THE FALL BEHAVIOR OF ROCK PTARMIGAN (*LAGOPUS MUTUS*) IN INTERIOR ALASKA

A

THESIS

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By

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ABSTRACT

Fall population characteristics, flocking, and territoriality of rock ptarmigan (Lagopus mutus) were studied at Eagle Creek in interior Alaska during a year of population decline and low ptarmigan density. The behavioral effects of certain marking techniques were also evaluated.

Most ptarmigan aggregated into flocks during September and moved about considerably. Many females left the area in October. Social hierarchies probably were established through aggressive encounters within fall flocks.

Some male ptarmigan established territories and, at least temporarily, paired with hens. Territorial males succeeded in defending their territories against other individuals, but frequently were overwhelmed by roving flocks.

Ptarmigan frequented progressively lower elevations throughout the fall, probably in response to changing environmental conditions.

Backtagging resulted in unusually high losses to eagle (Aquila chrysaetos) predation and subsequent replacement by unmarked birds. Properly installed backtags and radio packages did not prevent males from establishing territories or otherwise competing for social standing during September.

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INTRODUCTION

Although the life history of rock ptarmigan (Lagopus mutus) has been fairly well documented (DeLeonardis 1952; MacDonald 1970; Roberts 1963; Weeden 1959, 1965a, 1965b; Watson 1956, 1965a, 1972), most studies have been primarily concerned with the breeding biology. Watson's study of the annual cycle of ptarmigan in Scotland is an exception. Three investigators have reported on various facets of ptarmigan behavior: Theberge (1971) studied brooding behavior of the hens and differences in the agonistic qualities of chicks; MacDonald (1970) described behavior of ptarmigan during the breeding season; and Watson (1972) described the behavioral repertoire and compared the behavior of ptarmigan and red grouse (Lagopus lagopus scoticus).

Watson and Moss (1970a, 1970b, 1971) concluded that territorial behavior among red grouse males in the fall was the proximal mechanism for population regulation of that species. Rock ptarmigan were not studied as intensively; however, the investigators concluded that the population dynamics were essentially the same (Jenkins and Watson 1967).

In North America, Weeden (1965a, 1965b) had conducted long-term research on rock ptarmigan population dynamics in central Alaska. This study provided the basis for ancillary studies (Theberge 1971, Modafferi 1975, and this study). An attempt was made to coalesce these data into an evaluation of population regulation using key factor analysis (Theberge 1971, Weeden and Theberge 1972); however, the lack of information for the fall and winter periods hindered the effort. An important conclusion of this analysis was that "winter" losses (mid-August to

mid-May) accounted for most of the total loss in any year and was the most important factor affecting mean loss over the 10-year period. Furthermore, juvenile birds constituted the bulk of the winter loss. This is consistent with the thesis of Watson, Jenkins and Moss as expressed in the aforementioned references concerning red grouse and ptarmigan biology in Scotland.

Weeden did not study fall behavior in detail but did note a resurgence of aggressive behavior among male ptarmigan during the fall. The potential importance of the phenomenon was acknowledged: could the conclusions emerging from the thorough research in Scotland be applied to ptarmigan in Alaska? The present study was initiated to help answer this question.

OBJECTIVES

1. To observe and describe the fall behavior of rock ptarmigan in interior Alaska.

2. To observe the fall flock formation process and evaluate its significance.

3. To determine whether fall territoriality exists and, if so, evaluate its significance.

4. To evaluate the effect that marking techniques have on ptarmigan behavior and mortality.

STUDY AREA

The study area at Eagle Creek encompasses approximately 15.5 km^2 (6 mi^2) of alpine and subalpine habitat approximately 161 km (100 mi) northeast of Fairbanks in central Alaska (Fig. 1). It consists of low, rounded mountains rather completely covered with vegetation except for an occasional bare ridgetop or talus slope. The area is typical of the geographic area known as the Tanana Hills that extends across the Interior for 240 to 320 km (150-200 mi). Most of the study area is within the area used by Weeden during previous investigations and thus has been described elsewhere in detail (Weeden 1965a). Elevations range from 762 to 1219 m (2500-4000 ft) above sea level. Timberline varies from 792 to 914 m (2600-3000 ft) above sea level depending on aspect of the slope. Snow cover is usually complete from mid-September through April. Total annual precipitation is 250 to 380 mm (10-15 in). Wind is of considerable importance in its effects on the distribution and quality of the snow cover; large areas of worn and scarred vegetation attest to the harshness of the surface environment at certain times of the year.

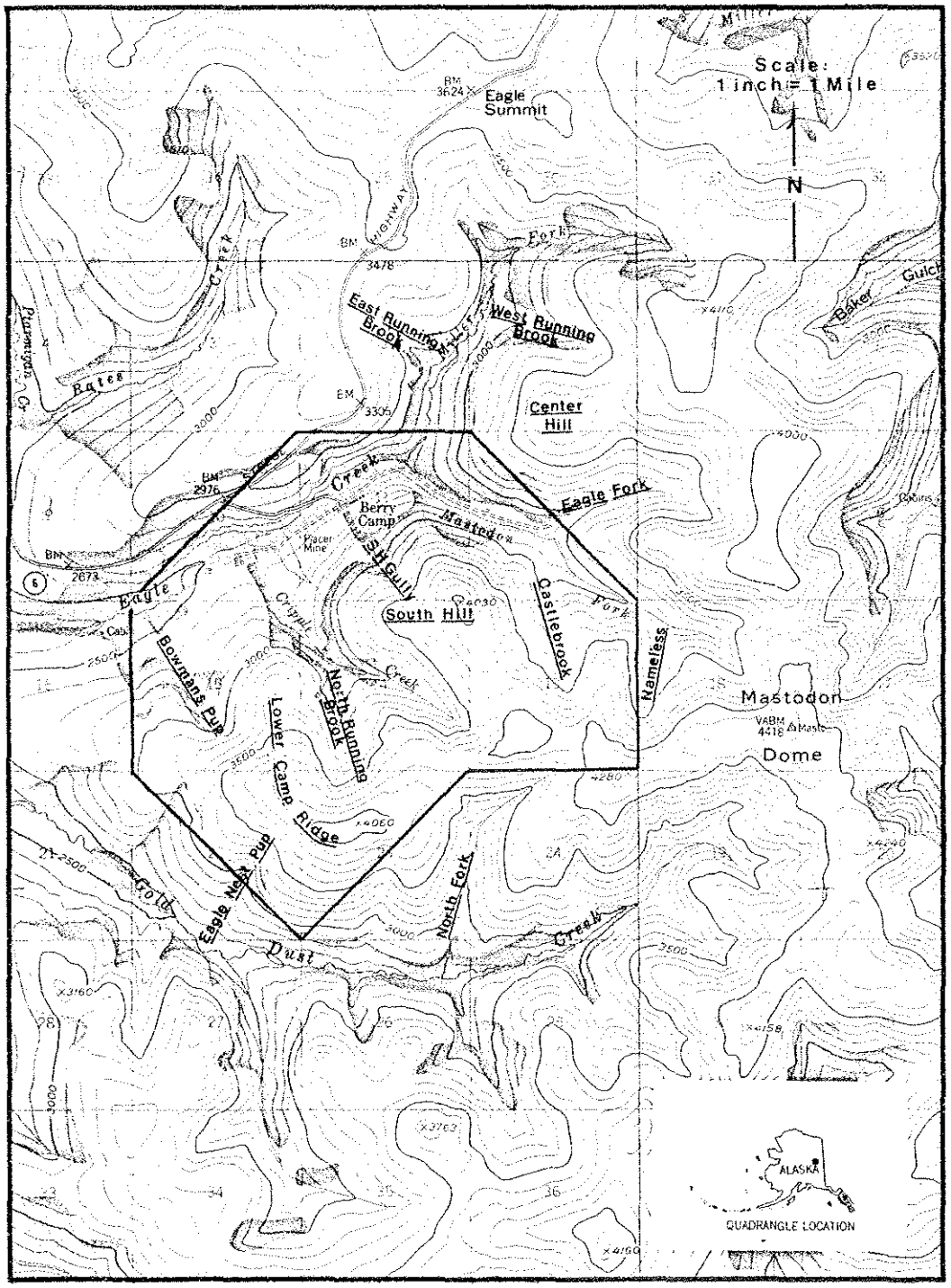

Fig. 1. Location of the study area in interior Alaska. (Note: underlined names are local derivations and are not officially recognized.)

ASPECTS OF THE LIFE CYCLE OF ROCK PTARMIGAN IN ALASKA

Most rock ptarmigan of Alaska's mainland are migratory. Each fall resident birds join into flocks and disperse from the breeding habitat. There appears to be a partial segregation by sex with females moving the farthest, often appearing in the forested lowlands a considerable distance away from the nearest breeding area (Weeden 1964). Most adult males remain near the breeding grounds, usually just above timberline. Most losses from the population occur during winter, with juveniles of both sexes incurring the majority of the mortality in nearly equal proportions (Weeden and Theberge 1972). Adult males are nomadic during this period and move about in small flocks with little sign of overt aggression.

In April the females return to the breeding grounds, the males begin displaying and defending territories, and pairing commences. Occasionally males mate with two hens, but most are monogamous. Some males defend territories but do not acquire hens (Weeden 1965b). The universal presence of brood patches among captured hens suggests that all hens mate (Theberge 1970). Evidently, females first develop an attraction to a suitable nesting site, irrespective of territories held by males; however, since males occupy all available breeding habitat, these nesting sites fall within established territories of the males. As courting progresses and a pair bond develops, the male's activities and displays center around the nesting site and the female becomes attached to feeding and sheltering spots within the male's territory

(MacDonald 1970). Eggs are laid in late May. When the hens begin to incubate, most males desert the territory and gather in flocks at the upper and lower edges of the breeding habitat (Weeden 1964). Females that lose their clutch or brood join these males. Productive hens lead their broods away from the nest site shortly after the hatch and wander erratically throughout the summer. Occasionally a male will be found with a brood during the summer. By mid-August broods are often found in the moist sedge-filled swales at the heads of the draws on the hillsides (Weeden 1965b) and males in the ridgetop flocks begin to display and vocalize in a manner reminiscent of spring territorial behavior. During September the broods join these flocks as the cycle comes full circle for yet another dispersal for the winter months.

SPRING DENSITIES AND TERRITORIAL SPACING

Each spring personnel from the Alaska Department of Fish and Game census rock ptarmigan at Eagle Summit by traversing the area on foot and observing males on their breeding territories. Males are conspicuous at that time of year because of their aggressive behavior and white plumage. Observers listen for vocalizations and scan the hillsides with binoculars. The birds are viewed long enough to determine which are established on territories on the hillside. Count data thus derived are thought to be accurate to within 5 percent (Weeden 1965a).

In 1973 I participated in the census. The count yielded 65 males, or 1.7 per square km (4.5 per mi^2). Department of Fish and Game records show that the population was still declining from the previous peak in 1969 (Fig. 2).

The spacing of male rock ptarmigan on the study area and adjacent lands during spring 1973 is shown on Figure 3. The presence of a female was not always confirmed, since females are less conspicuous and observations were made from a distance. Males were presumed to be occupying territories at the time of observation; however, observations were not lengthy enough to permit delineation of territory boundaries. Based on the number of males observed and the area involved, a mean territory size of 33 ha (81 a) can be calculated if all available habitat were occupied. However, no males were observed above 1128 m (3700 ft) elevation during May and it was likely that some of the area above that altitude was not used by territorial males (although these high ridges

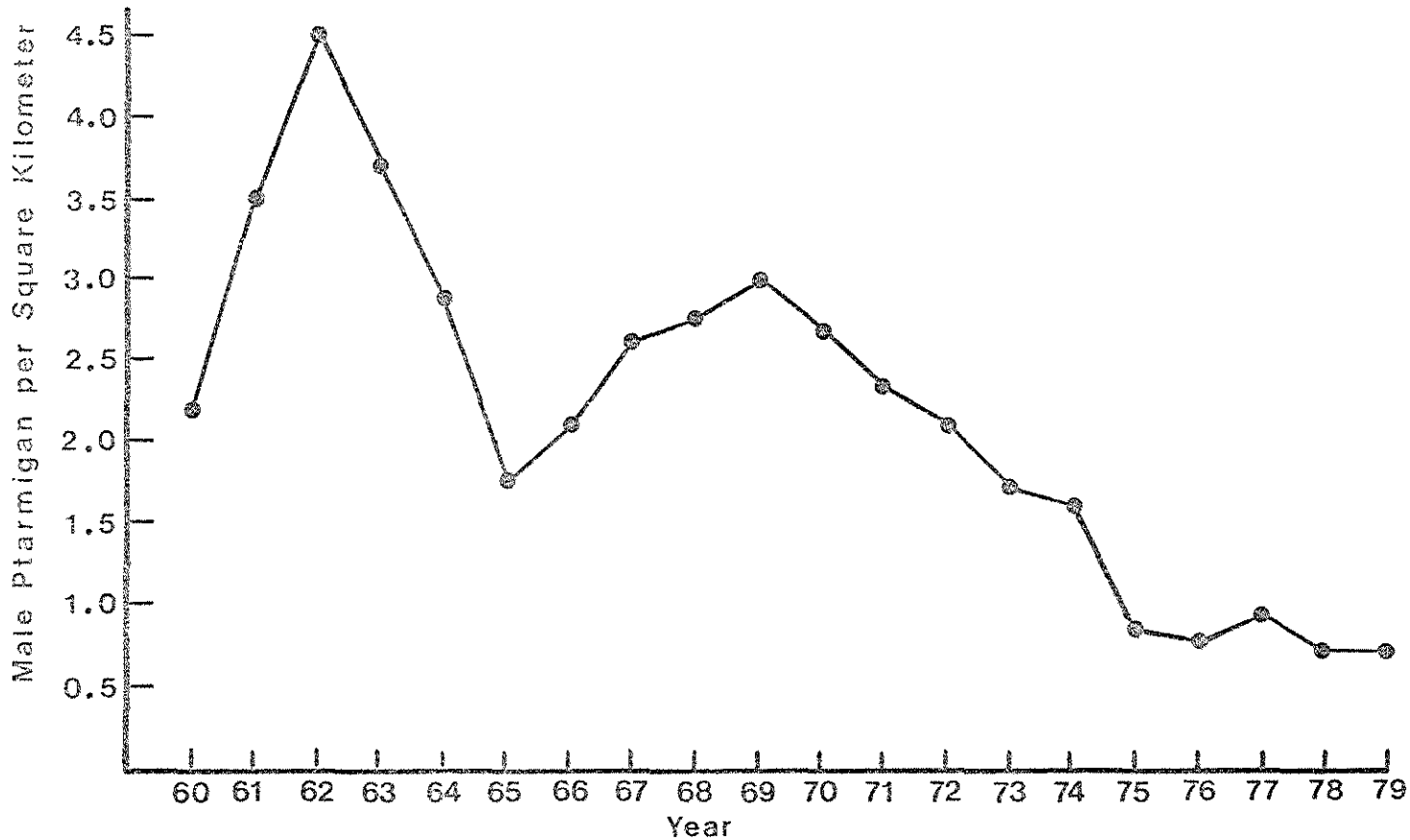

Fig. 2. Spring densities of male rock ptarmigan on 39 km^2 (15 mi^2) of breeding habitat at Eagle Creek, 1960-1979 (Annual Reports of Survey-Inventory Activities, Alaska Department of Fish and Game, Juneau).

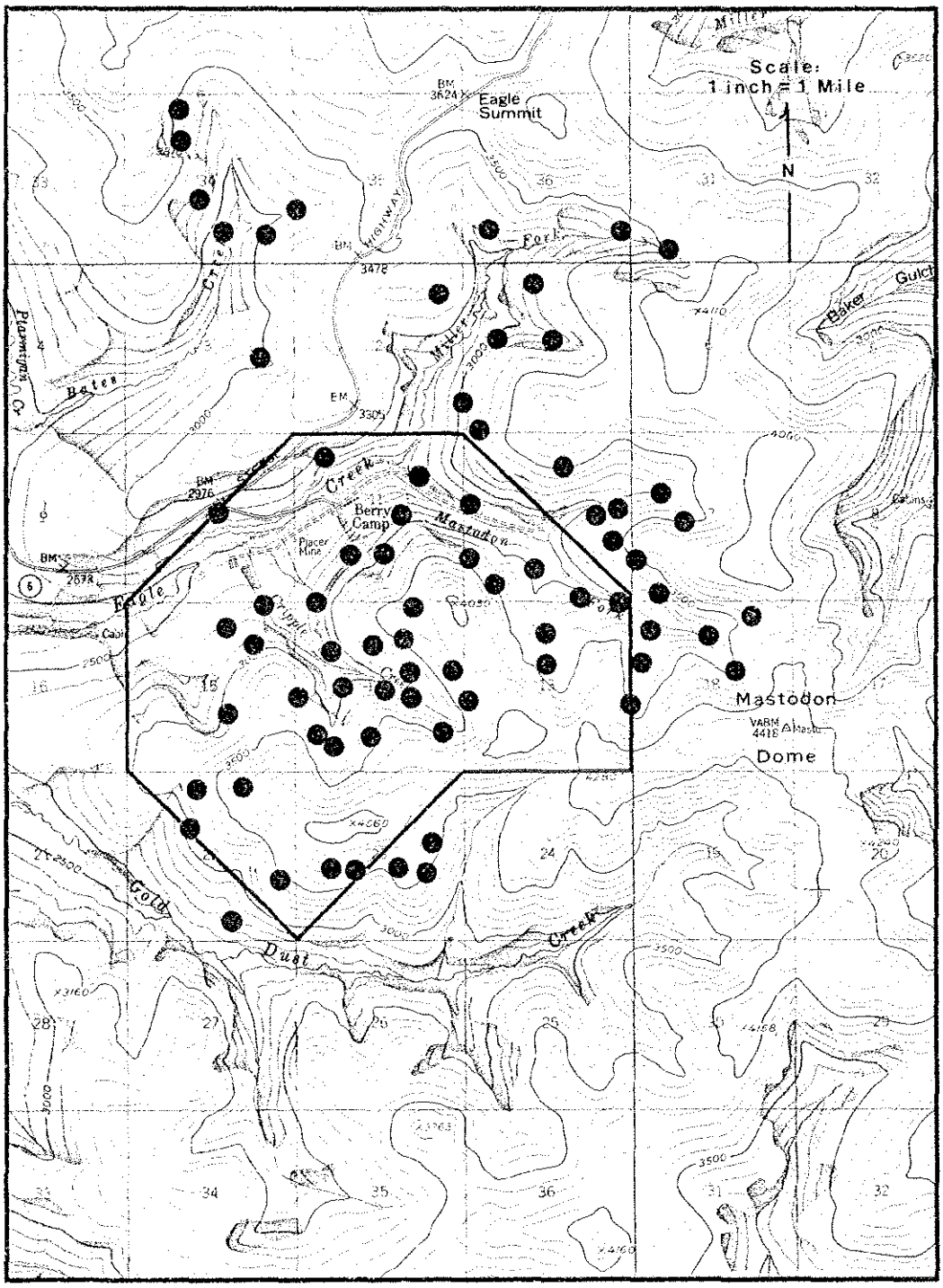

Fig. 3. Distribution of male rock ptarmigan at Eagle Creek, 15-18 May 1973. Study area boundaries are superimposed for reference.

are occupied in some years, according to ADF&G records). If the area above 1158 m (3800 ft) is deleted from the calculations, mean territory size would approximate 31 ha (77 a). These figures should be viewed as maxima. There were noticeably fewer interactions between territorial males during 1973 than in 1968 when I observed ptarmigan at this same location during a population high. Distances between territorial males were often so great that they seldom saw or encountered each other. By way of comparison, territories in Scotland ranged from 8 to 30 ha (20-75 a) during years when ptarmigan numbers were low (Watson 1965b).

Some portions of the Eagle Creek area apparently are better ptarmigan habitat than others. For example, few birds are ever found in the Miller Fork drainage (Fig. 3). The area selected for this study consistently supports relatively high densities of ptarmigan. In 1973 there were 2.9 males per square km (7.4 per mi^2) on the study area compared to 1.7 males per square km (4.5 per mi^2) on the larger census area of which it was a part.

METHODS

Forty-one territorial males were counted on the study area during May 1973. Of these, 27 were captured with a noosing pole (Zwickel and Bendell 1967) and marked with colored backtags. The release of a tagged male often aided in the location of other males, since the fleeing male often disregarded territorial boundaries and elicited responses from neighboring males. By 1 June males had become so secretive that further efforts at tagging were not warranted. Tagging locations are shown on Figure 4, and pertinent data are available in Appendix A.

Backtags were constructed from vinyl-coated nylon (Saflag) similar to those described by Blank and Ash (1956) and Labesky and Mann (1962). Three colors were used: fluorescent red for adult males, fluorescent green for adult females, and light blue (non-fluorescent) for chicks of the year. Backtags measured 120 mm by 30 mm (approximately 4.75 in by 1.19 in) and were attached to the bird with 7 mm (0.28 in) wide straps of the same material. Average weight was 3 gm (0.11 oz). Black letter and number combinations measuring 35 mm by 22 mm (1.38 in by 0.88 in) provided for individual identification.

Female rock ptarmigan were captured after their eggs had hatched to avoid disturbance during the nesting period. Backtags were installed on 22 hens between 4 July and 20 August. The maternal protectiveness of the female permitted captures to be made using a long-handled net (Weeden 1965b). Chicks were captured late in the summer when they were large enough to backtag. This was done incidental to the tagging of adults, and only 13 chicks were marked.

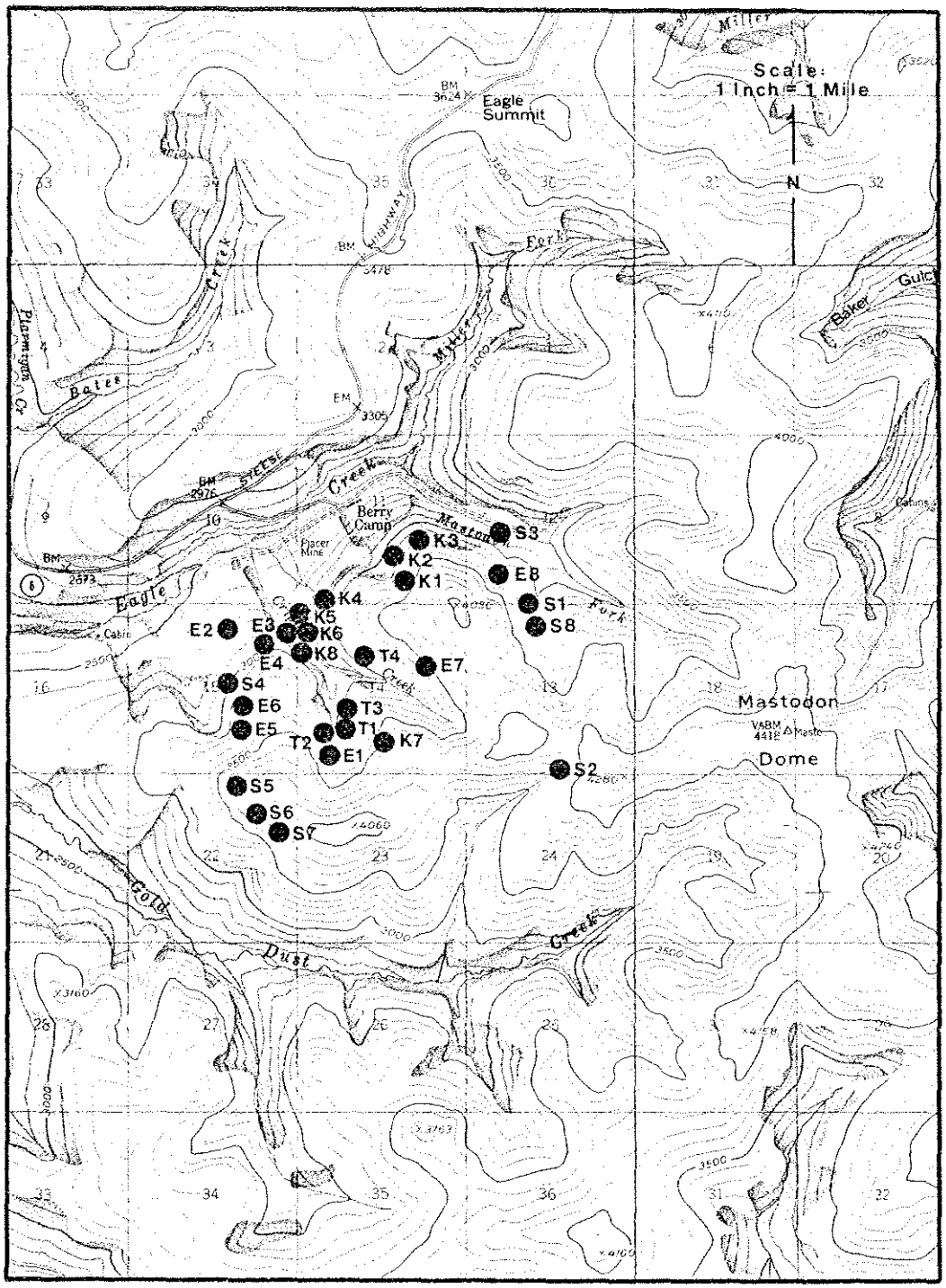

Fig. 4. Locations of adult male rock ptarmigan captured and marked at Eagle Creek during May 1973.

Radio transmitters were placed on seven adult males and one juvenile female (bird hatched in 1973) during August. Backtags (without Saflag harness straps) were incorporated into the radio package design to permit visual identification from a distance.

Transmitters were of the single stage type and emitted pulsing signals at separable frequencies near 150 megahertz. Circuitry was patterned after that used by AVM Instrument Company (810 Dennison Dr., Champaign, IL 68120). Harness design was adopted from Brander (1968) with only slight modification.

Radio packages were carried dorsally like the backtags. Each unit measured approximately 35 mm long by 17 mm wide by 9 mm high (1.38 in by 0.67 in by 0.35 in), not counting the 305 mm (12.0 in) whip antenna. Weight, including the backtag, totaled 17.5 g (0.64 oz). This represents 3 to 4 percent of the body weight of adult male ptarmigan in late September.

Birds with backtags could be easily distinguished from other ptarmigan whether on the ground or in flight. However, lengthy observation was often required to identify an individual. The dorsal location of the tag reduced its usefulness, particularly when birds were above the observer on the hillside. Under ideal conditions, markings could be read as far away as 150 m (500 ft) with a 10-60 power spotting scope; however, closer observations were usually necessary.

The presence of a few radio-marked males proved to be an excellent means of locating flocks of birds to observe. However, these transmitters proved to be rather short-lived (Table 1). Two radios (A5, A3)

Table 1. Signal life for radio transmitters installed on rock ptarmigan at Eagle Creek, 1973.

Backtag color and designation	Date Radio activated	Date installed	Date last heard	Date last observed	Min. No. of days on bird	Min. No. of days of operation
Red A1	30 July	4 Aug	27 Aug*	14 Aug	24	28
Red A3	7 Aug	7 Aug	30 Sept**	2 Oct	56	54
Red A5	7 Aug	16 Aug	22 Sept**	6 Oct	51	46
Red A6	7 Aug	20 Aug	30 Sept*	30 Sept	41	54
Red A7	20 Aug	20 Aug	23 Sept*	23 Sept	34	34
Red A8	20 Aug	30 Aug	4 Oct*	30 Sept	37	45

* Radio either ceased functioning or the bird moved out of range.

** Radio known to have ceased functioning.

were known to have expired during the observation period and a third (A6) was noticeably weakening when last heard. Only one (A8) is known to have remained functional into October.

Preliminary observations were made during August and September 1972, and during May through July 1973. Data for this thesis were collected during the period 30 July 1973 through 2 November 1973. Activities were based out of the old Berry Mining Company camp on Eagle Creek (Fig. 1). Most of the observation time was spent along the hillsides between the 823 m (2700 ft) and 1128 m (3700 ft) contours; however, the ridgetops (1200 m [4000 ft] elevation) were visited periodically. The entire study area was not covered each day since some observations were quite lengthy. Sightings, ptarmigan movements, and routes taken during the course of observation were recorded daily on field maps of the study area. Flock size and composition, individual identities, and descriptions of activities were recorded when possible. Particular attention was paid to the activities of the males; i.e. which individuals were interacting, the results of encounters, the intensity of displays and aggressiveness, and whether or not any defense of area was evident. Visual estimates were made of distances and heights involved in these interactions.

RESULTS AND DISCUSSION

Effects of Marking on Behavior

Several males (K1, K2, K3, K4, K6, K7) flew erratically after backtags were installed too tightly, but recovered after preening their feathers into position around the tags and harness. One male (K6) was recaptured in order to loosen the tag. Some investigators have reported a loss of birds from backtags being installed too loosely (Labisky and Mann 1962, Schladweiler and Tester 1972), but there was no evidence of this occurring during the present study, even though properly fitted backtags appeared rather loose.

In this study there was no evidence that ptarmigan needed to adjust to properly installed backtags. Ten ptarmigan were resighted within 2 weeks of tagging and their behavior appeared normal. For example, 3 days after being fitted with a backtag, male E4 was observed chasing other males from his spring territory, copulating with the hen, displaying on the territory, and successfully evading a goshawk (Accipter gentilis).

Radio-tagged birds required up to 19 days to adjust to the transmitter packages. Reactions that were observed during this adjustment period were a hesitancy to fly (A1, A3, A5, A6, A7) and temporary erratic movements (A5, A7). Lance and Watson (1977) reported similar observations for radio-tagged red grouse. Presumably, it is the added weight of the radio package that affects the birds, since no similar adjustment period has been reported for backtagged birds.

It is not known what social disadvantage, if any, backtags may impose on the recipients. Certain colors, particularly in the vicinity of the head and neck, have been shown to greatly affect behavior in other species, at least during the breeding season (Bennett 1939, Frankel and Basket 1963, Goforth and Baskett 1965, Lensink 1968, Smith 1972). In particular, red may have been a poor choice of color for tags applied to male ptarmigan. Red combs are an integral part of the threat displays. Thus, red tags may have enhanced the aggressive appearance of marked males.

On the other hand, the presence of a backtag did not cause male E6 to abandon either his spring territory or his mate. Likewise, radio-tagged male A5 went on to establish a fall territory, and radio-tagged male A8, who did not become territorial in the fall, was successful in competing for social standing within the fall flocks. Thus it was evident that tagging did not preclude an individual from attaining high social stature. However, it has been suggested that marked birds may tend to seek out other marked birds or gather as a result of common exclusion from the flock social structure (Mercer and McGrath 1963, Unpubl. rep., Department of Mines, Agriculture and Resources, St. John's, Newfoundland). In the present study there were six instances where aggregation consisted entirely, or almost entirely, of tagged birds.

Effects of Marking on Mortality

Survival of marked ptarmigan was exceedingly poor (Fig. 5). Sixty-two percent of the marked adult ptarmigan were either killed by predators

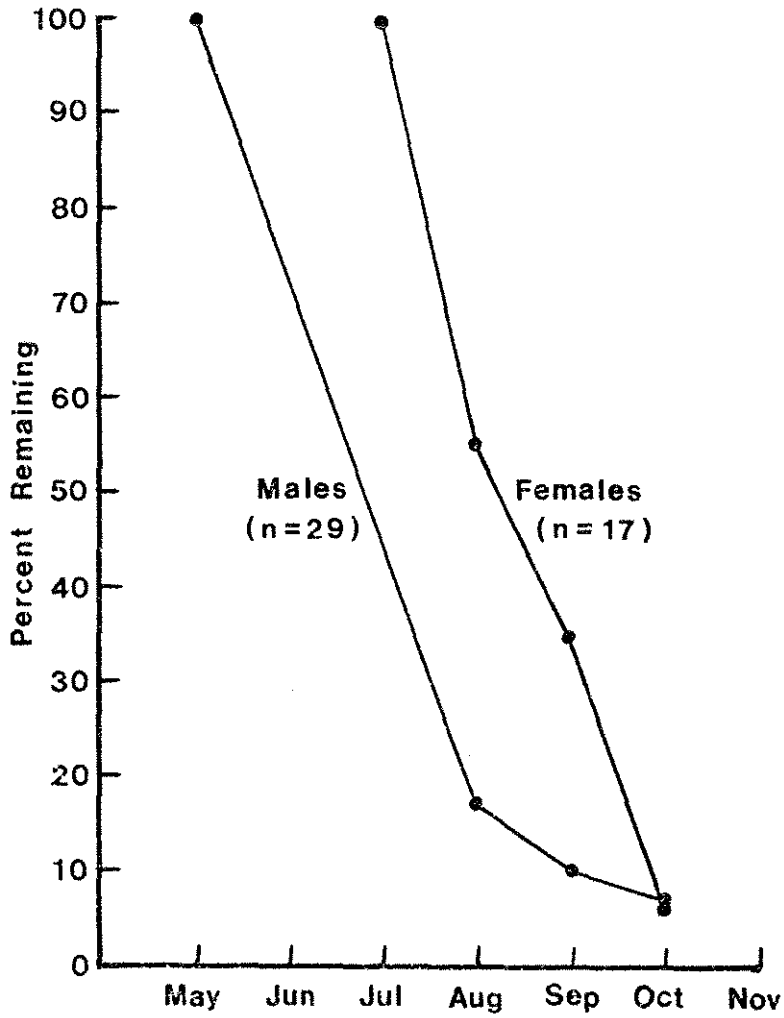

Fig. 5. Marked ptarmigan remaining at intervals following tagging.

or never resighted after the initial tagging (Table 2). Efforts were made to locate the missing marked birds in areas adjacent to the study area on the chance that they had emigrated. None were found; however, the probability of locating marked birds off the study area would greatly decrease as the search area is enlarged outward. Nonetheless, I feel that it is very likely that these birds were killed by predators and simply not found. Data in Table 1 suggest that the likelihood of observing radio-marked males after the radios cease transmitting is good, providing that they remain in the study area and are alive.

A variety of predators frequented the Eagle Creek area during all or part of fall 1973, several of which were capable of killing adult rock ptarmigan. Golden eagles (Aquila chrysaetos) and harriers (Circus cyaneus) were the most frequently observed predators (13 and 5 observations, respectively). Others included goshawks, gyrfalcons (Falco rusticolus), peregrine falcons (Falco peregrinus), red foxes (Vulpes vulpes), and wolves (Canis lupus).

A pair of golden eagles that nested in the southwest corner of the study area in 1973 killed at least 13 backtagged and 2 radio-tagged adult male ptarmigan (42% of the marked males) and 1 backtagged chick (Table 2). Too few identifiable bones were found in the nest to permit evaluation of predation on marked versus unmarked birds. However, despite the fact that only 51 percent of the backtags in use were red, 94 percent of the remains attributable to eagle predation were so marked (Chi-square = 9.72, $P < 0.005$, 1 df). This suggests that these eagles selected for ptarmigan with red backtags. Red is the color most likely

Table 2. Attrition of marked ptarmigan at Eagle Creek, 1973.

Age/Sex	Type of marking	Number marked	Number never relocated	Number killed by golden eagle	Number killed by red fox
Adult males	backtags	29	10	13	1
Adult males	radios	7	0	2	0
	Subtotal	36	10	15	1
Adult females	backtags	22	9	0	1
Juveniles*	backtags	14	7	1	0
	Grand total	72	26	16	2

* Sex of chicks was not determined.

to be noticed by avian predators (Kessler 1964), and raptors often select prey that contrast with their environment and are conspicuous (Dice 1945; Rudebeck 1950, 1951; Mueller 1968, 1971; Sparrowe 1972; Kaufman 1973). Furthermore, the formation of a "specific search image" (Tinbergen 1960), in this case ptarmigan with red tags, may result in the greatest return for the effort (MacArthur and Pianka 1966).

The loss of adult ptarmigan between early May and mid-August has been estimated to be 9-10 percent (Watson 1965c; Weeden 1966, P-R Segment Rep., Proj. 2-6-R-6 and W-13-R-1, Alaska Dept. Fish and Game, Juneau). Watson's study involved unmarked birds, while Weeden used leg bands and color-coded remiges for identification. Losses in the present study, where the majority of the adult birds were backtagged, amounted to 36 percent and heavily favored the male segment. Thus, many males who defended territories in the spring were not alive the following fall and therefore not available to reoccupy those territories.

Population Characteristics

Unsuccessful hens and those that have lost their broods generally join the males in flocks on the rocky ridgetops or in streamside willow thickets (Weeden 1965b); however, throughout August and part way into September many female rock ptarmigan are with broods and are usually apart from the flocks. Gradually, family groups lose their identity as broods join and intermingle to varying extents (Weeden 1965b). Five (38%) of the chicks backtagged in this study later were observed either with a hen other than the one originally present at the time of tagging

or in the company of other chicks with no hen present. Between 1 August and 6 October lone chicks or groups of chicks without adult birds present accounted for 9.3 percent of 140 encounters. Similarly, 50 percent (n=10) of the broods of marked hens for which there were subsequent observations either intermingled or otherwise substantially changed in number.

During September hens with chicks joined the flocks of males and unsuccessful females; however, hens accompanied by chicks were often still identifiable within the large flocks well into the month because of their tendency to remain apart from the other birds.

Throughout September and October the aggregating process remained a dynamic one with flock sizes changing frequently. Certain members of a flock seemed to respond differently to stimuli which elicit a flight response. Family groups, chicks, and displaying males seemed most likely to remain behind when a flock flushed. These individuals were variously preoccupied with other activities and seldom seemed party to the social facilitation that increased awareness and alarm among the rest of the flock. Also, at the height of the periods of male interactions, there was a continual flow of displaying males across the hillside, causing constant fluctuations in the numerical makeup of the flocks.

The largest aggregation observed during fall 1973 was approximately 70 birds; however, large flocks comprised only 3 percent of all observations. Sixty-six percent of the total encounters (n=232) consisted of flocks of 2-25 birds. Single birds comprised 31 percent of all observations.

Flock size was quite variable throughout the fall, but overall a very weak trend toward larger average flock size as the season progressed was evident (Fig. 6). Pooling the flock size data by weekly intervals produced groups for which the variance between weeks was 4.5 times the variance within the groups, suggesting that the variability in flock size could be examined by looking at factors affecting several days at a time (e.g., weather). Mean flock sizes for weekly intervals throughout the study period were found to differ significantly (Table 3).

Visual comparison of flock sizes with general weather conditions suggests that weather greatly influences fall flocking (Fig. 6). Ptarmigan flocks are largest during periods of favorable weather (i.e., clear skies and calm winds) and decline during protracted periods of bad weather. Flock size was significantly correlated with precipitation but did not correlate significantly with either windspeed or ambient temperature (Table 4). However, it is probably unrealistic to consider each parameter separately when, in reality, it is the combined effect that results in harsh weather conditions.

Weeden observed two periods of rather abrupt changes in flock size during fall 1959: one in late August when broods combined to form small flocks, and another in mid-September when males and broodless hens joined the hens with chicks to form large flocks (Weeden 1961, P-R Segment Rep., Proj. W-6-R-1, Alaska Dept. Fish and Game, Juneau). In 1960 Weeden observed large flocks at Eagle Creek from mid-September until he left on 28 September (Weeden 1962, P-R Segment Rep., Proj. W-6-R-2, Alaska Dept. Fish and Game, Juneau). My observations in 1973

Table 3. Results of analyses of variance involving flock size, percent males in flocks, and elevations of observations.

Parameter Analyzed	Analysis of Variance (F)		
	Week	Month	Flock Size
Mean flock size	4.46*		
Percent males in flocks of 3 or more birds	1.34	4.34*	0.35
Elevation of observation (broods)	5.03*	6.69*	
Elevation of observation (mixed flock)	14.29*		
Elevation of observation (single birds)	17.98*		

* Mean values are significantly different at the 95 percent level.

Table 4. Correlation of environmental and flock parameters at Eagle Creek, 1973.

Variables (Y_1)	(Y_2)	Correlation coefficient (r)	Probability of larger value of r	Degrees of freedom (n-2)
Max. temp. (°F) @ 2900'	Flock size	+0.0321	ns	209
Min. temp. (°F) @ 2900'	Flock size	-0.1187	ns	207
Max. wind (mph) @ 2900'	Flock size	-0.0383	ns	202
Elevation of flock	Flock size	-0.0799	ns	222
Precipitation @ 2900'	Flock size	-0.1873	<.01	209
Precipitation @ 2900'	Elevation of observation	-0.0231	ns	222
Max. wind speed @ 2900'	Elevation of observation	-0.0831	ns	217
Difference in wind speed	Elevation of observation	-0.1573	<.05	159
Max. temp. (°F) @ 2900'	Elevation of observation	+0.4570	<.001	225
Flock size	% male (transformed)	+0.0922	ns	69

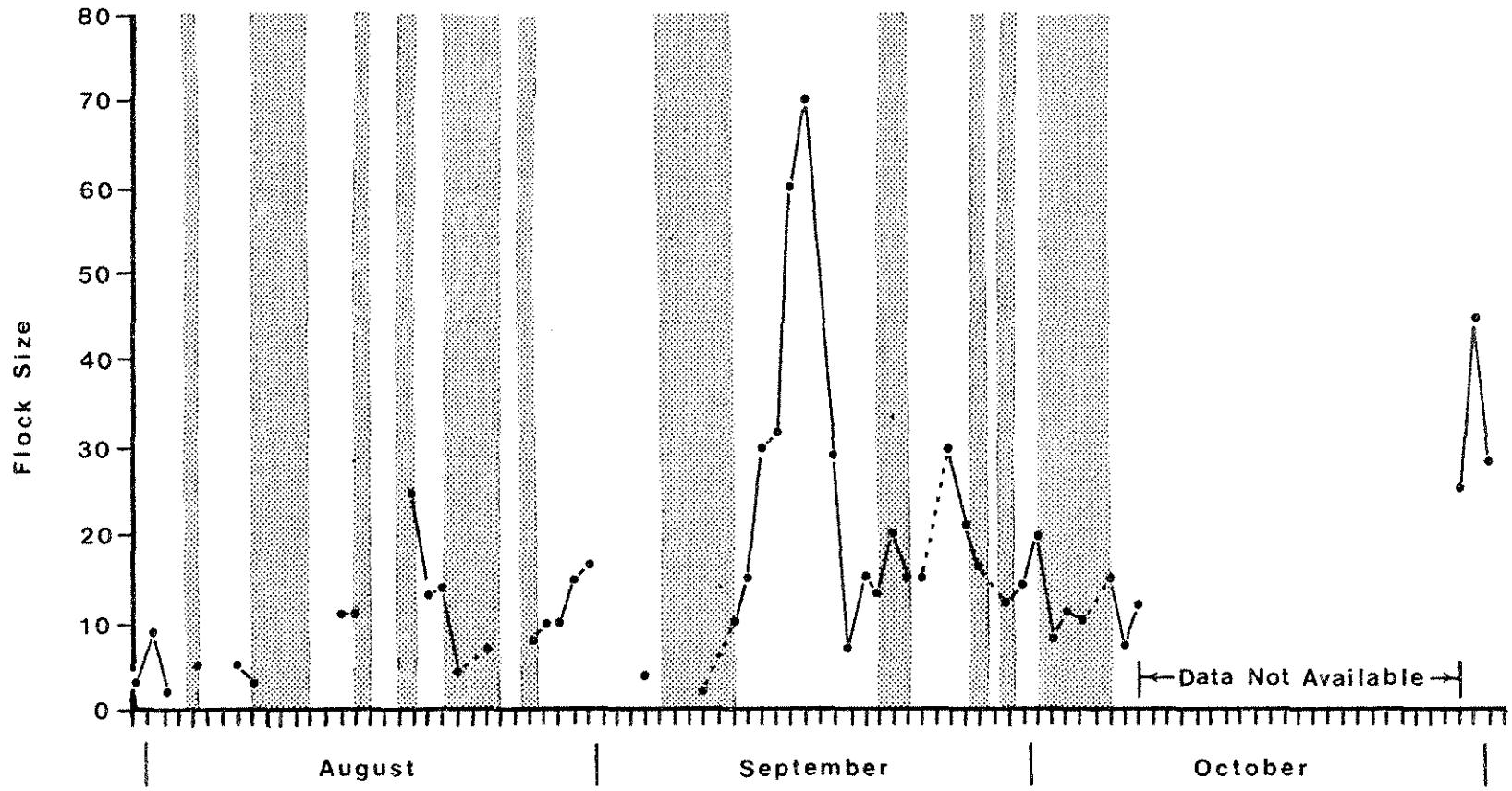

Fig. 6. Relationship between flock size and weather. Plotted points represent maximum flock sizes seen. Stippled areas represent periods of inclement weather.

parallel Weeden's earlier ones. I began to encounter small flocks of mixed broods on 19 August, and the first large flock (65 birds) appeared on 14 September. There was an obvious peak in flock size during mid-September (Fig. 6). However, the absence of extremely large flocks in late September may have been a result of the inclement weather that occurred during this period. Large flocks were again evident when I visited Eagle Creek in late October.

The increase in flock size and the increase in gregarious flocking behavior made ptarmigan appear more abundant during the fall; however, fall census data are lacking, so absolute changes in numbers cannot be ascertained. My observations suggest that there is considerable movement within the population during fall, which may result in local increases in areas of favorable habitat. Sixty-six percent of the resident males on the study area were marked in the spring. Of these, 67 percent died prior to September. Yet unmarked males seemed abundant during fall observations, implying that new birds had moved in from surrounding areas. One radioed male (A5) provided some evidence that replacement may have taken place. The area that male A5 utilized in fall and on occasion defended (Fig. 7) included that area claimed the previous spring by males K1 and K2, both of which died during the summer. Also, leg bands returned from birds killed in the fall by hunters (Weeden 1972) confirmed that some adult males moved at least 5 km (3 mi) from the point of tagging during the previous spring. In fact, only 40 percent of the birds shot within 0.8 km (0.5 mi) of the road during the fall had been summer residents there. Since the study

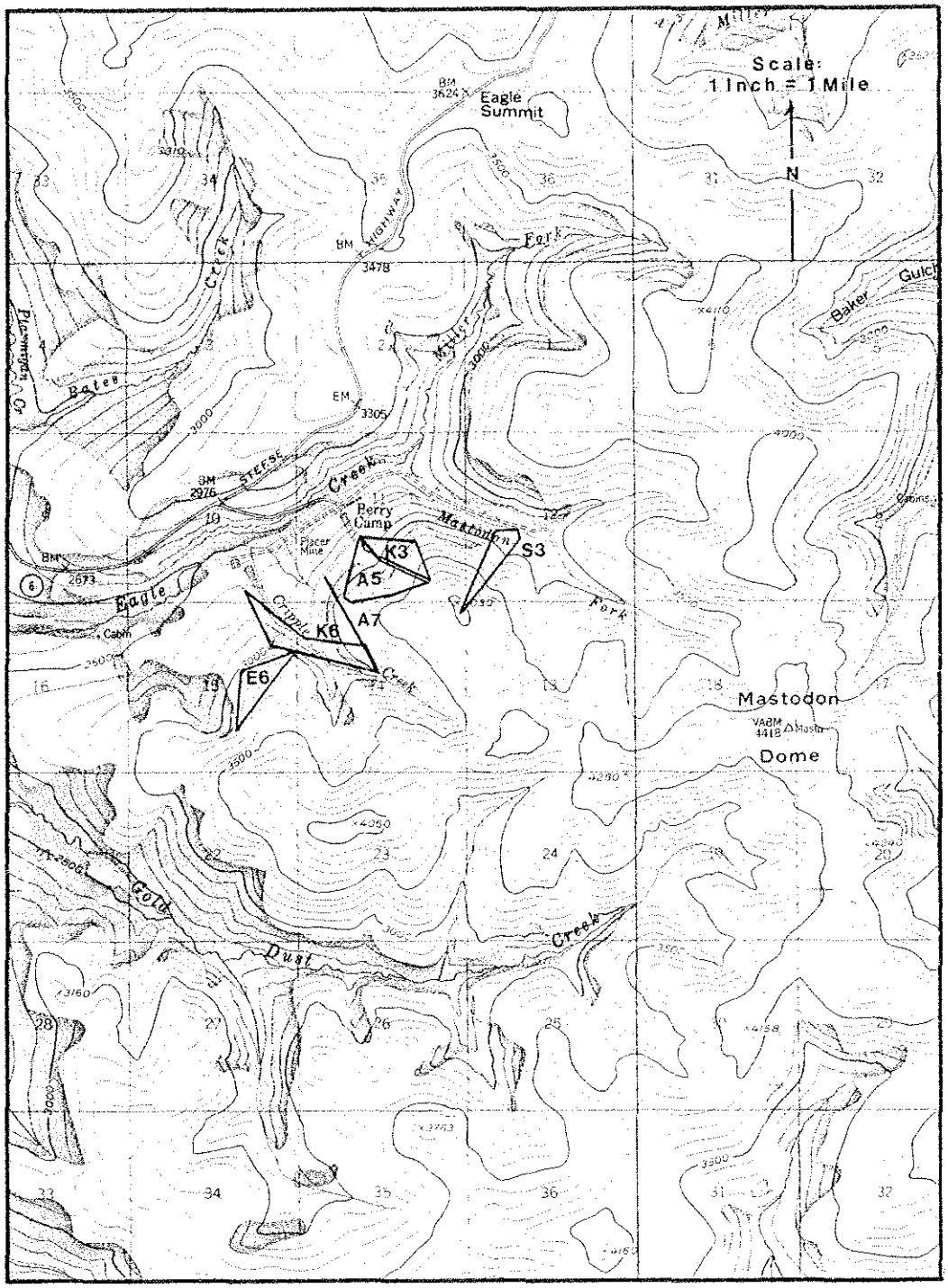

Fig. 7. Fall use areas of marked male rock ptarmigan at Eagle Creek, 1973.

area presumably comprises some of the better ptarmigan habitat in the Eagle Creek area (spring density of territorial males was 1.6 times that of the total census area in 1973), it seems reasonable that new birds would move into the area as the resident birds are removed.

The composition of the ptarmigan population also changed substantially during fall 1973. Juvenile birds normally comprise 59-71 percent of the population at the beginning of August (calculated from data presented by Weeden in various Federal Aid to Wildlife Restoration Progress Reports, 1961-1969). In 1973, juveniles comprised 49 percent of the 193 birds identified during the month of August (Table 5). Family groups were the least conspicuous segment of the population at this time and therefore are probably under-represented in this sample. Although I purposely attempted to locate family groups during much of August by searching areas where they would most likely be found and by imitating chick distress calls in order to attract hens, only 50 adult hens were located for every 115 adult males observed, compared to an expected ratio of 50 adult females per 54 adult males (Weeden 1964).

Juvenile birds were identified by body size, plumage characteristics, and behavior; however, these characteristics are only valid until late September at best. The mean weight of juvenile birds nearly equals that of adults of the same sex by 30 September (Weeden 1961, P-R Segment Rep., Proj. W-6-R-1, Alaska Dept. Fish and Game, Juneau). This is particularly true of females.

Thus the apparent decrease in juvenile birds in September and October (Table 5) may not be real. However, data obtained from birds

Table 5. Sex and age composition[a] of rock ptarmigan at Eagle Creek, 1973.

Month	Number identified	Percent of total seen	Percent adult male	Percent adult female	Percent chicks
Single birds only:					
August	21	88	52	19	29
September	29	85	72	17	10
October	7	70	100	0	0
Flocks[b] plus singles:					
August	193	56	36	16	49
September	313	36	68	17	15
October[c]	164	36	79	18	4

[a] Determined by external body characteristics such as body size, stage of molt and feather appearance, and by behavior. After mid-September the presence or absence of the black loral stripe was used to sex birds in winter plumage.

[b] Only includes flocks that were completely classified.

[c] Most chicks are indistinguishable from adults at this time.

killed in areas away from the breeding grounds suggest a decline in juveniles on the breeding areas at this time of year. During October rock ptarmigan begin to appear in areas where they are not known to breed in spring. In 1977 and 1978 hunters on Murphy Dome near Fairbanks saw the first flocks of rock ptarmigan during the last week of September. Examination of the wings of 132 rock ptarmigan shot on Murphy Dome revealed that 73 percent were juveniles.

The proportion of males in the population increased steadily during the fall (Table 5). Differences between months are statistically significant (Table 3). Weeden (1964) reported that males comprised 58 percent of the population at Eagle Creek during mid-October 1963 and that, while single males were common, lone hens were never seen. All single birds seen during October during the present study were also males (Table 5). Earlier in the fall, however, lone females and chicks were occasionally seen.

During August and September only adult birds were classified according to sex, since only occasionally could the sex of juveniles be readily determined. During October any juveniles that were mistaken for adults were in turn classified according to sex, since the black eyestrip characteristic of the males was evident even among young birds. Thus the effect would be to inflate the observed percentage of "adult" males.

Overall, approximately two-thirds of the single birds encountered during fall were males. Thirty-seven percent of all flocks observed were comprised entirely of adult males and 51 percent consisted of adult males and females (Table 6). Twenty-seven percent of those encountered

Table 6. Composition of rock ptarmigan flocks[a] at Eagle Creek during fall 1973. Numbers in parentheses are percent of total.

Category	August	September	Combined
Flocks of adult males only	11(34)	12(39)	23(37)
Flocks of adult females only	1(3)	0(0)	1(2)
Flocks of both adult males and females	4(13)	4(13)	8(13)
	16(50)	16(52)	32(51)
Flocks of adult females plus chicks	10(31)	7(23)	17(27)
Flocks of adult males plus chicks	0(0)	1(3)	1(2)
Flocks of chicks only	3(9)	1(3)	4(6)
Flocks of all sexes and ages combined	3(9)	6(19)	9(14)
Total	32(100)	31(100)	63(100)

[a] Only includes flocks of two or more birds for which the sex and age of all members are known.

were hens with chicks. Adult males were seldom found with chicks; however, it was not uncommon to find a mixed flock that consisted of cocks, hens, and chicks.

The composition of flocks of ptarmigan was quite variable; thus, the percentage of males in flocks of three or more birds was not significantly different when analyzed by weekly intervals (Table 3). However, comparison by monthly intervals reduces the variability within groups and differences become significant. There was no significant correlation between the percentage of males in a flock and flock size (Tables 3 and 4).

The range of elevations at which ptarmigan were found appeared to change as fall progressed. All elevations were not searched with equal intensity or frequency, since that was not necessary to the prime objective of observing behavior. However, the alpine zone, extending from approximately 790-1220 m (2600-4000 ft) elevation, was traversed repeatedly during the course of this study. These observations suggested that ptarmigan restricted their activities to lower elevations as fall progressed, and that the range of elevations at which ptarmigan occurred was greatest early in the fall (Fig. 8). During September ptarmigan were only found at higher elevations during the protracted period of favorable weather that occurred during mid-month. Generally speaking, the shift to lower elevations appeared to coincide with the progressive movement of the snow line down the hillsides and the increasing snow depths at higher elevations. However, analysis of individual weather parameters against observed elevations provided mixed results. The

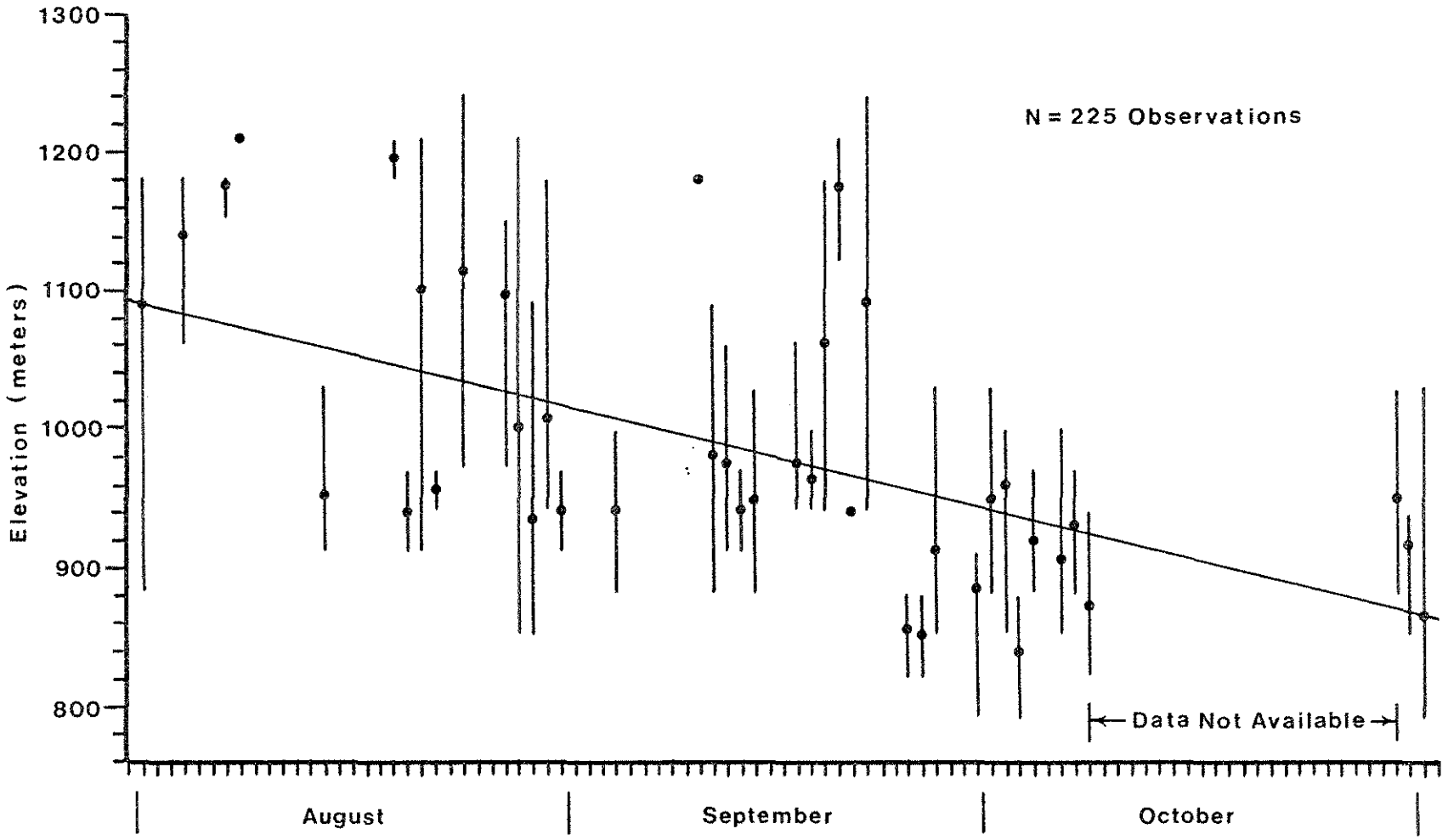

Fig. 8. Daily means (dots) and ranges (vertical lines) for elevations frequented by ptarmigan at Eagle Creek, 1973, with the calculated line of regression superimposed to indicate trend.

elevations at which ptarmigan were found did not correlate well with either precipitation or maximum wind speed (Table 4), although these elevations did correlate significantly ($P < 0.05$) with both ambient temperatures and the difference in wind speed between the 1100 and 1190 m (3600 and 3900 ft) levels.

Three categories of observations could be distinguished easily: 1) single birds, 2) mixed flocks, and 3) broods. The elevations at which observations were made were compared (t-test) for each category. Elevations at which single birds were observed did not differ significantly ($P > 0.05$) from those recorded for mixed flocks in either September ($t=0.25$, 71df) or October ($t=0.75$, 86df), the months in which male activities were greatest; however, a significant difference ($P < 0.05$) existed between values obtained for August and September for both mixed flocks ($t=5.45$, 62df) and broods ($t=3.17$, 20df). When the data were grouped by weekly intervals, differences between weeks were significant (Table 3).

My observations suggest that environmental factors are responsible for the progressive shift to lower elevations. Wind, which is an ever present influence in the Tanana Hills, is of consistently greater magnitude at higher elevations (Appendix B). Throughout the fall daily temperatures decline, snow depths increase, and wind alters snow density and distribution, resulting in an increasingly severe microclimate at all elevations. The effects are felt first and remain most pronounced at the higher elevations. Ptarmigan are well adapted to the arctic environment but even so they must increase their metabolic rate at

temperatures below -1.3°C (29°F) in order to survive (West 1972). Roosting beneath the snow allows ptarmigan to achieve a more favorable microclimate; however, snow quality greatly affects the thermal advantage incurred. Dense, windblown snow is hard to penetrate, and it has much less insulative value. These factors would make it advantageous for ptarmigan to move to lower altitudes at this time of year.

The onset of snow cover also reduces the availability of preferred food plants, since ptarmigan apparently restrict their feeding to the exposed vegetation. Although ptarmigan can dig down to depths of approximately 300 mm (12 in) in search of preferred foods (Gardarsson and Moss 1970), they apparently do not routinely dig through snow deeper than 10-50 mm (0.4-2.0 in) in order to feed, especially where the snow is hard packed by wind (Watson 1965a). As the snow level progresses down the mountainside during the fall, ptarmigan may move to lower elevations to take advantage of the exposed berry-producing plants, dryas (Dryas octopetala) and sedge (Carex spp.). This was obviously the case for some of the flocks I observed at Eagle Creek and has been likewise reported for ptarmigan in Scotland (Watson 1965a).

Timberline is at approximately 900 m (3000 ft) in the study area. The calculated line of regression in Figure 8 passes through the 900 m (3000 ft) coordinate at a point corresponding to 15 October on the X-axis. As shown earlier, flock composition by this date heavily favors adult males. Also flocks comprised of mostly adult females and juveniles of both sexes have already begun appearing in non-breeding habitats some distance away. These observations substantiate Weeden's (1964) ideas

concerning dispersal of ptarmigan in early winter. Data obtained from radio-marked birds lend additional support. Juvenile female A6 and non-territorial adult male A8 both appeared to be moving away from the study area when last contacted despite earlier histories of observations confined within the study area. The last signal reception (4 October 1973) from male A8 seemed to originate from a ridge about 2 km (1.25 mi) southwest of the study area.

Seasonal movements and partial segregation by sex have also been described for willow ptarmigan (Lagopus lagopus) in arctic Alaska (Irving et al. 1967b) and white-tailed ptarmigan (Lagopus leucurus) in Colorado (Braun and Schmidt 1971). The latter study suggested that seasonal movements were a reaction to environmental conditions, primarily snow depth and wind, that affect the availability of food and roosting sites, and the difference in movements between males and females was attributed to different habitat preferences.

Flocking Behavior

Ptarmigan are sedentary and quiet during August. Most males are in flocks on the ridgetops, and usually do not display or threaten other males unless provoked by some external stimulus such as the presence of the observer. The accidental flushing of a male often results in a flight song display or a chain reaction of flight songs and brief chases as the fleeing male in turn excites nearby males.

Watson (1965a) reported that cock ptarmigan in Scotland occasionally stay with the hens and chicks all summer or rejoin the families

later in the summer after a period of flocking together. Weeden (1965b) wrote that cocks rarely stay with the hen and chicks in midsummer, but that some males, those whose territories contain thickets of tall alder or willow, remain on territories all summer. When a cock was observed with a brood in June or July, the cock never displayed or otherwise attempted to defend the brood. Typically, the cock flew away before the hen or chicks flushed. According to Weeden, broods often combine in early August and attract lone cocks, small groups of cocks, or unproductive hens, resulting in small mixed flocks throughout the breeding habitat.

On two occasions during August I observed a male in the company of hens and chicks at lower elevations. During the first encounter on 1 August the cock lingered nearby while I netted the hen. However, once the brood had scattered, he became unapproachable. On 20 August I captured and tagged a male (A7) after a 50-minute chase during which he refused to leave the vicinity of a hen (or hens) and nine chicks. Male A7 flushed six times and called flight song (Watson 1972) eight times during the encounter, and the erect combs, sleeked feathers, and erect stance clearly indicated a threat posture. Male A7 was not intimidated by my approach and allowed me to get very close (5-6 m) (16-20 ft) each time before flushing. In addition, he was very aggressive when in hand and hard to handle.

During the two encounters that I have noted, both males were extremely hesitant to leave the hens and chicks. However, both sightings were in areas where thickets were available, so it is possible that

these were males that had remained near or on their territories all summer. The behavior noted in these encounters may be a result of ties of the males toward the areas involved, rather than toward the hens and chicks; however, the presence of a hen may heighten the territorial tendencies of these particular males. This would explain why the male observed on 20 August was aggressive at a time when other males rarely displayed or called.

During September males began to appear at lower elevations in more frequent association with hens and their broods. Displays and vocalizations became commonplace. Many males were in flocks that wandered back and forth throughout the alpine area; however, some remained alone, frequented relatively small areas, and interacted with the wandering flocks only when they overran the areas that the lone males were occupying. Usually these lone males remained after the flocks moved on. Thus interactions occurred between males within a flock and between males in a flock and whatever lone males they encroached upon. Interactions were most intense in these latter situations.

Behaviorial interactions between males appeared to peak in late September or early October, and were very similar to those observed during spring, although of generally lower intensity. The various postures, displays, and vocalizations that have been described for territorial males during the breeding season (Hjorth 1970, MacDonald 1970, Watson 1972) also occur during the fall. However, by late October rock ptarmigan appeared to spend most of the short daylight period feeding, as reported by Irving et al. (1967a) for the conspecific willow ptarmigan in northern Alaska, and aggressiveness appeared to have waned.

This resurgence of activity during the fall is rather common among members of the family Tetraonidae, and is not unique to rock ptarmigan in interior Alaska. Fall song and displaying have been noted during observations of hazel grouse (Tetrastes bonasia), ruffed grouse (Bonasa umbellus), spruce grouse (Canachites canadensis), capercaillie (Tetrao urogallus), black-billed capercaillie (Tetrao parvirostris), black grouse (Lyrurus tetrix), caucasian black grouse (Lyrurus mlokosiewiczi), greater prairie chicken (Tympanuchus cupido), lesser prairie chicken (Tympanuchus pallidicinctus), sharp-tailed grouse (Pediocetes phasianellus), willow ptarmigan, and white-tailed ptarmigan (Hjorth 1970). For most of these species, fall activities are also similar to those performed during the spring, but of lesser intensity. In only one case (sharp-tailed grouse in Wisconsin) were fall displays claimed to be as vigorous as in spring.

Involvement of females apparently varies from species to species (Hjorth 1970). For some no mention was made of female participation in or response to fall displays and song. However, it remained unclear whether there actually was no involvement or whether observations of fall behavior were simply insufficient to document such involvement. Investigators believe that pairing of male and female red grouse (Watson and Moss 1970a) and hazel grouse (Hjorth 1970) occurs during the fall as well as in the spring and that this pairing coincides with re-establishment of territorial ties. In addition, males of at least four of the collectively displaying species (black grouse, sharp-tailed grouse, greater and lesser prairie chicken) apparently return to their

respective leks in the fall to display and call. These activities attract some females to the leks, but to a lesser extent than in spring.

Fall song is also very common among birds other than tetraonids (Dorst 1974). Davis (1963) wrote that "innumerable recent studies indicate that territorial behavior occurs at times and under conditions different from courtship behavior." Starlings (Sturnus vulgaris) (Kessel 1957, Davis 1959), song thrushes (Turdus philomelos) (Davies and Snow 1965), blackbirds (Turdus merula) (Lind 1955), and European robins (Erithacus rubecula) (Lack 1943) defend territories in fall, for instance, which are not related to courtship activities.

Investigators noted quite early that spring territorial behavior coincided with an increase in gonad size and that aggressiveness could be enhanced and, in some cases, social rank could be altered through the experimental implantation of androgens (Davis 1963). However, fall territorial behavior in some species was not associated with a commensurate increase in gonad size. For example, starlings actively defended their nest hole in fall when their gonads were small (Kessel 1957). Implantations of large doses of testosterone in starlings had little effect on either aggressiveness or social rank (Davis 1963). Further experimentation revealed that another hormone (Luteinizing hormone) of pituitary origin was responsible for the observed fall aggressiveness in starlings, thus explaining why courtship behavior was not being manifested at the same time. Davis (1963) suggested that the control of aggressive behavior in all birds was originally controlled by gonadotrophins like LH but, in specialized species such as domestic fowl, this

control has shifted to the gonadal hormones for increased efficiency of breeding. This would explain why androgen implants in red grouse cocks resulted in increased courtship and pairing, in addition to increased aggressiveness (Watson and Moss 1970). These investigators also noted that the sudden increase in strife among resident red grouse in the fall was associated with gonad maturation in the juvenile birds, resulting in a reshuffling of the number, size, and shape of territories previously established by the older cocks. Thus it seemed to be an inescapable conclusion that fall behavior is closely tied to physiological conditions that promote or permit certain behavior patterns. The frequent observation that fall song and display among tetraonids does not reach the level noted in spring would appear to reflect a similar limited increase in gonad size during the fall. Indeed this seems to be the case for rock ptarmigan in interior Alaska. So little gonad enlargement was noted among adult males shot during fall that measurements were seldom taken (Weeden, pers. comm.). The few measurements that are available (3 adult males, 1 juvenile male) indicate that testes size in the fall (6 October) is approximately 5.0 mm by 3.2 mm (the juvenile's measurements were slightly smaller). These compare with spring (May) measurements that average 14.4 mm by 10.7 mm (n=21).

This situation evidently exists among many species of birds other than tetraonids. Dorst (1974) concluded that most bird song is under the control of male sexual hormones and that, rather than expressing itself throughout the year, song follows cyclic fluctuations which are closely correlated to testes development. Photoperiod, environmental

conditions, and the quantity and quality of available food have all been shown to influence testes development, and therefore the manifestation of song, display, and overt aggression.

In interior Alaska photoperiod does not seem to be the primary factor involved since the period of greatest fall activity occurs approximately 3 weeks after the time period in August where daily daylight duration matches that found in late April and early May (Johnson and Hartman 1969). The most likely possibility seems to be temperature. Investigators have noted that display activities usually cease or greatly diminish after the first real cold spell associated with winter (Dorst 1974). With regard to tetraonids, it has been observed that males seldom return to their respective leks or territories during winter except on clear sunny days and that usually they only sit there or display weakly (Hjorth 1970). At Eagle Creek the period of fall activity occurred from about 10 September through early October (Fig. 9). Mean air temperatures during this period come closest to approximating those that occur during spring when territorial displays are most pronounced (unpublished chart prepared by Institute of Water Resources, University of Alaska). Furthermore, by the time I returned to Eagle Creek in late October, display activities had virtually ceased, perhaps in response to the onset of cold weather. Temperatures on 1 November plunged to -25°F. A similar pattern was reported for wintering white-tailed ptarmigan in Colorado, where extreme weather conditions were noted to inhibit ptarmigan activity (Brown and Schmidt 1971).

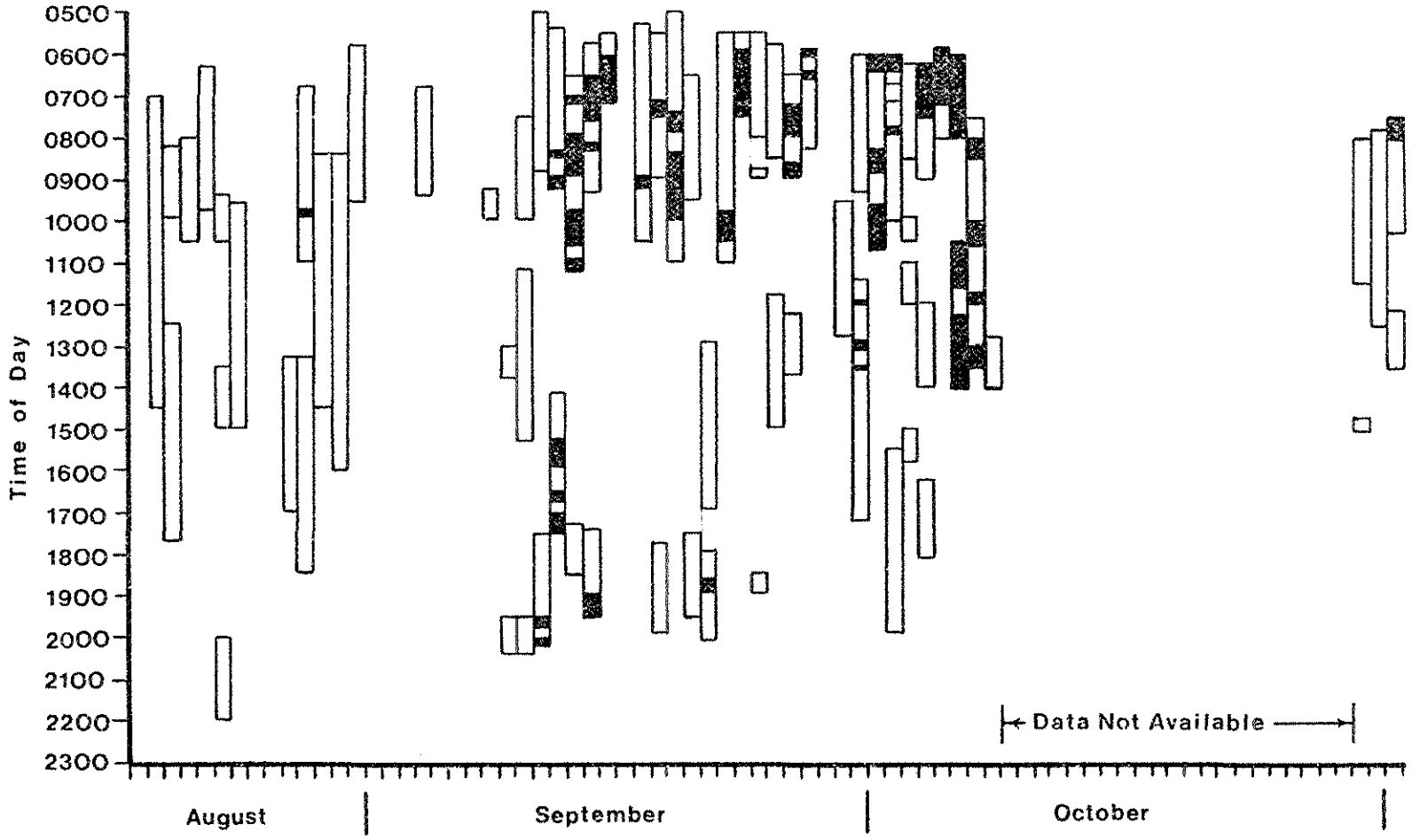

Fig. 9. Activity of male rock ptarmigan during periods of observation at Eagle Creek, 1973. Interactions provoked by the observer's presence are not included. Solid bars represent periods of display and interaction. Empty bars represent periods when birds were resting, feeding, or preening.

The weather in a more general sense also affects ptarmigan on a day-to-day basis. As previously noted, ptarmigan at Eagle Creek gathered into the largest flocks on clear days immediately following periods of inclement weather and on slightly overcast days. Likewise, ptarmigan males seemed to be most active when skies were either clear or slightly overcast. Interactions were less frequent on windy or snowy days. However, the brief snow flurries that often moved through the area frequently stimulated calling among male ptarmigan.

Ptarmigan at Eagle Creek were generally more active early in the day (Fig. 9). This activity was not continual, however. Ptarmigan in flocks often rested quietly without any physical or vocal exchanges. At other times they would move about slowly while feeding, preening, or stretching. Sometimes interactions resumed for no apparent reason; at other times an external stimulus such as other birds calling in the distance, other birds flying overhead, the noise of an airplane or truck, or movement on the part of the observer would apparently trigger the activity. Social facilitation was common; the activity of a few would soon result in a flurry of activity among the rest of the flock. Dorst (1974) confirms that this is to be expected. Evidently psychological influences can release hormonal mechanisms that result in the production of song.

Most of the vocalizations can be categorized as flight song, ground song, flight intention, and social contact (Watson 1972). Social contact ("Krr") and flight intention ("Ka-Ka-Ka...," "Kuk-Kuk-Kuk...") are generally heard whenever birds are observed, while flight song and ground song are more specific to agonistic situations.

The complexity of the vocalization and accompanying display depended on the intensity of the interaction. Low-intensity displays were most common; often the cock fluttered to a landing without a pronounced "stall" during the flight and failed to assume much of a threat posture after landing. Low-intensity displays were characteristic of the interactions prevalent among males in flocks. The activities of these males often resulted in the flock slowly moving across the area in "leap-frog" fashion, each male in turn flying just beyond the previous one in short successive flights.

The most common aggressive activity among males in flocks was the "brief encounter" (Watson and Jenkins 1964, Watson 1972). Often this activity seemed to center around a hump on which the dominating cock would stand in alert fashion overlooking the others. Typically, one male would approach another in a threatening manner, but, in instances where the advancing male was not clearly dominant, the approach would be interrupted by occasional pauses to peck at the ground. Usually the threatened male assumed a submissive posture and walked away, but occasionally the male toward which the aggressive behavior was directed stood his ground, faced the oncoming male, and did not display the appropriate submissive features (lowered combs, raised crest feathers, etc.). In such cases the advancing male would either lunge at the resisting bird and chase it some distance away or quietly withdraw.

Brief encounters rarely involved hens and chicks early in the fall. Chicks would peck at other chicks or even chase other chicks short distances, but chicks were rarely seen threatening adult males. However,

during feeding situations adult males would threaten every individual close to them, including hens and chicks. Hens nearly always scurried away when the aggression was directed toward them; however, in one case where an adult male landed among several chicks, scattering them in all directions, the hen pecked at the male before fleeing. The male chased the hen a short distance, but quickly lost interest and turned to confront a nearby male.

An interesting variation of this behavior was observed among members of a small flock on 13 September. A juvenile male who had been slowly walking about suddenly ran toward a nearby adult male, stopped abruptly, spun around to face the opposite direction, "squiggled" among the vegetation in a low crouching manner, then spun around again to face in the original direction. A short time later an adult male performed similar antics; he stood tall on tiptoes while flapping his wings, ran forward in a low crouching erratic manner, and stopped a few feet short of another male. Although I observed this behavior only once, "jumping" (Watson and Jenkins 1964) apparently is fairly common among fall flocks of ptarmigan in Scotland (Watson 1972), and has been previously observed among fall flocks of ptarmigan at Eagle Creek (Weeden 1963, P-R Segment Rep., Proj. W-6-R-3, Alaska Dept. Fish and Game, Juneau). Weeden observed both young and old males (but not females) engaged in jumping, which he described as a "squiggle." Watson reported that jumping involved birds of either sex and represented a communal aggressive encounter not associated with territory defense. Perhaps this activity is ambivalent in nature since elements of both flight and aggression appear to be present.

By the end of September brood identity was nonexistent and chicks were almost indistinguishable from adults. Hens were more involved in the social interactions among flock members and their vocalizations always elicited further calling and displaying from nearby males.

The higher intensity displays were observed whenever roving flocks encroached upon lone males in areas where spring territories had existed. Song flight "stalls" were higher, reaching an estimated 23 m (75 ft), and males often landed with their tails fanned, feathers sleeked, and combs erect. Frequently a male would either walk or run in a horizontal threat posture toward another male after landing. The most exaggerated ground song displays were also observed during these encounters. Again, very erect combs were frequently observed. The male would bow low to the ground and bring his head up in an arc as he called. The longer "kohwaa-kohwaa-ah" version frequently was voiced. I also observed "walking-in-line," aerial chases, and avoidance during these encounters and ambivalent behavior in the form of displacement feeding was very common.

I believe these lone males were territorial in the sense that they restricted their activities to relatively small areas and attempted to defend them against intruding flocks. Evidence for this will be presented in a later section.

The significance of behaviorial interactions among members of these autumn flocks was not clear. Individual involvement was sporadic and inconsistent. Several times I observed aggressive behavior among males,

only to find them resting amiably beside each other a short time later. I had only one marked male (A8) for which repeated, lengthy observations of interactions within the flock were available (Appendix C). The activities of this male were not restricted to any particular locale. He was observed among members of a flock on four different occasions in widely separated areas, and each time he was vigorously calling and displaying. In most instances this male was the most vocal and aggressive, but at least during a portion of one observation he continually yielded to another male. Usually the interactions were between males in the flock, but on one occasion the aggressive behavior was also directed toward females and juveniles. My impression from these and similar flock observations is that some sort of social structuring was taking place, but the scarcity of marked birds precluded an adequate assessment. One possibility is that these interactions serve to establish a social hierarchy among flock members that may be food related.

The existence of flock behavior among non-territorial birds in the fall could provide the mechanism for accommodating larger numbers of ptarmigan per unit area, if indeed an area held some special attraction (e.g., a preferred food source). Whereas individuals might be excluded by a territorial male, a flock of birds might simply overwhelm the defending male and allow for limited use of the territory by other birds. This situation has been reported for other species. For example, song thrushes will descend en masse on a preferred food source that has ripened, temporarily overwhelming the defending territory owner on which

the resource is located (Davies and Snow 1965), and solitary black-capped chickadees (Parus atricapillus) will respond less aggressively to chickadee flocks than to other solitaries (Barash 1974). Thus, flocking may serve to buffer the aggressiveness of territorial individuals and allow some access to resources contained within defended territories.

Furthermore, if a dominance hierarchy exists among members of these fall flocks, it would, once established, also serve to reduce fighting between individuals thus freeing more time for feeding and other basic functions (Huxley 1966). Murton et al. (1971) found that even subordinate members of wood-pigeon (Columba palumbus) flocks fed more efficiently than did solitary individuals. They suggested that flock members were better able to exploit certain food items because of the combined feeding experience of the group and that individuals within a flock could devote more time to feeding and less to watching for predators.

Territorial Behavior

Although the boundaries of spring territories were not delineated at the time of tagging, subsequent resightings of surviving males (Table 7) were close enough to the initial capture points to suggest that some males that defend territories in the spring return to the same areas during the following fall. Resightings were plotted on maps of the study area, after which the outermost observation points were connected to form polygons (except for male A7) depicting the area of use for each individual (Fig. 7). Observations of the radio-tagged individuals that

Table 7. Distances traveled by adult male rock ptarmigan after tagging on spring territories at Eagle Creek, 1973.

	Distance from Point of Capture (in kilometers)				
	K3	K6	E6	S3	K7
Observation #1	0.24	1.50*	0.68	0.89*	0.27
Observation #2	0.40	0.52	0.32	0.27	
Observation #3	0.48	0.81	0.37	0.31	
Observation #4	0.48	0.37			
Observation #5	0.48	0.77			
Mean distance	0.42	0.61	0.45	0.29	

* Observation while in "molting flock" during summer period. Distance is not used when calculating mean distance from initial capture point.

occurred within the first 2 to 3 weeks after tagging were discarded as abnormal due to a period of adjustment to the transmitter package (Boag 1972). These "fall use areas" show the general fall distribution of solitary males, but the paucity of repeat observations renders the boundaries I have drawn somewhat arbitrary. Only three observations were available for either male E6 or S3, and just five were available for either male K3 or K7. Thirteen observations were available for male A5; thus his fall use area probably comes the closest to approximating reality. The others should be viewed as minima. The polygon described by male A5's movements encompassed 21.3 ha (52.6 a). This figure seems reasonable when compared with the 31 ha (77 a) mean calculated earlier for spring territories at Eagle Creek in 1973 and the 8 to 30 ha (20 to 75 a) territories reported for Scottish rock ptarmigan during a population low.

Territoriality may be defined as the pattern of behavior associated with the defense of a preempted area (Carpenter 1958). Several observations were made where the aggressive behavior of the male involved could be construed as territorial in nature. Most of these observations were of radio-tagged male A5; however, a few observations of unmarked males in similar situations lend support to the hypothesis that some males are territorial during the fall.

Male A5 was captured in mid-August for tagging and reappeared at the capture site about 2 weeks later, presumably after undergoing a period of adjustment to the radio package. Male A5 spent most of the fall in an area only 0.8 km (0.5 mi) from camp and carried a radio

transmitter; thus, he was observed more frequently than other marked ptarmigan. Ninety-four percent (n=18) of the observations of male A5 subsequent to the period of adjustment to the radio package were confined to a relatively small area on South Hill (Fig. 7). The only observation after 1 September in which male A5 was located away from this site occurred on 3 October at a time when many ptarmigan were dispersing from the breeding habitat and territoriality may have been waning.

Male A5 was extremely aggressive during all encounters (n=6) with other ptarmigan on South Hill as long as the interactions were not interrupted by the observer's presence (Appendix D). Most of the more intense displays were observed during these encounters. For example, male A5 often performed very exaggerated ground song threat displays in which he would bow low to the ground and bring his head up slowly while calling. Watson (1972) described this as characteristic of territorial males.

Throughout these observations several consistencies were evident: Male A5 exhibited considerable fidelity to one small area of habitat; he interacted with males that moved into his area of localized use; he often was apart from the other males at the onset of the observations; and he remained in the area when other males left. This suggested that the association of this male with roving flocks was temporary and resulted from their intrusion into his area. During these encounters male A5 aggressively resisted the encroachment by other birds, and was the dominant male during most interactions. Male A5 successfully

challenged other males, causing them to flee, and in time intruding flocks would also leave, although for a while they appeared to simply overwhelm his attempts to defend the area.

Some observations of unmarked birds may also reflect some degree of territorial involvement (Appendix E). For example, on 19 September I observed a lone male behave as if he were defending a territory. A large flock had flushed before me and flown near this lone male. He pursued the flock for approximately 230 m (750 ft) to what may have been a boundary of his territory, where he landed in an impressive song flight display, and stood in an alert posture looking in the direction of the departing flock. In two other instances, two males were observed interacting in the absence of any other ptarmigan. In both cases the participants appeared to be neighboring males involved in territorial activities. The latter observation (30 October) in particular was highly reminiscent of territorial behavior seen in the spring. Two males that were first observed spatially separated along a hillside flew to a spot between them for a series of exchanges.

Female ptarmigan did not seem to be involved in these interactions until about mid-September. I recorded the first instance of a male/female "pair" on 17 September. In this case no other ptarmigan were near and their behavior suggested that the association was deliberate, not chance. The male assumed a threatening posture when disturbed by the observer and followed the female when she flushed. A second, and perhaps more significant, observation occurred on 6 October (Appendix D). During a series of interactions between male A5 and some intruding

males, a female joined male A5 and remained in close proximity to him. During this time, the activities of male A5 appeared to center about the hen. In view of the adherence of male A5 to the area and his continual interactions with other males that entered the area, I find this association with a hen quite consistent. Data are not available to demonstrate the persistence of this association; however, it is suggestive of the pairing characteristic of ptarmigan in the spring and similar to observations reported from Scotland (Watson 1965a).

These observations lead me to believe that some males are territorial during all or part of the fall. However, it is difficult to determine the extent of fall territoriality. The high losses of marked male birds prior to September greatly reduced the opportunity to gather data on the extent of fall territorial behavior. Only eight marked males survived into the fall and remained on the study area (however, six of the eight exhibited the localized movements suggestive of territorial behavior). Even the proportion of single males present in the population at any time is not known, since the greater detectability of the more mobile flocks resulted in their over-representation in daily observations.

There is some indication that the previous history of the males determines whether they are subsequently territorial in the fall. All four of the surviving males that were backtagged on spring territories subsequently exhibited localized movements in the fall, suggesting territorial involvement. The previous history of the radio-tagged males is not known since they were marked during August. However, the two

(A3, A8) that were captured from flocks on the ridgetops did not subsequently confine their activities to discernible areas, whereas the two (A5, A7) captured in willow thickets low on the hillside within the breeding habitat subsequently exhibited localized use patterns around their capture sites. One of these (male A7) was extremely aggressive when captured and was suspected of being territorial even at that time. Both may represent males that elected to remain on or near their spring territories throughout the summer.

Although I feel that these observations indicate that fall territoriality exists, they are not extensive enough to rule out the possibility that male ptarmigan are alternately territorial, then gregarious. In fact, some observations appear to support the idea. For example, male A5 occasionally was encountered near either neighboring male K3 or other males without any sign of aggression being evident, and backtagged males E6, K3, and K6 were never aggressive when encountered in areas judged to be their territories. However, in all such instances I had unknowingly walked within close proximity of the birds. I feel that behavioral interactions among males were disrupted by the closeness of the observer in these instances; therefore, these observations do not necessarily represent periods of non-territorial activity.

A review of the observations of the surviving backtagged males supports this assumption. In all six encounters where these birds were alone, I failed to see the individual before I was within 30 m (98 ft) ($\bar{x}$=15 m), and in each instance the male reacted in a submissive manner. Similarly, backtagged males did not interact with other males during

encounters in which the birds were disturbed by the observer. In contrast, aggressive behavior was evident during the single observation during favorable weather in which the birds were not disturbed by the observer (no interactions were noted during two similar encounters that occurred during poor weather conditions). Thus, I conclude that the visible presence of the observer inhibits behavioral interactions among males and that the paucity of observed aggression among backtagged males exhibiting localized use areas was a function of the nature of the observations and should not be construed as evidence that they were not territorial.

Although the scant data available from backtagged birds suggest that males that are territorial in spring are subsequently territorial in fall, observations of fall flocks confirm that many adult males are in flocks all or part of the fall. Where do the latter males come from if the first premise is correct? One possible source would be surplus males that did not breed the previous spring. There is some evidence that surplus males are present in spring during some years (McGowan 1973, P-R Final Rep., Proj. W-17-3, W-17-4 and W-17-5, Alaska Dept. Fish and Game, Juneau). However, no investigations have been undertaken to demonstrate that a surplus exists beyond the spring breeding period. Among red grouse, the few territorial cocks that die in spring before breeding are replaced by birds from this non-territorial surplus. The remaining non-territorial segment is then forced onto marginal habitat off the breeding areas, and not more than 1 percent survives the summer (Watson and Moss 1970a). However, this has not been demonstrated for

other species in which a surplus exists. Bendell et al. (1972) could find no direct evidence that surplus male blue grouse (Dendragapus obscurus) that are chased away from spring territory sites subsequently leave the area and die. Likewise, Herzog and Boag (1978) concluded that yearling male spruce grouse (Canachites canadensis) that do not establish spring territories remain peripheral to the main group of displaying males and are available during autumn to fill any vacancies created by the death of resident adults.

Another possible source would be males that occupied territories in marginal habitat during the preceding spring. Presumably these males, which establish territories but do not necessarily attract mates, would have less reason to reestablish ties with the territory during the subsequent fall, and would either seek new territories or remain in flocks.

The other alternative, of course, is that not all birds that are territorial in spring resume territorial activities the following fall. Band returns (Weeden 1972) from earlier studies revealed that only 31 percent of the banded adult male ptarmigan shot during the fall were killed within 0.4 km (0.25 mi) of the point of banding during the previous spring, while 88 percent of the banded adult males recaptured during the following spring were within 0.4 km (0.25 mi) of the original capture sites of the previous spring (Table 8). It is assumed that these birds were originally banded while on spring territories and that many resightings of less than 0.4 km (0.25 mi) from the site of a spring territory represent a return to the original territory site. An obvious

Table 8. Leg band recoveries from adult male rock ptarmigan captured on spring territories at Eagle Creek, 1960-1968 (unpubl. data, Alaska Dept. Fish and Game).

Distance from banding site	Recovered in fall of same year banded	Recaptured next spring	Recaptured in spring 2 or more years later
up to 0.4 km	12	21	8
greater than 0.4 km but not more than 0.8 km	5	0	2
greater than 0.8 km but not more than 1.2 km	3	0	1
greater than 1.2 km but not more than 1.6 km	8	3	1
more than 1.6 km	11	0	1

problem with this analysis is that the samples were obtained in different ways; thus, I am not convinced that the comparison is valid. Each spring researchers systematically searched the entire area for ptarmigan to capture and mark, whereas hunters in the fall obtained birds in a manner that favored the inclusion of birds comprising fall flocks. Flocks are more visible because of the number of birds involved and their tendency to move around. In contrast, a person can easily walk past lone birds. The same territorial males that react aggressively to other males entering their territories will usually not respond to a similar intrusion by a person.

If these two strategies, territoriality and flocking, are present within the ptarmigan population in the fall, what advantages are accorded by being territorial? The resurgence of territorial activities among males in the fall and the tendency for males to remain near the breeding areas in winter suggests that territorial ties are paramount. Data that show that females move farther to overwinter than males and that juveniles move farther than adults (Weeden 1964, Irving et al. 1967, Hoffman and Braun 1975) may reflect the differing degrees of involvement of different segments of the population in activities relevant to territorial spacing. In other words, the males and few hens (primarily adults) that establish fall territories may be hesitant to leave the breeding grounds and thus not move as far, even though remaining near the breeding habitat may subject them to less favorable conditions than faced by individuals moving farther away. Food shortages in winter and

poorer conditions for winter survival (other than food supplies) in breeding habitats have been posed as possible reasons for the differential movement of ptarmigan in winter (Weeden 1964). However, those remaining may not necessarily be placed at a disadvantage. With the departure of a large portion of the population, resources may be adequate for those remaining. In addition, the remaining birds are thought to remain near, but not necessarily on (at least all the time), the breeding grounds; thus, they may avoid harsh environmental conditions by temporarily moving to nearby timbered areas in the subalpine zone. Braun et al. (1976) suggested that males wintering closest to the breeding areas may be more successful than those wintering farther away; however, there is no evidence for this at Eagle Creek. Nonetheless, fall territoriality may provide familiarity with an area that gives an individual a competitive advantage during the following spring when breeding takes place. The dominance that males enjoy on their own ground is an important psychological factor that affects gonad maturation and the subsequent ability to reproduce successfully (Dorst 1974). However, as long as the question of whether the number of breeding males is determined in the fall as postulated for red grouse (Watson and Moss 1970a) or in the spring as postulated for blue grouse (Bendell et al. 1972, Zwickel 1972) remains unanswered, the full role that fall behavior plays in the annual cycle remains speculative.

CONCLUSIONS

Properly fitted backtags did not appear to reduce the ability of males to continue defending spring territories. Radio tagging did not prevent one male from establishing and defending a new territory or another male from successfully competing for social standing within fall flocks.

Ptarmigan apparently do not need to adjust to the presence of backtags. However, up to 19 days were required for birds to adjust to the heavier radio packages. During this adjustment period radio-marked birds were hesitant to fly and moved erratically about the area.

Brightly colored backtags probably increase susceptibility to avian predation. Likewise, the losses in this study suggest that red is a poor choice where avian predation is concerned.

Most ptarmigan aggregate into flocks in the fall and range widely over the area. The process is a dynamic one that reflects both the gradual involvement of family groups into the flock social structure and changes in local weather conditions. Generally speaking, flock sizes increase as fall progresses; however, flocks also are largest immediately following periods of inclement weather. Extremely large flocks are uncommon. Most flocks are comprised of less than 25 individuals.

Behavioral interactions among males in flocks are commonplace throughout September and early October, and contain most elements common to territorial encounters in spring; however, they are of generally lower intensity and do not appear to be related to specific parcels of

land. Activity is greatest early in the day, and on calm days when skies are either clear or slightly overcast. Brief encounters are the most frequent aggressive encounters involving males. Hens and chicks seldom are involved until after brood breakup in late September. Individual involvement (and conversely, tolerance of others) is sporadic. Interactions between flock members probably result in the establishment of a social hierarchy within the flock.

Flock members, through sheer advantage of numbers, appear to be able to temporarily overwhelm territorial males. Thus, flocking may serve to allow access to preferred food resources that are made generally less available by the onset of snow cover at higher elevations and the establishment of territories by some males in the population. Ptarmigan flocks frequent progressively lower elevations throughout the fall, probably in response to locally harsh environmental conditions resulting from the onset of winter. Adult males comprise an increasing proportion of the flocks as fall progresses, suggesting that most females and juveniles leave the breeding grounds by early October as previously reported.

Some male ptarmigan confine their activities to readily discernible areas in the fall and tend to remain apart from the roving flocks. The repeated attempts by one frequently observed male to defend his area of localized use from incursions by other males suggests that some males become territorial all or part of the fall. It was not possible to determine the extent of territoriality among the population; however, certainly not all adult males are territorial, since many can be found

in flocks during the fall. Males that occupied territories in the same area during the previous spring may be more prone to reestablish territories in the fall. One female was observed closely associated with a territorial male, suggesting that males may pair with hens (at least temporarily) during the fall. It is suggested that, while limited food supplies, harsh winter conditions in the breeding habitat, and the urge to disperse may be responsible for most ptarmigan wintering away from the alpine areas, the ties that certain adult males (and a few hens) have to territories may be responsible for them remaining. Such a strategy may give these territorial individuals an advantage during the following spring when breeding takes place.

Appendix A. Tagging data for rock ptarmigan at Eagle Creek, 1973.

Leg Band number	Backtag designation	Backtag color[a]	Date marked	Sex	Age[b] (yrs.)	Location
2302	K1	R	22 May	M	2+	SHG
2303	K2	R	22 May	M	1	SHG
2304	K3	R	22 May	M	2+	SHG
2305	K4	R	23 May	M	2+	LCC
2306	K5	R	23 May	M	1	LCC
2307	K6	R	23 May	M	2+	LCC
2308	K8	R	23 May	M	2+	LCC
2309	E3	R	23 May	M	2+	LCC
2310	E4	R	23 May	M	2+	LCR
2311	E2	R	23 May	M	1	LCR
2312	K7	R	24 May	M	2+	NRB
2313	E1	R	24 May	M	2+	NRB
2314	E5	R	24 May	M	2+	BP
2315	E6	R	24 May	M	2+	BP
2316	E7	R	24 May	M	1	UCC
2317	E8	R	25 May	M	2+	SH
2318	S1	R	25 May	M	2+	CB
2319	S2	R	25 May	M	1	NFGD
2320	S3	R	25 May	M	1	LMF
2321	S4	R	26 May	M	2+	BP
2322	S5	R	26 May	M	2+	LCR
2323	S6	R	26 May	M	2+	LCR
2324	S7	R	26 May	M	2+	LCR
2325	S8	R	30 May	M	1	CB
2326	T1	R	31 May	M	1	NRB
2327	T2	R	31 May	M	1	NRB
2328	T3	R	31 May	M	2+	NRB
2329	T4	R	31 May	M	2+	UCC
2330	K1	G	4 July	F	2+	SHG
2331	K2	G	4 July	F	2+	SHG
2332	A1	G	4 July	F	1	SH
2333	A2	G	4 July	F	1	CB
2334	A3	G	6 July	F	2+	NRB
2335	A6	G	6 July	F	2+	UCC
2336	A7	G	6 July	F	2+	SH
2337	A8	G	6 July	F	2+	SHG
2338	T1	G	7 July	F	1	LCR
2339	T2	G	7 July	F	2+	BP
2340	T3	G	11 July	F	1	SH
2341	A4	G	11 July	F	2+	SHG
2342	A5	G	11 July	F	1	SHG
2343	K3	G	13 July	F	1	NRB
2344	S1	G	13 July	F	1	LCR

Appendix A. Continued.

Leg Band number	Backtag designation	Backtag color[a]	Date marked	Sex	Age[b] (yrs.)	Location
2345	S2	G	30 July	F	2+	BP
2346	T4	G	31 July	F	1	SHG
2347	K4	G	1 Aug	F	A	NRB
2348	K5	G	1 Aug	F	A	NRB
2349	K6	G	1 Aug	F	2	NRB
2350	A1	R	4 Aug	M	A	NRB
2351	A2	R	4 Aug	M	A	NRB
2352	T5	R	4 Aug	M	A	NRB
2353	A1	B	7 Aug	-	C	LCR
2354	A3	R	7 Aug	M	A	LCR
2355	A2	B	7 Aug	-	C	LCR
2356	A4	R	7 Aug	M	A	LCR
2357	K1	B	7 Aug	-	C	LCR
2358	K2	B	7 Aug	-	C	LCR
2359	K7	G	8 Aug	F	A	SH
2360	K3	B	8 Aug	-	C	SH
2361	A5	R	16 Aug	M	A	SHG
2362	A6	R	20 Aug	F	C	SHG
2363	A7	R	20 Aug	M	A	UCC
2364	K8	G	20 Aug	F	A	UCC
2365	A5	B	20 Aug	-	C	SH-UCC
2366	A3	B	20 Aug	-	C	SH-UCC
2367	A4	B	20 Aug	-	C	SH-UCC
2368	K4	B	20 Aug	-	C	SH-UCC
2369	K5	B	20 Aug	-	C	SH-UCC
2370	K6	B	20 Aug	-	C	SH-UCC
2371	K7	B	22 Aug	-	C	SH-SHG
2372	K8	B	22 Aug	-	C	SH-SHG
2373	A8	R	30 Aug	M	A	LCR

[a] B= blue, G=green, R=red.

[b] determined by feather development and comparison of the pigmentation on primaries P9 and P8 (Weeden and Watson 1967). After P9 moults in late summer, long-yearlings can no longer be distinguished from birds two years of age or older and are combined as "adults" (A). Chicks (C) are birds of the year.

[c] Location codes: South Hill (SH), South Hill Gully (SHG), Lower Cripple Creek (LCC), Upper Cripple Creek (UCC), North Running Brook (NRB), Lower Camp Ridge (LCR), Bowmans Pup (BP), Lower Mastodon Fork (LMF), and North Fork of Golddust Creek (NFGD).

Appendix B. Weather data for Eagle Creek for the period 31 July 1973 through 1 November 1973 (U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, New Hampshire).

Date	Max. Temp. (°F) at 2900 ft.	Min. Temp (°F) at 2900 ft.	Precipitation at 2900 ft. (water equiv. in inches)	Max. Wind Speed (miles per hour) 2900 ft.	3620 ft.
July 31	59	40	0	4	15
Aug 1	62	39	.11	4	10
2	61	37	0	4	8
3	59	45	0	7.5	15
4	61	47	.03	2	5
5	70	45	0	4	10
6	59	43	0	7.5	20
7	60	42	0	3	7.5
8	61	39	.11	5	10
9	52	42	.21	-	20
10	-	39	.47	-	30
11	45	38	.20	-	15
12	46	31	.06	-	15
13	45	27	0	7	10
14	47	32	0	5	10
15	48	32	.15	3	7.5
16	55	30	.01	3	3
17	49	36	0	5.5	20
18	53	38	.10	7.5	20
19	55	48	0	4	15
20	76	48	0	7.5	15
21	53	43	.45	2.5	14
22	50	39	.46	4	10
23	60	35	.02	3	10
24	60	40	.01	5	14
25	49	41	.06	4	14
26	51	39	0	6	10
27	52	27	.06	4	10
28	49	37	0	5	20
29	44	33	0	5	20
30	47	29	0	2	5
31	53	34	0	3.5	7.5
Sept 1	54	33	0	5	7.5
2	58	30	0	2.5	10
3	58	34	0	5	7.5
4	58	30	0	5	10
5	58	37	.02	5	7.5
6	59	34	.04	5	7.5
7	56	32	.01	5	10
8	52	38	.02	3.5	10
9	41	36	.33	2.5	15

Appendix B. continued.

Date	Max. Temp. (°F) at 2900 ft.	Min. Temp. (°F) at 2900 ft.	Precipitation at 2900 ft. (water equiv. in inches)	Max. Wind Speed (miles per hour) 2900 ft.	3620 ft.
Sept 10	49	33	.03	3	10
11	56	31	0	4	10
12	57	34	0	5	10
13	61	38	0	7.5	20
14	58	37	0	3	15
15	66	35	0	6	7.5
16	68	42	0	5	15
17	59	38	0	5	15
18	62	36	0	4	7.5
19	40	32	0	2.5	15
20	39	32	.11	1.3	-
21	38	31	.05	-	10
22	32	29	.04	-	15
23	33	27	0	-	15
24	33	23	0	-	20
25	42	24	0	1	10
26	40	30	0	7.5	7.5
27	34	25	.03	10	30
28	29	20	0	5	15
29	33	24	.09	5	15
30	45	25	0	5	30
Oct 1	38	31	.17	2.5	15
2	34	28	.12	7.5	20
3	31	24	.18	10	15
4	29	23	.07	6	15
5	31	27	.04	7.5	15
6	34	24	.28	3	-
7	28	20	0	2.5	-
8	32	17	0	1	-
9	28	20	.20	7.5	10
10	25	18	0	3	-
11	23	13	.08	3	-
12	16	12	.05	7.5	-
13	15	12	.04	7	10
14	13	10	0	7	5
15	13	2	0	7	-
16	25	0	0	1	-
17	33	15	0	1	-
18	24	18	0	5	-
19	25	9	0	2.5	-
20	22	11	o	2	-

Appendix B. continued.

Date	Max. Temp. (°F) at 2900 ft.	Min. Temp. (°F) at 2900 ft.	Precipitation at 2900 ft. (water equiv. in inches)	Max. Wind Speed (miles per hour) 2900 ft.	3620 ft.
Oct 21	20	5	0	1	-
22	20	0	0	1	-
23	25	4	0	1	-
24	25	3	0	1	-
25	25	3	0	1	20
26	31	11	0	5	-
27	25	6	0	1	-
28	30	16	0	1	-
29	27	18	0	7.5	-
30	19	14	.01	5	-
31	14	5	.01	2.5	-
Nov 1	14	-4	0	1	-

Appendix C. Summary of observations involving marked male A8 which may suggest development of a social hierarchy within fall flocks.

Male A8 was captured on 8 August from a flock of eight adult males on the ridgetop, and marked with a backtag and transmitter. On 15 September male A8 was observed within a flock numbering approximately 70 birds. Male A8 was responsible for most of the calling that occurred and spent most of the observation period walking about with erect combs. Other males voiced ground song also but not as frequently. No physical interactions among adult males were noticed, although several times male A8 or another male ran among the chicks in the flock and scattered them in all directions. On 19 September male A8 was observed in another drainage with a flock of 16 birds. When first observed, five adult males (including A8) were on the hillside above the rest of the flock interacting with one another through successive song flights and threatening postures. During the first half hour of observation male A8 was submissive to another male, who kept following male A8 either on the ground or in short song flights. Finally, every time the pursuing male landed nearby, male A8 would fly farther down the hill. Eventually these males worked their way to where the rest of the flock was quietly sitting among low vegetation. For the next hour most of the flock remained quiet while feeding and preening. Male A8, however, now became aggressive and on two occasions ran toward other males, causing the other males to flee a short distance. Later male A8 ceased threatening these males and began to roost near them. On 21 September what may have

been the same flock was observed at the same location, and again relatively few individuals (4 males, including A8) were doing all the calling. On 27 September male A8 was observed at still another site within a flock containing two adult males, three adult females, four male chicks, and four female chicks. Male A8 was extremely aggressive and deliberately made repeated short thrusts at the other members of the flock causing them to scurry to one side. Throughout the observation period male A8 walked about with very erect combs and voiced ground song.

Appendix D. Summary of interactions involving marked male A5 which may indicate territorial behavior.

13 September 1973 (0945-1037 hours): A flock of approximately 25 ptarmigan (mostly males) was observed interacting on South Hill within male A5's "use area." Much calling and displaying took place between the adult males. Male A5 was recognizable during two encounters:

During the first interaction an unmarked male flew 137-183 m (450-600 ft) downhill from the flock, performed a song flight display, and landed on a solifluction lobe. Male A5 immediately followed suit and landed within 3 m (10 ft) of the first male after executing a song flight display comparable to that of the first male. Both males exchanged several ground song threats and grunts, then became quiet and stood alongside one another. Occasionally one would peck at the ground. After approximately 1 minute the unmarked male gave the flight intention call and flew away. Male A5 remained behind and voiced ground song.

During the second encounter, male A5 was first noticed standing on a hump in an alert posture. Another male began to run uphill toward male A5 but then turned back. Then male A5 flew in a low song flight display and landed with his tail fully spread. This was followed by a ground song after which he ran uphill.

14 September 1973 (0615-0750 hours): A flock of approximately 30 ptarmigan (mostly males) was observed interacting on South Hill within male A5's "use area." Male A5 was first seen approximately 60 m (200

ft) from the flock, which was feeding among the dryas and bearberry (Arctostaphylos spp.). Male A5 ran toward the flock, stopping occasionally to call. He gave seven ground song displays in close succession, each time by bowing low to the ground while calling. Male A5's combs became erect and bright red each time he called. This calling resulted in most of the flock moving toward male A5. A flurry of activity erupted that included many song flight displays by several males. Many of the individuals were pecking at the vegetation, but I could not tell if they were actually feeding or whether this was displacement activity. About half of the flock were either hens or chicks. One juvenile male gave an off-key ground song call.

Male A5 was relocated in the flock at 0650. His combs were erect and very red as he walked about giving ground song calls. Many males were calling at once and it was impossible to keep track of the activity.

At 0700 male A5 preened and stretched for about 3 minutes. During this time his combs were only partially erect, but he continued to be very alert and glanced around frequently. This activity changed abruptly and male A5 began running in short spurts with pauses to call ground song and peck vigorously at the vegetation. He gave six ground song calls in close succession, then relaxed and appeared to begin feeding.

At 0730 most of the flock flushed on their own and left the area. Three males including A5 remained behind. Two of these flew into South Hill Gully, one after the other. Seconds later one returned and, along with the third one, flew in the direction the flock had flown earlier. The male remaining in South Hill Gully turned out to be A5.

18 September 1973 (0830-0838 hours): A flock of six males flew into male A5's "use area," landing approximately 45 m (150 ft) from A5. Male A5 began calling, resulting in a barrage of vocalizations between A5 and other males. Other males approached male A5 and displayed weakly before flying from the area as a flock. Male A5 remained and ceased calling.

1 October 1973 (0740-1020 hours): I observed male A5 on his "fall use area" with a flock of five other birds. Composition of this flock was uncertain but was believed to contain an adult female and juveniles of both sexes. Another flock of nine birds (mostly males) flew into the upper portion of South Hill Gully. These new birds ran across the hill, calling as they went. Male A5 flew halfway up the gully toward the males and landed in a frontal display. Then male A5 ran across the hill parallel to the path of the birds uphill of him. Male A5's combs were erect and he gave several ground song calls. Then male A5 flew back to the center of the gully in a song flight display. The other birds (both male and female) that A5 had been with ran to where A5 had flown, milled about, and joined A5 in the calling. Male A5 quit calling after the flock uphill from him had moved out of sight.

Thirty minutes later another small flock flew into the area and began calling. Male A5 responded by running to a hummock approximately 8 m (25 ft) away where he assumed an alert stance and called ground song twice. Then A5 flew in a song flight display to a point approximately 60 m (200 ft) downhill. The vocalizations and short song flights continued for the next half hour and included one loud screaming call by

a female that flew into the gully. Finally one of the males flew downhill in a high song flight display. Minutes later male A5 and this other male flew back uphill, and landed about 5 m (15 ft) apart with fanned tail feathers. Both began to walk parallel to one another, but the unmarked male appeared hesitant, voiced flight intention calls, and finally flew off. Male A5 stood erect and looked in the direction of the departing unmarked male.

At 1000 several more males flew into the upper part of South Hill Gully. Their arrival set off a whole barrage of ground song calls, short chases, and song flight displays. One or two of the hens became excited and added their voices to the racket. Five males, including A5, engaged in a series of short pursuits in which they would briefly plop into the snow, only to take off again as soon as another male landed nearby. By this time their activities had taken them across the hill to my position of observation, but the males appeared oblivious to my presence.

4 October 1973 (0638-0745 hours): Ground song calls were heard coming from South Hill Gully during the first half hour. Five ptarmigan (4 males, 1 female) flew to the south side of the gully at 0645. The males, which included A5, began running in spurts, one after another, and called constantly. But when another male in the gully called, these males stopped to listen. Male A5 responded with a ground song call. Then A5 and one other male flew back into the gully toward the calling male. For the next half hour interactions continued at a low level of intensity. Finally at 0720 most of the birds flew out of the gully.

Shortly thereafter (0730), one male flew in song flight display to the upper part of the gully. Male A5 followed and landed nearby. After a period of walking about and exchanging ground song calls, both settled down to rest only 1 m (3 ft) apart.

6 October 1973 (1030-1245 hours): A small flock of about six birds (including male A5) was observed just north of the base of South Hill Gully. Males in the flock were slightly apart from the others and gave occasional ground song calls. At 1040 a male flew in song flight display to a point halfway up the south side of the gully. Male A5 flew to the base of the gully and called. Another male flew up to nearly the same spot to challenge, and lots of low-intensity threat calls resulted. The latter male flew back downhill a few minutes later. At 1108 male A5 flew in song flight display to a point near the flock located downhill of the gully, but sat apart from them.

At 1215 I walked through the gully causing four males, including A5, to fly up the gully in song flight displays. At 1226 the calling of a female at the bottom of the gully caused two males to fly down to that location in song flight displays. Male A5 gave two ground song displays before also flying down. He was joined in flight by a hen and both landed on top of a hump to one side of the gully. Male A5 called loudly after landing and the female could be heard faintly clucking. Two of the other males in the gully then glided out of the gully to the flat below. Male A5 and the hen walked about 30 m (100 ft) during this time. Finally A5 climbed onto a rock and stood in an alert stance while the

female preened nearby. After a short pause, male A5 called and flew away, with the hen in close pursuit. Male A5 landed in a low song flight display approximately 90 m (300 ft) away and the hen flew in beside him.

Appendix E. Observations of unmarked birds that may indicate territorial behavior.

19 September 1973 (0725-0810 hours): A flock of 15 ptarmigan flew from the head of Eagle Nest Pup as I approached. Nearby I noticed a single adult male standing in an alert stance atop a hump somewhat apart from where the flock had flushed. His feathers were sleeked (an aggressive characteristic) and he stood tall in an attempt to see where the other birds had flown to. After a few moments another 11 ptarmigan flushed about 90 m (300 ft) away. The lone male immediately flew after them, performed a flight song display, and landed approximately 230 m (750 ft) away in an obvious threat display. He remained standing in an alert posture with sleeked feathers for more than 15 minutes after the departure of the other birds.

7 October 1973 (0950-1038 hours): Two male ptarmigan on the south side of West Running Brook were heard calling several times before I visually located them. At 1034 a male flew into view and plopped into the snow among the alders. A pursuing male landed behind the first male, calling flight song as he landed, then took off again toward the first. The lead male immediately took flight again and fluttered down in flight song display about 90 m (300 ft) away. The second male landed nearby. Another flight song was heard and the second male returned, landed in a song flight display, fanned his tail, and began to strut about. By 1038 the activity ceased and the remaining male was quiet.

30 October 1973 (1010-1025 hours): Two male ptarmigan were located in upper Castle Brook, in the same area used by territorial males each spring. No other males were seen in the vicinity. The male in the uppermost part of the drainage flew downstream and landed on the south side in song flight display. The other male was high on the south side above the spot where the first landed. This second male called and flew across the valley to the north side, then quickly returned and walked briskly uphill in spurts, calling as he went. This activity was very similar to what was often seen in the spring between neighboring males.

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