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ASPECTS OF MORPHOLOGY IN FEMALE ROCK PTARMIGAN (*LAGOPUS MUTUS*) DURING OVARIAN RECRUDESCENCE

A

DISSERTATION

Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

by

Ronald D. Modafferi, B.S., M.S.

Fairbanks, Alaska

December, 1975

ASPECTS OF MORPHOLOGY IN FEMALE ROCK PTARMIGAN (LAGOPUS MUTUS)
DURING OVARIAN RECRUDESCENCE

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ABSTRACT

This study of gross morphology of prelaying female Rock Ptarmigan (Lagopus mutus) in Interior Alaska during 1969 to 1971, a period of population decline, revealed seasonal differences and differences between age classes, between areas and between years in weights and/or measurements of component parts of the body. Variation in weight and/or size of various components of the body was attributed to the influences of weather, slope exposure, age class, ovarian recrudescence and body size. Seasonal variation in morphology was associated with reproductive recrudescence, however the ovary and oviduct were not the only components which contributed to variation in body weight. Ovarian follicle size was the only variable that exhibited statistically significant season, age class, area and year effects. Juveniles did not attain adult body weight prior to egg laying and they probably did not do so until their second autumn of life. Seasonal and annual variation in morphology and the reproductive cycle were attributed to the effects of winter and spring weather and melting of the snow pack on availability of food resources. During the prelaying period, females accumulate reserves of minerals in the skeleton and reserves of fats in subcutaneous depots, however no protein reserves were found to accumulate in the breast muscles. Increases in weight and/or size of component parts of the alimentary tract were probably an adaptive response to the increased bodily demands during reproduction.

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INTRODUCTION

Periodic fluctuations in numbers of breeding birds are a common characteristic among tetraonid species of the temperate and arctic regions. There is no agreement yet on the cause of these fluctuations. Siivonen (1957) demonstrated that early spring temperatures and the appearance of snowless spots on the breeding areas correlated with annual fluctuations in numbers of Blackgame (Lyrurus tetrix) and Capercaillie (Tetrao urogallus); he believed that variation in the nutritive condition of prelaying females, associated with the availability of early green plants, may help explain this phenomenon.

Data obtained during a long term study of Rock Ptarmigan (Lagopus mutus) at Eagle Creek, Alaska verified that annual changes in clutch size correlated with fluctuations in spring breeding population levels (Weeden 1965a). Moss (1968) found that Icelandic Rock Ptarmigan, which lay clutches of about 11 eggs, consume a diet higher in nitrogen, phosphorus and soluble carbohydrates than Scottish Rock Ptarmigan, which lay clutches of six to seven eggs. This information pointed to the possibility that annual changes in the population levels of Alaskan Rock Ptarmigan, as in Blackgame and Capercaillie, varied in relation to the nutritive condition of prelaying females.

I postulated that if this combination of events were related to annual changes in the levels of nutrition of prelaying hens this would be reflected in the relative "condition" of the birds which would in turn be evidenced in their gross morphology.

The objectives of this study were: first, to document the changes in morphology which occur in free-living, prelaying female Rock Ptarmigan and second, to test the hypothesis that morphology of prelaying females is different between years of increasing and decreasing populations. Because data collected on a nearby control study area in a complimentary study indicated that numbers of ptarmigan decreased through the duration of this study (1969-71), only the first objective could be met. Therefore, the purpose of this paper is: (1) to describe the dynamics of morphology in free-living, prelaying female Rock Ptarmigan and (2) to relate these findings to the environment and breeding biology of Rock Ptarmigan.

Although gross morphology has been used to appraise the nutritive condition of birds (Hanson 1962; Breitenbach et al. 1963), there is little detailed information on morphological changes among prelaying females in fluctuating populations, nor are there sufficient data to show the range of morphological variation occurring throughout a population cycle. In addition, there are relatively few data available that itemize morphological changes among prelaying females in any avian species and among those that are available some are contradictory (Kirkpatrick 1944; Lewin 1963).

Numerous studies of birds have been directed at describing variation of total body weight (Nice 1938; Baldwin and Kendeigh 1938) or the weight of individual component parts of the body (Oakeson 1953, 1956; Hartman 1955; Fisher and Bartlett 1957; Brush 1966). Investigations involving both aspects are few (Quiring and Bade 1943; Wilson 1952, 1954a, 1954b; Stegman 1954; Anderson 1972) and information on weight and size dynamics of the body and its component parts in free-living females during ovarian recrudescence is scarce and fragmentary. While it is generally accepted that the total body weight of females increases prior to egg laying, there is disagreement as to which body components contribute to this increase.

Two studies representing contrary data are those by Lewin (1963) on free-living California Quail (*Lophortyx californica*) and Kirkpatrick (1944) on pen reared, captive Ring-necked Pheasants (*Phasianus colchicus*). Lewin (p. 266) stated that

> the factors responsible for the nearly 20-gram increment in the females just prior to and during the laying period is obviously due to the increased size of the reproductive organs.

Whereas Kirkpatrick (p. 181) reported that

> the weight of the ovary itself was not enough to account for the spring weight increases in the hens, because the ovary did not enlarge significantly until late March, sometime after the body weights had begun to increase.

It is possible, but doubtful, that both interpretations are correct and the discrepancy is due to captivity or species differences in breeding biology.

The literature, however, contains reports from numerous studies on many different species in which ovarian recrudescence is paralleled by increases in the weight of other body components. Taylor and Moore (1954) demonstrated that many parts of the skeleton in domestic fowl increased in weight during the prelaying period. Lorenz *et al.* (1938) furnished evidence that liver weights of domestic fowl increased during ovarian recrudescence. Similarly, Brenner (1967) reported that abdominal, cervical and subscapular fat deposits of Red-winged Blackbirds (*Agelaius phoeniceus*) increased in weight prior to egg laying.

In contrast to increases in weight, some body components may be expected to decrease in weight and size from winter to spring. Using rationale developed by Leopold (1953), that intestinal weight and length increase with the fiber content or physical harshness of the diet, one would hypothesize a decrease in the length and weight of these components of the alimentary tract as birds change from a relatively harsh fibrous winter diet to the spring or prelaying diet of more tender and newly growing plant parts as is the case in Rock Ptarmigan (Weeden 1969).

Additional factors may contribute to variation of total body weight and weight or size of body components in birds. Koskimies (1958) demonstrated seasonal, geographical and yearly variations in the body weight of Capercaillie and Blackgame. Helms *et al.* (1967) partitioned variation in weight of major body components in Dark-eyed Juncos (*Junco hyemalis*) into categories of individual size (wing length), time of day and air temperature. Nestor *et al.* (1967) considered genetic components in studying variation of body weight and body measurements in domestic turkeys.

Described in this paper are changes in average body weight and average weight and/or size of body component parts for two age classes of prelaying female Rock Ptarmigan collected during three periods in three successive years. For the same sample of individuals, variation in morphology is related to year, age class, area, photoperiod, follicle size, individual size, snow cover, prenuptial molt and air temperature.

The relevance of these findings to the environment and breeding biology of Rock Ptarmigan is discussed.

Ultimately, data such as these should be used in part to test Siivonen's (1957) hypothesis that the spring diet which is "decisive" for restoring nutritive condition of females during the "fattening season" (prelaying period) is responsible for annual fluctuations in numbers of tetraonids.

MATERIAL AND METHODS

Study Area

This study was conducted in the Yukon-Tanana upland (65°30' N, 147°30' W), approximately 160 km north of Fairbanks, Alaska in a 44 sq km area drained by the upper third of Porcupine Creek (Fig. 1). This area of rounded, essentially treeless hills is characteristic of the arctic-alpine tundra in Interior Alaska as described by Weeden (1968). It is accessible to hunters from the Steese Highway by an eight km walk or a rough 19 km mining road and remains relatively undisturbed by man except for this access road, a few cabins and some tailing piles from previous placer mining operations. Disturbances removing stands of riparian spruce (Picea sp.) have favored growth of willow (Salix sp.) and alder (Alnus sp.).

The climate of the area is continental subarctic with the exception of winds characteristic of alpine areas. Annual precipation is from 25 to 40 cm. Except for a few large snow drifts and occasional snow showers, the area is free of snow cover from mid-May to mid-September. Annual temperatures vary from -50° to 30°C with -17° and 22°C being the extremes recorded during the three field seasons (Fig. 2).

Aspects of the Rock Ptarmigan Life Cycle

Territorial behavior intensifies in breeding and nesting areas in late April following the arrival of females and it spaces males over the available alpine tundra nesting habitat. It has been reported that

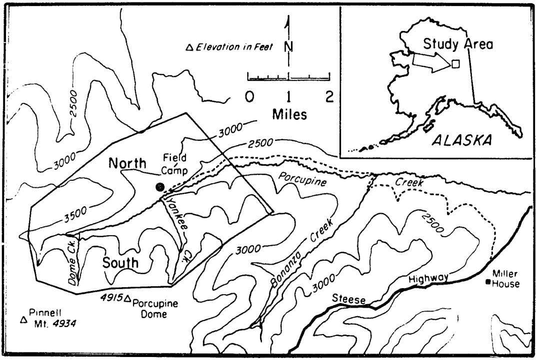

Figure 1. Location of the study area in Alaska, the boundaries of the study area and the subdivision of the study area into two slope exposure categories.

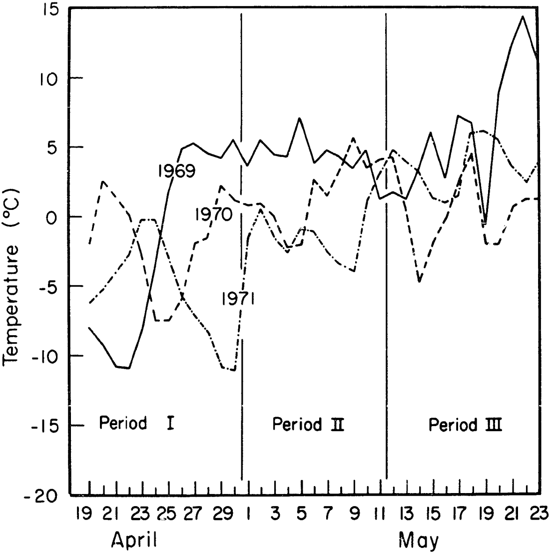

Figure 2. Mean daily temperatures recorded hourly at Porcupine Creek from April 19 to May 23, 1969-71. Periods I, II and III roughly correspond to initial, intermediate and final stages of ovarian recrudescence in female Rock Ptarmigan.

Rock Ptarmigan are monogamous but it is not uncommon to see a single male associated with two or three females.

Females appear to wander and until egg laying are not confined in their movements by the boundaries of territories maintained by a specific male. Eggs are laid in late May or early June and hatch about 21 days later. The hatch correlates with plant phenology, occurs within a one to two week period and usually peaks on June 21 (Weeden 1968). Hens unsuccessful in nesting rarely renest but move altitudinally and join cocks in loose flocks on the ridge tops (Weeden 1965b).

In early August successful females and their broods form flocks which frequently move to moist areas at the headwaters of small streams; later they are joined by cocks and unsuccessful hens. Most birds have joined these flocks by mid-September.

During winter age classes behave similarly but sexes segregate, most males remaining in the alpine tundra habitat, while females form flocks and move to lower elevations at the fringe of forested areas. The sexes are again united by mid- to late April as the females move back to the breeding and nesting areas.

Censuses conducted on the breeding and nesting areas in May indicate that there are annual fluctuations in the numbers of breeding birds (Weeden 1965a).

Field Procedures

Daily excursions for collecting female ptarmigan commenced on April 19 during each year and were terminated on May 22 in 1969, May

21 in 1970 and May 23 in 1971. In 1971 no females were found on the study area until April 22. In 1969 birds were collected primarily between 0800 and 1000 hr; in 1970 and 1971 familiarity with the study area and with ptarmigan behavior enabled me to collect birds between 1800 and 2000 hr. An attempt was made to collect four females each day and to distribute sampling intensity equally throughout the area and over the collecting period. However, weather conditions and availability of birds disrupted this plan frequently. Birds were collected by shooting them in the head with a scope-sighted 22 caliber rifle. Collecting was terminated each year when samples became dominated by females possessing postovulatory follicles.

Notes recorded at the site of collection were: percent of snow cover in a 30 m diameter circle (snow cover index) and the study area subdivision.

Air temperature was recorded at the field camp on a recording hygrothermograph housed in a louvered box 1-1/4 m above ground level. Temperature records were transcribed for each day (0800 to 0800 hr) by averaging the recorded temperature for each hour, summing these hourly averages for each day and averaging by 24 hr. In some instances the daily 24 hr means were converted to °F and accumulated (cumulative temperature) over each respective field season.

In 1969, birds were autopsied immediately after returning to the field camp. In 1970 and 1971, since birds were collected late in the day, they were kept on ice and processed the following morning. In all years, materials collected in the field and destined for oven or freeze drying were kept frozen until the appropriate time. For dried materials, weights were determined with a balance accurate to 1.0 mg.

At the field camp, weights were determined with a triple beam balance accurate to 0.1 g and linear measurements were made with either a dial caliper accurate to 0.01 mm or a meter rule divided into 1 mm segments. Prior to weighing, all organs and tissues were blotted dry of blood and other excess fluids.

The age of each bird was determined by comparing the amount of dark pigment on primary feather number eight with the amount on primary feather number nine (Weeden and Watson 1967).

The extent of prenuptial molt was determined and ranked in order according to the presence or absence of new, darkly pigmented summer plumage feathers on various locations of the body. Fifteen points of reference were used for this index; zero being no new feathers present, 15 being new feathers present in all reference areas of the body.

To indicate the status of the population of Rock Ptarmigan on the study area, data collected by the Alaska Department of Fish and Game on an area located five km to the southeast were used. Annual spring censuses, conducted on this 38 sq km area, indicated that the number of male Rock Ptarmigan varied in the following manner: 88 in 1960, 134 in 1961, 170 in 1962, 141 in 1963, 109 in 1964, 66 in 1965, 80 in 1966, 98 in 1967, 120 in 1968, 113 in 1969, 102 in 1970, 92 in 1971, 79 in 1972, 65 in 1973, 61 in 1974 and 34 in 1975 (Robert B. Weeden and Jerry McGowan, pers. comm.).

Autopsy Procedures

The total body weight was determined by weighing the fresh intact bird.

The quantity of subcutaneous fat was visually estimated for three deposits, the cervicular, the clavicular and the substernal. These deposits were exposed by making a lateral incision through the skin in the region of the sternum and peeling it anteriorly to the gullet and posteriorly to the abdomen. The cervicular fat deposit refers to the fat body found on the anterior surface of the crop; the clavicular fat deposit is that fat body between the posterior surface of the crop and the breast muscle and the substernal deposit is the fat body that extends laterally along the posterior edge of the sternum. The amount of fat in each of the three deposits was ranked subjectively on an index of zero to 30. It was later found that an index value of 30 would equal approximately 1.5 g of fat in that particular deposit. The index values were multiplied by 0.05 g to give "gram estimates". The three site estimates were summed to furnish a single value referred to as the "subcutaneous fat index".

Muscular tissues of the breast, Pectoralis thoracica (Pectoralis major) and Supracoracoideus ventral head (Pectoralis minor) (nomenclature by Hudson and Lanzillotti 1964) were removed from the left half of the sternum and weighed.

The crop and contents, liver, heart, thoracic esophagus and proventriculus, ventriculus, small intestine, ceca, large intestine, spleen, pancreas, kidneys, ovary and oviduct were excised from each bird, freed from adhering tissue, blotted dry of blood and other excess fluids and weighed.

The crop was separated from the alimentary tract by cutting at the constrictions leading to the cervical esophagus and thoracic esophagus and weighed along with the contents.

The liver was excised by cutting restraining mesenteries and severing hepatic blood vessels as close to the organ as possible. The liver was then blotted dry and weighed.

The spleen was removed by severing blood vessels as near to the organ as possible, blotted dry, then placed in a vial, capped and frozen. Spleen dry weight was determined after freeze drying for 24 hr.

After major blood vessels were severed at the atria, the heart was firmly squeezed and pulsated to expel any remaining blood, blotted dry and weighed. The deposit of fat encircling the heart in the atrial region was not removed and was weighed along with the heart.

The weight determined for the proventriculus included the weight of that portion of the esophagus posterior to the crop (thoracic esophagus) and the small constricted portion immediately following the proventriculus and preceding the ventriculus. For length measurements, the proventriculus was defined by shape and coloration of the tissue.

The ventriculus was removed from between the proventriculus and the small intestine by severing immediately at their ventricular origin. After slicing through the ventriculus muscle, it was peeled away and separated from the cornified lining and its contents. Both parts were weighed.

The pancreas was freed from the small intestine by severing all blood vessels and ducts as near to the organ as possible; the organ was weighed.

The small intestine and large intestine were severed at their junction with the ceca which were separated at the junction of the former two organs. The large intestine included the cloaca and was separated from the carcass at the lip of the vent. The lengths of the intestines and ceca were determined by cutting the mesenteries and blood vessels with scissors thus permitting the organs to be laid out straight, unrestricted, without loops or twists, under slight tension but not stretched. Each cecum was weighed and measured and the respective parameters summed for each bird. The small and large intestines were weighed.

The oviduct was freed from the carcass by trimming off mesenteries and severed from the large intestine at its junction with the cloaca. Oviductal eggs were weighed along with the oviduct.

Size of the largest ovarian follicle was determined by measuring with dial calipers the greatest diameter of the largest ovarian follicle. This measurement was usually taken along the stigma. Because large follicles were soft and any pressure would cause changes in shape, they were always laid on a flat surface when measurements were taken. Occurrence of ruptured (postovulatory) follicles was noted. The ovary was weighed.

The kidneys were removed from each specimen with scissors and forceps. Small curved forceps were used to pull the kidneys out and free from the vertebral region. The average of weights from both kidneys was recorded.

Adrenal gland size was assessed by measuring (in situ) with dial calipers the greatest linear distance from one edge to its opposite. The average of measurements from both adrenals was recorded.

The femur and tibiotarsus were removed from both legs, scraped free of adhering muscle tissue and tendons, and measured with dial calipers to determine the length of each bone. The measurements for opposite and like bones were summed and recorded. Weights were determined after oven drying at 100°C to constant weight.

The pelvic bone was dissected from the carcass, freed from the vertebral column at the last thoracic and the first caudal vertebrae, and scraped clean of most adhering tissues. A "width" measurement was taken with dial calipers across the dorsal surface of the bone and between outer surfaces of the acetabuli. Weight was determined following the tissue and fat removing process described by Taylor and Moore (1954) and oven drying at 100°C to constant weight.

The following composite weights were also calculated:

Body weight - total body weight minus the weight of the crop and its contents;

Reproductive organ weight - ovary plus oviduct weight. The oviduct weight, where appropriate, includes that of oviductal eggs;

Internal organ weight - the sum of weights of the thoracic esophagus and proventriculus, ventriculus, small intestine, ceca, large intestine, kidneys, pancreas, liver and heart; and

Carcass weight - the value obtained by subtracting the sum of internal organ weight and reproductive organ weight from the body weight. This term may be somewhat misleading because included in it is the weight of the integument, feathers and lungs.

Data Analysis

Calculations for data analyses were done on IBM 360/40 and 360/50 digital computer systems. Programs used were BMD01D (Data Description), BMD02R (Stepwise Regression) and BMDX64 (Analysis of Covariance) from Dixon (1970a, 1970b).

Significance levels were determined from tables in Snedecor (1956) and Zar (1974).

Birds collected in this study were grouped by age, period, year and/or area. Weight and size data were analyzed by correlation, variance or covariance techniques.

Birds determined to be less than 12 months of age (referred to as juveniles) have been grouped and separated from birds determined to be older than 12 months of age (referred to as adults).

To test for seasonal effects on morphological variables, data were grouped into three periods based on calendar dates: period I refers to the inclusive 12 day period April 19-30; period II refers to the inclusive 11 day period May 1-11; and period III refers to the inclusive 11, 10 and 12 day periods May 12-22, 1969, May 12-21, 1970 and May 12-23, 1971, respectively. In Table 1, these three periods have been described and defined in terms of annual cycle phenomena of Rock Ptarmigan.

Table 1. Periods based on calendar dates and characterized by manifestations in the annual cycle of Rock Ptarmigan.

	Period		
Sex	I April 19 to April 30	II May 1 to May 11	III May 12 to May 23
Females	Arrival on breeding areas; birds in groups composed of both sexes or one sex; few are paired.	Movement to breeding areas completed; groups of birds dissolved.	
	Very flighty; females flush before males; apt to fly great distances when flushed.	All females associated with males but movements not restricted to territory of specific male; most males flush before females.	Hesitant to fly, secretive in activities and movements more or less confined to a specific area.
	Few snow free patches of ground; feed mostly on plant species protruding through snow cover.	Amount of ground free of snow cover equal to amount covered by snow; feed along edges of melting snow banks.	Most ground free of snow, only a few large snow drifts remain.
	White winter plumage.	Prenuptial molt commences; most birds with brown feathers at least on head and neck.	Prenuptial molt extending to wing coverts, back and breast.
	Prior to any significant ovarian recrudescence.	Early phase of ovarian recrudescence, slow rate of growth.	Late and final phase of ovarian recrudescence, fast rate of growth.
	Condition of birds representative of winter environment; essentially a winter bird on spring range.	Effects of spring environment on condition being realized.	Peak body condition achieved prior to egg laying in part a result of spring environment.
Males	Present on or near breeding area through winter.		
	Males may be found in groups with or without females.	All males separated spatially and associated with none, one or more females.	Males starting postnuptial molt; brown feathers around eyes and on crown; physically somewhat removed from females.
	First sporadic signs of territoriality, varying with local weather conditions and time of day.	All males appear to be associated with a parcel of ground; still minor boundary disputes; disputes associated with females intensifying.	Disputes range over period from very intense to almost nothing.
	Males flush after females.	Males flush before females.	Males flush before females.

Included with results of analyses of variance and covariance are a series of hypotheses concerning the equality of various group means for a number of different variables. These tests enable one to determine which specific groups were involved in yielding significant overall F-values and/or significant F-values for the interaction terms in analyses of variance and covariance.

A correlation analysis was performed using snow cover index, date of collection, cumulative temperature, molt index, tibiotarsus length, femur length, pelvic bone width, ovarian follicle size, reproductive organ weight and body weight to assess the association between environmental variables, morphological variables and annual cycle phenomena. For these analyses, data were first grouped by age class and then further subdivided on the basis of two "physiological" periods. The physiological periods roughly correspond to a preovarian recrudescence period (I) and an ovarian recrudescence period (II', period II plus period III). Correlation coefficients were used to appraise the intensity of association between any two of the variables.

Covariance techniques were used to assess annual variation in snow cover index, body weight, reproductive organ weight, ovarian follicle size and adrenal gland size. To make between year comparisons more meaningful, variation attributed to age class and area were measured and excluded from experimental error, and date of collection was used as the covariate to hold constant mean dates of collection in all categories. To isolate effects of the breeding area environment on morphological variables from effects of the wintering area environment, data were analyzed for two periods (period I and period II'). Birds collected in period I have been influenced by the wintering area environment more than by the breeding area environment and birds collected in period II' were exposed to the breeding area environment longer than birds collected in period I. Tests for "year effects" were based on comparisons between data collected in 1969, 1970 and 1971. Tests for "area effects" were based on a comparison between data from birds collected in two areas differing in direction of slope exposure and separated by Porcupine Creek which runs from west to east. Data from birds collected on the South side of Porcupine Creek, terrain predominately facing to the north are represented by area S and data from birds collected on the North side of Porcupine Creek, terrain predominately facing to the south are represented by area N (Fig. 1). Tests for "age effects" were based on a comparison between data collected from birds in two age classes, juvenile (J) and adult (A).

A copy of the original data on which this paper is based is filed in the University of Alaska library in Fairbanks, Alaska.

RESULTS

Seasonal Variation

In variance tests to assess seasonal variation in morphology, variation attributed to age class was measured and excluded from experimental error. Seasonal variation in morphology was appraised in three periods. These periods are characterized in relation to ptarmigan behavior, snow cover, the prenuptial molt and ovarian recrudescence in Table 1.

Statistics and analyses used to determine period and age class effects on morphological variables are summarized in Table 2.

These data demonstrate that when female Rock Ptarmigan arrive on the breeding areas, adults are approximately 25 g (six %) heavier than juveniles. Several different components of the body are responsible for this discrepancy.

Between the time of arrival on the breeding area and egg laying, females in each age class gain more than 40 g in body weight. Along with the ovary and oviduct, many other components of the body contribute to the increase in total body weight and accentuate the difference between age classes.

The mean values for most morphological variables exhibited statistically significant period effects. In nearly all cases, the means for each variable were less in period I than in period III. For most variables, the means of measurements within each age class were similar in periods I and II. Only the means for femur weights

Table 2. Means, standard errors and results of analysis of variance on morphological variables for juvenile (J) and adult (A) female Rock Ptarmigan collected from April 19-30 (period I), from May 1-11 (period II) and from May 12-23 (period III) in Interior Alaska, 1969-71. (No entry, * (or <) and ** (or <<) denote statistical significance at $P>0.05$, $0.01<P\leq0.05$ and $P\leq0.01$, respectively.)

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	Period	Age(N)	Mean ± SEM^a	Period Effect	Significant Differences	Age Effect	Significant Differences	
Femur Length (mm)	I	J(40)	105.0 ± 0.5					
		A(40)	105.4 ± 0.4					
	II	J(61)	105.5 ± 0.3					
		A(45)	104.9 ± 0.4					
	III	J(64)	104.7 ± 0.4					
		A(59)	105.1 ± 0.3					
Femur Weight (mg)	I	J(40)	940.2 ±12.5	**	$I_J<II_J<<III_J$ $I_A<II_A<<III_A$	**	$I_J<I_A$ $II_J<II_A$ $III_J<<III_A$	
		A(40)	993.5 ±13.1					
	II	J(61)	993.6 ±11.3					
		A(45)	1041.2 ±18.1					
	III	J(64)	1172.8 ±17.3					
		A(59)	1229.9 ±18.7					
Tibiotarsus Length (mm)	I	J(40)	130.8 ± 0.6					
		A(40)	131.2 ± 0.6					
	II	J(61)	131.0 ± 0.4					
		A(45)	130.4 ± 0.7					
	III	J(64)	130.4 ± 0.4					
		A(59)	130.6 ± 0.4					
Tibiotarsus Weight (mg)	I	J(40)	1340.9 ±21.0	**	$I_J<II_J<<III_J$ $I_A=II_A<<III_A$	**	$III_J<III_A$	
		A(40)	1401.3 ±18.5					
	II	J(61)	1408.9 ±14.9					
		A(45)	1432.8 ±23.8					
	III	J(64)	1592.7 ±21.1					
		A(59)	1658.7 ±20.4					

Table 2. Continued.

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	Period	Age(N)	Mean ± SEM[a]	Period Effect	Significant Differences	Age Effect	Significant Differences	
Pelvic Bone Width (mm)	I	J(40)	44.9 ± 0.3					
		A(40)	45.5 ± 0.3					
	II	J(61)	45.1 ± 0.2					
		A(45)	44.9 ± 0.2					
	III	J(64)	44.9 ± 0.2					
		A(59)	45.2 ± 0.2					
Pelvic Bone Weight (mg)	I	J(40)	1647.1 ±29.6	**	$I_J=II_J<<III_J$ $I_A=II_A<<III_A$	**	$I_J<I_A$ $III_J<<III_A$	
		A(40)	1756.8 ±28.5					
	II	J(61)	1732.0 ±22.7					
		A(45)	1807.0 ±33.3					
	III	J(64)	2005.3 ±33.9					
		A(59)	2165.2 ±34.2					
Body Weight (g)	I	J(40)	376.9 ± 5.3	**	$I_J=II_J<<III_J$ $I_A=II_A<<III_A$	**	$I_J<<I_A$ $II_J<II_A$ $III_J<<III_A$	
		A(40)	398.2 ± 4.2					
	II	J(61)	380.4 ± 3.4					
		A(45)	394.7 ± 4.2					
	III	J(64)	398.8 ± 3.8					
		A(59)	430.1 ± 3.9					
Carcass Weight (g)	I	J(40)	287.9 ± 4.2	**	$II_A<<III_A$	**	$I_J<<I_A$ $II_J<<II_A$ $III_J<<III_A$	
		A(40)	308.9 ± 3.5					
	II	J(61)	292.1 ± 2.7					
		A(45)	306.1 ± 3.7					
	III	J(64)	295.8 ± 2.8					
		A(59)	318.2 ± 2.9					
Internal Organ Weight (g)	I	J(40)	88.3 ± 1.6	**	$I_A=II_A<<III_A$		$III_J<<III_A$	
		A(40)	88.3 ± 1.4					
	II	J(61)	86.6 ± 1.3					
		A(45)	85.8 ± 1.1					
	III	J(64)	88.1 ± 1.1					
		A(59)	92.5 ± 1.1					

Table 2. Continued.

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	Period	Age(N)	Mean ± SEM[a]	Period Effect	Significant Differences	Age Effect	Significant Differences	
Reproductive Organ Weight (g)	I	J(40)	0.6 ± 0.0					
		A(40)	0.8 ± 0.1					
	II	J(61)	1.7 ± 0.2	**	$I_J = II_J \ll III_J$	*	$III_J \ll III_A$	
		A(45)	2.7 ± 0.3		$I_A = II_A \ll III_A$			
	III	J(64)	14.2 ± 1.3					
		A(59)	19.2 ± 1.7					
Ovary Weight (g)	I	J(40)	0.2 ± 0.0					
		A(40)	0.3 ± 0.0					
	II	J(61)	0.4 ± 0.0	**	$I_J = II_J \ll III_J$	*	$III_J \ll III_A$	
		A(45)	0.8 ± 0.1		$I_A = II_A \ll III_A$			
	III	J(64)	5.9 ± 0.7					
		A(59)	8.2 ± 0.8					
Oviduct Weight (g)	I	J(40)	0.4 ± 0.0					
		A(40)	0.5 ± 0.1					
	II	J(61)	1.3 ± 0.1	**	$I_J = II_J \ll III_J$	*	$III_J \ll III_A$	
		A(45)	2.0 ± 0.2		$I_A = II_A \ll III_A$			
	III	J(64)	8.3 ± 0.8					
		A(59)	11.2 ± 1.2					
Subcutaneous Fat Index (g Estimates)	I	J(40)	1.45 ± 0.11					
		A(40)	1.62 ± 0.10					
	II	J(61)	1.36 ± 0.10	**	$I_J = II_J \ll III_J$	**	$II_J < II_A$	
		A(45)	1.73 ± 0.11		$I_A = II_A \ll III_A$			
	III	J(64)	2.25 ± 0.11					
		A(59)	2.40 ± 0.11					
Crop Weight (g)	I	J(40)	18.1 ± 2.2					
		A(40)	15.8 ± 1.7					
	II	J(61)	9.2 ± 0.8	**	$I_J \gg II_J \gg III_J$			
		A(45)	7.8 ± 0.9		$I_A \gg II_A = III_A$			
	III	J(64)	4.9 ± 0.4					
		A(59)	6.4 ± 0.5					

Table 2. Continued.

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	Period	Age(N)	Mean ± SEM[a]	Period Effect	Significant Differences	Age Effect	Significant Differences	
Proventriculus Length (mm)	I	J(40)	18.9 ± 0.2	**	$I_J<<II_J<<III_J$ $I_A=II_A<<III_A$	**	$III_J<<III_A$	
		A(40)	19.6 ± 0.3					
	II	J(61)	19.7 ± 0.2					
		A(45)	20.0 ± 0.2					
	III	J(64)	20.5 ± 0.2					
		A(59)	21.3 ± 0.2					
Proventriculus Weight (g)	I	J(40)	1.63± 0.04	**	$I_J=II_J<<III_J$ $I_A=II_A<<III_A$	**	$III_J<<III_A$	
		A(40)	1.73± 0.04					
	II	J(61)	1.70± 0.02					
		A(45)	1.77± 0.04					
	III	J(64)	1.88± 0.03					
		A(59)	2.02± 0.05					
Ventriculus Muscle Weight (g)	I	J(40)	8.41± 0.13	**	$I_J<II_J<<III_J$ $I_A=II_A<<III_A$			
		A(40)	8.35± 0.14					
	II	J(61)	8.88± 0.12					
		A(45)	8.76± 0.16					
	III	J(64)	9.54± 0.15					
		A(59)	9.39± 0.15					
Ventriculus Lining and Contents Weight (g)	I	J(40)	7.03± 0.15	*	$III_J<<I_J>II_J$			
		A(40)	6.57± 0.14					
	II	J(61)	6.45± 0.14					
		A(45)	6.55± 0.18					
	III	J(64)	6.23± 0.14					
		A(59)	6.56± 0.17					
Small Intestine Length (cm)	I	J(40)	102.5 ± 1.2	**	$II_J<III_J$ $I_A=II_A<<III_A$			
		A(40)	100.9 ± 1.1					
	II	J(61)	101.3 ± 0.8					
		A(45)	101.0 ± 0.9					
	III	J(64)	104.0 ± 1.1					
		A(59)	104.9 ± 0.9					

Table 2. Continued.

Variable (units)	Period	Age(N)	Mean ± SEM[a]	Analysis of Variance: Period 2 df		Analysis of Variance: Age 1 df		Analysis of Variance: Period x Age Effect 2 df
				Period Effect	Significant Differences	Age Effect	Significant Differences	
Small Intestine Weight (g)	I	J(40)	24.1 ± 0.6					
		A(40)	23.1 ± 0.5					
	II	J(61)	23.3 ± 0.4	**	$I_A=II_A<<III_A$		$III_J<<III_A$	*
		A(45)	22.6 ± 0.4					
	III	J(64)	23.7 ± 0.4					
		A(59)	24.9 ± 0.4					
Ceca Length (cm)	I	J(40)	84.2 ± 1.1					
		A(40)	84.6 ± 1.0					
	II	J(61)	86.1 ± 0.9	**	$I_J<<III_J$ $I_A=II_A<<III_A$			
		A(45)	86.5 ± 0.9					
	III	J(64)	87.9 ± 0.8					
		A(59)	89.3 ± 0.9					
Ceca Weight (g)	I	J(40)	21.7 ± 0.8					
		A(40)	22.2 ± 0.6					
	II	J(61)	20.9 ± 0.7	**	$I_J>III_J$ $I_A>II_A=III_A$			
		A(45)	20.2 ± 0.6					
	III	J(64)	19.6 ± 0.4					
		A(59)	20.2 ± 0.5					
Large Intestine Length (cm)	I	J(40)	10.4 ± 0.1					
		A(40)	10.7 ± 0.1					
	II	J(61)	10.4 ± 0.1			**		
		A(45)	10.6 ± 0.1					
	III	J(64)	10.5 ± 0.1					
		A(59)	10.6 ± 0.1					
Large Intestine Weight (g)	I	J(40)	4.1 ± 0.2					
		A(40)	4.7 ± 0.2					
	II	J(61)	4.2 ± 0.1			**	$I_J<I_A$ $III_J<III_A$	
		A(45)	4.5 ± 0.1					
	III	J(64)	4.1 ± 0.2					
		A(59)	4.6 ± 0.2					

Table 2. Continued.

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	Period	Age(N)	Mean ± SEM[a]	Period Effect	Significant Differences	Age Effect	Significant Differences	
P. Major (g)	I	J(40)	44.22± 0.70					
		A(40)	46.71± 0.57				$I_J \ll I_A$	
	II	J(61)	43.92± 0.43			**	$II_J \ll II_A$	
		A(45)	46.29± 0.64				$III_J \ll III_A$	
	III	J(64)	44.11± 0.45					
		A(59)	46.79± 0.43					
P. Minor (g)	I	J(40)	10.69± 0.18					
		A(40)	11.33± 0.16				$I_J \ll I_A$	
	II	J(61)	10.69± 0.09			**	$II_J < II_A$	
		A(45)	11.08± 0.16				$III_J \ll III_A$	
	III	J(64)	10.75± 0.12					
		A(59)	11.39± 0.10					
Heart Weight (g)	I	J(40)	7.83± 0.13					
		A(40)	8.49± 0.12					
	II	J(61)	7.67± 0.10	**	$I_A \gg II_A = III_A$	**	$I_J \ll I_A$	*
		A(45)	7.77± 0.13					
	III	J(64)	7.73± 0.08					
		A(59)	7.94± 0.12					
Liver Weight (g)	I	J(40)	8.54± 0.31					
		A(40)	8.89± 0.20		$I_J = II_J \ll III_J$			
	II	J(61)	8.88± 0.23	**		**	$III_J \ll III_A$	*
		A(45)	8.82± 0.20		$I_A = II_A \ll III_A$			
	III	J(64)	10.58± 0.23					
		A(59)	11.73± 0.26					
Spleen Weight (mg)	I	J(40)	30.17± 2.78					
		A(40)	32.27± 2.28		$I_J < III_J$			
	II	J(61)	34.29± 2.72	**				
		A(45)	39.47± 3.68		$I_A \ll III_A$			
	III	J(64)	39.41± 2.68					
		A(59)	44.53± 2.42					

Table 2. Continued.

				Analysis of Variance				
				Period 2 df		Age 1 df		Period x Age Effect 2 df
Variable (units)	**Period**	**Age(N)**	**Mean ± SEM[a]**	**Period Effect**	**Significant Differences**	**Age Effect**	**Significant Differences**	
Kidney Weight (g)	I	J(40)	1.89± 0.05	*	$I_A<III_A$ $II_A \ll III_A$	**	$I_J<I_A$ $III_J \ll III_A$	
		A(40)	2.04± 0.05					
	II	J(61)	1.92± 0.04					
		A(45)	1.96± 0.04					
	III	J(64)	1.96± 0.04					
		A(59)	2.17± 0.04					
Pancreas Weight (g)	I	J(40)	1.08± 0.03	**	$II_J<I_J \ll III_J$ $I_A=II_A \ll III_A$		$I_A \ll I_J$ $III_J \ll III_A$	**
		A(40)	0.96± 0.03					
	II	J(61)	0.99± 0.02					
		A(45)	1.00± 0.03					
	III	J(64)	1.15± 0.02					
		A(59)	1.27± 0.03					

[a]SEM = Standard error of the mean.

exhibited a progressive increase in size between each period in each age class.

Though most variables increased in size from period I to period III, three exhibited a decrease. The means of weights of the crop plus its contents and the ceca showed a statistically significant decrease in weight from period I to period III in each age class. The means of weights of the ventricular contents demonstrated a similar trend but it was not statistically significant in the adult age class.

Variables that did not exhibit statistically significant period effects were the following: lengths and weights of the large intestine; weights of the pectoral muscles and linear measurements of the skeletal structures.

The means of measurements for each component of the alimentary tract, except those for the large intestine and the proventriculus, did not demonstrate significant age class effect. Additional variables that did not exhibit significant age class effects were the following: pancreas weight; spleen weight; linear measurements of the skeleton and the composite measurement, internal organ weight. All remaining variables illustrated statistically significant age class effects.

For most variables, age class differences were present at least in period III. The means of adult heart weights were greater than those of juveniles in each period but only the difference in period I was statistically significant. Similarly, the means in each period indicated that adults had more subcutaneous fat than juveniles, but only in period II was the difference statistically significant. The means for large intestine length exhibited age class effects but no statistically significant difference was detected in any single period. Femur weight, pelvic bone weight, breast muscle weights, kidney weight, large intestine weight and heart weight are variables that exhibited age class effects in period I.

Data on incidence of postovulatory follicles indicated that in general adults commenced egg laying prior to juveniles. Considering all years, 15% (five out of 33) of the juveniles collected subsequent to the first observation of a ruptured ovarian follicle in each year had postovulatory follicles; for the same sample of individuals 56% (14 out of 26) of the adults had ovulated. These data demonstrate that in a given season, adults are nearly four times as likely to commence egg laying prior to juveniles.

Statistically significant period x age class effects were detected for means of weights for the small intestine, the heart, the ventricular contents, the pancreas and the liver. This is interpreted to mean that in each of these instances the effect of the period on these variables is different in adults from the effect in juveniles, i.e., the effect of the period is dependent on age class.

Correlation of Environmental and Morphological Variables

The means and standard deviations of variables used in correlation analysis of changes in the environment and morphology of female Rock Ptarmigan are summarized in Table 3. The variables were measured for two age classes of female Rock Ptarmigan during two periods. The first

Table 3. Means and standard deviations of variables used in correlation analysis of changes in the environment and morphology of juvenile and adult female Rock Ptarmigan collected from April 19-30 (period I) and from May 1-23 (period II') in Interior Alaska, 1969-71.

Variable (units)	Mean ± SD[a]			
	Period I April 19 to April 30		Period II'[b] May 1 to May 23	
	Juveniles(40)[c]	Adults(40)	Juveniles(125)	Adults(104)
Snow Cover Index (Percent)	84.5 ± 21.9	75.5 ± 24.6	51.8 ± 35.8	44.8 ± 35.0
Date of Collection (Days)	7.3 ± 2.7	6.5 ± 3.5	24.2 ± 6.7	24.3 ± 6.2
Cumulative Temperature (Degree Days)	188.6 ± 81.8	167.9 ± 96.9	728.4 ± 251.7	760.5 ± 232.9
Molt Index (Rank, 1-15)	1.2 ± 0.4	1.2 ± 0.5	10.2 ± 5.5	12.2 ± 4.7
Femur Length (mm)	105.0 ± 2.9	105.4 ± 2.6	105.1 ± 2.8	105.0 ± 2.5
Tibiotarsus Length (mm)	130.8 ± 3.8	131.2 ± 3.7	130.7 ± 3.3	130.5 ± 3.0
Pelvic Bone Width (mm)	44.9 ± 1.6	45.2 ± 1.9	45.0 ± 1.6	45.1 ± 1.5
Ovarian Follicle Size (mm)	3.3 ± 0.7	3.9 ± 0.7	10.8 ± 7.8	13.7 ± 8.1
Reproductive Organ Weight (g)	0.6 ± 0.3	0.8 ± 0.6	8.1 ± 9.9	12.0 ± 13.0
Body Weight (g)	376.9 ± 33.6	398.2 ± 26.8	389.5 ± 29.6	414.8 ± 34.0

[a] Standard deviation.

[b] Period II' = period II plus period III.

[c] Number of individuals.

period (I), April 19-30, preceded any appreciable reproductive recrudescence, the second period (II'), May 1-23, which included periods II and III, covered essentially all reproductive recrudescence up to egg laying. Environmental variables examined were snow cover, date of collection and cumulative temperature; morphological variables examined were molt index, femur length, tibiotarsus length, pelvic bone width, ovarian follicle size, reproductive organ weight and body weight.

Results of simple correlation analysis on environmental and morphological variables for each age class in periods I and II' are presented in Tables 4 and 5, respectively.

Period I

These data indicate that follicle size and reproductive organ weight were each related to date of collection. This association indicates that reproductive recrudescence commenced prior to May 1 and before period II'. Though the variables ovarian follicle size and date of collection exhibited statistically significant positive correlations in each age class, each of these variables exhibited negative correlations with body weight in each age class.

Although recrudescence was advancing in period I, it was not evidenced in the variable body weight. The only variables exhibiting statistically significant correlations with body weight were skeletal measurements. Skeletal variables exhibited more intense associations with body weight in adults than in juveniles; the association between femur length and body weight was significantly more intense in adults

Table 4. Correlation coefficients for environmental and morphological variables measured for juvenile and adult female Rock Ptarmigan collected from April 19-30 (period I) in Interior Alaska, 1969-71 (N = 40 juveniles and 40 adults).

Variable	Date of Collection	Cumulative Temperature	Molt Index	Femur Length	Tibiotarsus Length	Pelvic Bone Width	Ovarian Follicle Size	Reproductive Organ Weight	Body Weight
JUVENILES, PERIOD I:									
Snow Cover Index	0.101	0.108	0.138	-0.140	-0.191	0.041	-0.057	0.024	0.051
Date of Collection		0.951**	-0.031	0.144	-0.002	-0.174	0.316*	0.465**	-0.143
Cumulative Temperature			0.064	0.226	0.041	-0.107	0.355*	0.349*	-0.110
Molt Index				0.188	0.097	-0.049	0.401*	0.182	0.030
Femur Length					0.819**	0.604**	0.060	0.063	0.447**
Tibiotarsus Length						0.630**	-0.024	-0.000	0.443**
Pelvic Bone Width							-0.125	-0.021	0.457**
Ovarian Follicle Size								0.387*	-0.244
Reproductive Organ Weight									0.058
ADULTS, PERIOD I:									
Snow Cover Index	0.389*	0.345*	-0.194	0.062	-0.005	0.197	0.073	0.039	0.080
Date of Collection		0.970**	0.034	-0.069	-0.132	-0.091	0.547**	0.454**	-0.044
Cumulative Temperature			0.088	-0.066	-0.115	-0.082	0.584**	0.469**	-0.075
Molt Index				0.059	0.114	0.115	0.346*	0.196	0.155
Femur Length					0.819**	0.812**	-0.165	-0.239	0.749**
Tibiotarsus Length						0.674**	-0.241	-0.133	0.606**
Pelvic Bone Width							-0.150	-0.259	0.643**
Ovarian Follicle Size								0.383*	-0.143
Reproductive Organ Weight									-0.179

*0.01<P≤0.05.

**P≤0.01.

Table 5. Correlation coefficients for environmental and morphological variables measured for juvenile and adult female Rock Ptarmigan collected from May 1-23 (period II') in Interior Alaska, 1969-71 (N = 125 juveniles and 104 adults).

Variable	Date of Collection	Cumulative Temperature	Molt Index	Femur Length	Tibiotarsus Length	Pelvic Bone Width	Ovarian Follicle Size	Reproductive Organ Weight	Body Weight
JUVENILES, PERIOD II':									
Snow Cover Index	-0.622**	-0.709**	-0.727**	0.002	-0.050	-0.171	-0.707**	-0.652**	-0.470**
Date of Collection		0.964**	0.793**	-0.087	-0.064	-0.037	0.834**	0.718**	0.366**
Cumulative Temperature			0.848**	-0.076	-0.042	0.019	0.866**	0.907**	0.483**
Molt Index				-0.064	-0.043	0.088	0.746**	0.650**	0.455**
Femur Length					0.882**	0.392**	-0.040	0.003	0.470**
Tibiotarsus Length						0.324**	-0.025	0.024	0.486**
Pelvic Bone Width							0.030	0.034	0.381**
Ovarian Follicle Size								0.907**	0.483**
Reproductive Organ Weight									0.484**
ADULTS, PERIOD II':									
Snow Cover Index	-0.528**	-0.602**	-0.631**	0.082	-0.159	-0.139	-0.640**	-0.532**	-0.466**
Date of Collection		0.962**	0.734**	0.028	0.060	0.101	0.859**	0.760**	0.568**
Cumulative Temperature			0.782**	0.053	0.085	0.138	0.886**	0.782**	0.617**
Molt Index				0.061	0.079	0.145	0.695**	0.556**	0.532**
Femur Length					0.820**	0.515**	0.040	0.082	0.375**
Tibiotarsus Length						0.434**	0.114	0.138	0.403**
Pelvic Bone Width							0.094	0.146	0.421**
Ovarian Follicle Size								0.880**	0.663**
Reproductive Organ Weight									0.585**

*0.01<P≤0.05.

**P≤0.01.

han in juveniles ($Z = 2.13$, $P<0.05$).

The variable molt index was significantly correlated with follicle size in each age class. Though the variable follicle size was associated with date of collection, molt index was not significantly correlated with collection date.

In adults, snow cover index was positively correlated with date of collection, but in neither age class was snow cover index significantly associated with follicle size, reproductive organ weight or molt index.

The data for each age class indicated that cumulative temperature was more intensely correlated with follicle size than was either date of collection or snow cover index.

Period II'

Contrary to the data in period I, data in period II' in each age class exhibited statistically significant correlations between body weight and each of the following variables: snow cover index; date of collection; cumulative temperature; molt index; ovarian follicle size and reproductive organ weight.

Correlation coefficients for variables of each skeletal measurement and body weight were statistically significant, but in the adult age class more intense associations were exhibited between body weight and each of the following environmental variables: cumulative temperature; date of collection; snow cover index and molt index.

In each age class, among environmental variables, cumulative temperature exhibited the most intense correlation with reproductive organ weight and follicle size. The variable cumulative temperature was more intensely associated with molt index than was either date of collection or snow cover index.

Annual Variation

In covariance tests to assess annual variation in snow cover index, body weight, reproductive organ weight, ovarian follicle size and adrenal gland size; variation attributed to age class and area was measured and excluded from experimental error and date of collection was used as a covariate to hold constant mean dates of collection between all categories. To isolate effects of the prelaying environment on morphological variables, data were analyzed in two periods (period I and period II', where period II' = period II plus period III). If variables did not exhibit an area effect in period II', data for each area were then combined to test for year and age class effects. Adjusted means and statistical analyses used to evaluate year, age class and area effects on snow cover and morphology, are presented in Tables 6, 7 and 8 and 9, 10 and 11, respectively; results of these covariance analyses and tests for significant differences are tabulated in Appendices A, B and C.

The data indicate that ovarian follicle size was the only variable to exhibit statistically significant effects for year, age class and area. Annual variations in morphology were associated with local weather conditions.

Local Weather

In period I, the snow cover index was greatest in 1971, less in

Table 6. Adjusted means of body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index for juvenile and adult female Rock Ptarmigan collected from April 19-30 (period I) in Interior Alaska, 1969-71.

			Adjusted Mean[a]				
Year	Age	Sample Size	Body Weight (g)[b]	Reproductive Organ Weight (g)	Ovarian Follicle Size (mm)	Adrenal Gland Size (mm)	Snow Cover Index (%)
1969	Juvenile	15	365.7	0.68	3.14	4.66	74.4
1969	Adult	13	401.0	0.95	3.78	4.77	71.7
1970	Juvenile	18	375.4	0.54	3.44	4.82	83.1
1970	Adult	18	393.5	0.82	4.13	5.16	69.6
1971	Juvenile	7	406.0	0.50	2.93	5.00	98.0
1971	Adult	9	402.8	0.70	3.63	5.03	93.0

[a] Estimates of variable means with date of collection held constant in all categories.

[b] Units of measurement.

Table 7. Adjusted means of body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index for juvenile (J) and adult (A) female Rock Ptarmigan collected on two areas from May 1-23 (period II') in Interior Alaska, 1969-71. (S = south side of Porcupine Creek, primarily northern exposure; N = north side of Porcupine Creek, primarily southern exposure.)

				Adjusted Mean[a]				
Year	Age	Area	Sample Size	Body Weight (g)[b]	Reproductive Organ Weight (g)	Ovarian Follicle Size (mm)	Adrenal Gland Size (mm)	Snow Cover Index (%)
1969	J	S	22	400.2	11.73	12.63	4.92	40.5
1969	J	N	7	395.3	10.89	13.08	4.71	39.8
1969	A	S	33	424.4	14.79	14.89	4.80	34.4
1969	A	N	6	431.1	12.86	15.61	5.08	30.9
1970	J	S	21	397.8	8.01	9.65	4.82	26.3
1970	J	N	12	385.4	11.91	15.96	4.80	30.0
1970	A	S	22	411.9	9.99	13.61	4.91	45.4
1970	A	N	14	412.4	10.23	14.48	4.88	24.6
1971	J	S	40	380.1	5.64	9.09	4.82	62.0
1971	J	N	23	389.0	6.55	9.97	4.72	76.9
1971	A	S	17	401.3	10.85	10.46	5.01	66.9
1971	A	N	12	406.2	10.95	12.77	4.72	63.9

[a] Estimates of variable means with date of collection held constant in all categories.

[b] Units of measurement.

Table 8. Adjusted means for body weight, reproductive organ weight, adrenal gland size and snow cover index for juvenile and adult female Rock Ptarmigan collected from May 1-23 (period II') in Interior Alaska, 1969-71.

			Adjusted Mean[a]			
Year	Age	Sample Size	Body Weight (g)[b]	Reproductive Organ Weight (g)	Adrenal Gland Size (mm)	Snow Cover Index (%)
1969	Juvenile	29	399.0	11.54	4.87	41.2
1969	Adult	39	425.4	14.50	4.84	34.8
1970	Juvenile	33	393.5	9.40	4.81	28.7
1970	Adult	36	412.2	10.06	4.89	38.3
1971	Juvenile	63	383.3	5.99	4.78	68.5
1971	Adult	29	403.2	10.90	4.89	66.5

[a] Estimates of variable means with date of collection held constant in all categories.

[b] Units of measurement.

Table 9. Results of analysis of covariance on body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index with date of collection as a covariate for juvenile and adult female Rock Ptarmigan collected from April 19-30 (period I) in Interior Alaska, 1969-71. (N = 80. No entry, * and ** denote statistical significance at $P>0.05$, $0.01<P\leq 0.05$ and $P\leq 0.01$, respectively.)

		Variable				
Source of Variation	DF	Body Weight	Reproductive Organ Weight	Ovarian Follicle Size	Adrenal Gland Size	Snow Cover Index
Year	2	($P<0.10$)		*		**
Age Class	1	*	*	**		
Year x Age Class	2					
Covariate[a] - Date of Collection	1		**	**		**

[a] Regression coefficient of covariate.

Table 10. Results of analysis of covariance on body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index with date of collection as a covariate for juvenile and adult female Rock Ptarmigan collected on north- and south-facing slopes from May 1-23 (period II') in Interior Alaska, 1969-71. (N = 229. No entry, * and ** denote statistical significance at $P>0.05$, $0.01<P\leq0.05$ and $P\leq0.01$, respectively.)

		Variable				
Source of Variation	DF	Body Weight	Reproductive Organ Weight	Ovarian Follicle Size	Adrenal Gland Size	Snow Cover Index
Year	2	**	($P<0.025$)	**		**
Age Class	1	**	($P<0.025$)	**		
Area	1			**		
Year x Age	2					
Year x Area	2					
Area x Age	1					
Year x Area x Age	2			*		*
Covariate[a] - Date of Collection	1	**	**	**		**

[a] Regression coefficient of covariate.

Table 11. Results of analysis of covariance on body weight, reproductive organ weight, adrenal gland size and snow cover index with data of collection as a covariate for female Rock Ptarmigan collected from May 1-23 (period II') in Interior Alaska, 1969-71. (N = 229. No entry, * and ** denote statistical significance at P>0.05, 0.01<P≤0.05 and P≤0.01, respectively.)

Source of Variation	DF	Variable			
		Body Weight	Reproductive Organ Weight	Adrenal Gland Size	Snow Cover Index
Year	2	**	**		**
Age Class	1	**	**		
Year x Age Class	2				
Covariate[a] - Date of Collection	1	**	**		**

[a] Regression coefficient of covariate.

1970 and least in 1969. In period I of each year, areas from which juveniles were collected had more extensive snow cover than areas from which adults were collected.

In period II', the snow cover index was greater in 1971 than in either 1969 or 1970. In period II' of 1969 and 1971, areas from which juveniles were collected had more extensive snow cover than areas from which adults were collected (Table 8).

Though temperatures were relatively low early in the spring of 1969, it was generally a warmer spring than in either 1970 or 1971 (Fig. 2). Except for the later part of period II' (period III), air temperatures were warmer in 1970 than in 1971.

Body Weight

In period I, body weights did not exhibit a year effect. In period II', body weights in each age class were heavier in 1969 than in either 1970 or 1971.

In all instances except period I in 1971, adults were heavier than juveniles. Failure to detect an age effect in period I in 1971 may have been the result of small sample size.

Reproductive Organ Weight

In period I, the reproductive organs of adults were heavier than those of juveniles in each year but there was no statistically significant differences between years.

In period II' in each age class reproductive organs were heavier in 1969 than in either 1970 or 1971.

Ovarian Follicle Size

In each year and in each period, ovarian follicle size was greater in adults than in juveniles.

In period I, follicle size in each age class was greater in 1970 than in either 1969 or 1971.

In period II', in almost all age class x area categories follicle sizes were greater in 1969 than in either 1970 or 1971. Ovarian follicles in birds collected in 1971 were the smallest of all years. In each year and in each age class, birds collected from hills with predominantly southern exposure (area N) had larger follicles than birds collected from hills with predominately northern exposure (area S).

Adrenal Gland Size

Though not statistically significant, data from period I indicate in each age class that adrenal glands were smaller in 1969 than in either 1970 or 1971, data from period I and period II' indicate that adults generally had larger adrenal glands than juveniles and data from period II' indicate in all instances except for adults in 1969 that birds collected from hills with southern exposure (area N) had smaller adrenal glands than birds collected from hills with northern exposure (area S).

DISCUSSION

General

Many investigations have been designed to determine and describe the effects of various factors on morphology of birds. From these types of studies, we gain appreciation for the morphological adjustments that are available to birds in response to changes in their environment.

Studies of morphology lend themselves to two general methods of design; the major difference between techniques is in the amount of experimental control employed. In both methods of study an attempt is made to explain variability in a morphological parameter by partitioning its variation among various factors or treatments. By relating variation in morphology to ecological factors, one can better evaluate the biological significance of a morphological character.

In the "experimental" type method of study, the environment is controlled and its effects on a predetermined morphological parameter are evaluated. The controlled experiment is widely used in studying morphology and its shortcomings are by definition the controlled, "non-natural" conditions. After completing a controlled study, the investigator is confronted with the question: Is this the way it would have happened under natural conditions?

In the other approach to studying morphological adaptations, treatments are not willfully imposed upon the subjects of study but are the result of opportunistic use of natural circumstances and wise use of stratified sampling techniques. In this method of study, sample strata function as "natural" treatments.

Data on body weights and weights and measurements of body component parts are normally of limited value. However, in this study of morphology in free-living female Rock Ptarmigan, these data furnish a wealth of information on avian biology when used in conjunction with specific annual cycle phenomena and other relevant environmental variables.

Because birds were sacrificed for initial sampling, each individual furnished only one set of measurements. Hence, it was assumed that changes in the means of variables represented changes at the individual level. Under these circumstances, changes in morphology were evaluated with means of samples and deduced to the level of individuals; in contrast to studying changes within individuals and inducting these changes to the population level. Changes in morphology reported in this study were not observed within the same individual but were recorded as changes in the respective variables for the population of birds studied.

Numbers of Rock Ptarmigan on an area close to the study area were at a peak level in 1968 but have decreased since then with the decrease continuing to at least the spring of 1975 (Robert B. Weeden and Jerry McGowan, pers. comm.). A similar decrease probably also occurred on the study area. Perhaps these data are only representative of female Rock Ptarmigan in a declining population and the morphology of individuals in an increasing population may not be the same.

To interpret ecological implications of this study, comments are directed to the following topics for discussion: (1) weight and size dynamics of prelaying female Rock Ptarmigan; (2) environmental and morphological intra- and interassociations; and (3) effects of year and area on morphology and reproduction.

Weight and Size Dynamics of Prelaying Female Rock Ptarmigan

Primary Growth

In Table 2, the mean body weight of 165 juveniles and 144 adults collected in periods I, II and III is summarized. Body weights of adult female Rock Ptarmigan were significantly greater than body weights of juveniles. Differences in body weight between age classes of prelaying females have been reported in other studies of birds. Kirkpatrick (1944) reported that pen reared hen pheasants reached adult size and weight as early as 20 weeks of age. Koskimies (1958) noted that juvenile female Blackgame had reached a weight equal to the maximal adult weight by November but that female Capercaillie did not reach this level until sometime after their first winter. West and Meng (1968) documented age class differences in body weight of female Willow Ptarmigan (*Lagopus lagopus*) and stated that "juvenile females become fully grown or equivalent in size to the adult female in their first spring". Robel and Linderman (1966) believed that prelaying juvenile Bobwhite Quail (*Colinus virginianus*) weighed less than adults because the reproductive cycle of adults was slightly advanced. Roseberry and Klimstra (1971) had data indicating that adult Bobwhite Quail continued to outweigh subadults during the spring and summer. Redfield (1973) concluded that yearling female Blue Grouse (*Dendragapus obscurus*) were lighter than adults in their second summer of life and gained additional weight in their second winter of life. Zwickel and Brigham (1974) demonstrated that yearling Franklin's Grouse (Canachites canadensis franklinii) were lighter than adults in autumn following their first breeding season. Data for female Rock Ptarmigan indicated that adults were heavier than juveniles upon arrival on the breeding areas (period I) and that the age class difference may be more pronounced several weeks after arrival (period II) because of the adults' relatively advanced reproductive cycle and that this difference persists at least up to egg laying (period III). Similarly, if both age classes are behaving the same, it seems improbable that juvenile Rock Ptarmigan would gain weight relative to adults during egg laying, incubation and/or brooding. Under these assumptions, it is unlikely that juvenile female Rock Ptarmigan attain adult body weight until sometime after their first breeding season. They probably reached adult body size in their second autumn or winter of life as evidenced by Redfield (1973) and Zwickel and Brigham (1974) for Blue Grouse and Franklin's Grouse, respectively.

To explain age class differences in body weight that: (1) exist before any appreciable reproductive organ growth (period I); (2) that persist up to egg laying (period II and III); and (3) that are present through the summer and on into autumn, one would expect that body components other than those directly related to reproductive processes are involved. To evaluate this idea, the following null hypothesis was examined: body components not affected by the reproductive cycle do not exhibit age class differences in weight.

Presented in Table 2 is a summary of results of analyses of variance of age class and season effects on weights and sizes of component parts of the body. It may be seen that weights of the large intestine and breast muscles (P. major and P. minor) exhibit age class differences in weight but show no change in relation to the reproductive cycle (period effect). I rejected the null hypothesis and accepted the alternative hypothesis: in prelaying female Rock Ptarmigan, body components not affected by the reproductive cycle exhibit age class differences in weight. These data demonstrate that age class differences in body weight of prelaying females are not solely due to the adults' advanced reproductive cycle.

Why are weight dynamics of seemingly unrelated structures, the breast muscles and the large intestine, similar to each other, but different from the weight dynamics of many other body components? The answer may be the growth priority of these body components. Wilson (1954a) demonstrated in domestic fowl a low growth priority for musculature relative to other body components and that within all muscular tissues the breast muscles are the last of all the groups to attain mature size. Although the alimentary tract undergoes a relatively small posthatching increase in weight, it exhibits a postnatal growth gradient in an anterior to posterior direction (the large intestine being the last to mature) with the peak growth of the intestines occurring during or after the breast muscles (Wilson 1954b).

Although this evidence strongly suggests that incomplete primary growth was responsible for the observed age class differences in weight, this may not be the case. Wilson and Osborne (1960) summarized the findings of many investigations and furnished evidence that during periods of undernutrition animals metabolized tissues ("degrowth", Needham 1950, p. 525) in the reverse order of maturity and in conformity with "functional demand" (Bryden 1969); depleted first are those components and areas maturing last and of least functional importance. In theory, it is possible that differences in weight by age class resulted from retrogressive growth prior to arrival on the breeding grounds and not from incomplete primary growth.

Age class differences in ovarian follicle size and reproductive organ weight present during the prelaying period (Table 2) indicate that recrudescent activity was more advanced in adults than in juveniles. Similar findings have been reported for Bobwhite Quail (Robel and Linderman 1966). However, this does not necessarily mean that when laying commenced in the respective age classes adults had larger reproductive organs.

Labisky and Jackson (1969) demonstrated that in Ring-necked Pheasants egg laying was advanced in adults but that there was no age class difference in the size of eggs laid. Likewise, though data on incidence of postovulatory follicles in female Rock Ptarmigan indicated that laying was delayed in juveniles, it is probable that when laying commenced in juveniles their reproductive organs had attained adult size.

Supplemental Regrowth

The mean body weights of female Rock Ptarmigan summarized in Table 2 exhibit the general tendency of avian species to gain in weight prior to egg laying.

Studies of captive, pen reared hen Ring-necked Pheasants indicate that a variety of body components contribute to the prelaying increase in body weight. Kirkpatrick (1944) and Breitenbach _et al._ (1963) demonstrated in hen Ring-necked Pheasants that in addition to the reproductive organs the digestive organs and increased fat accumulation contributed to weight gains prior to egg laying.

These findings are contrary to those reported by Lewin (1963) for wild, unconfined California Quail. Lewin compared weight curves for total body weight and reproductive organ (ovary plus oviduct) weight in prelaying female California Quail. He found that the area and shape of the body weight curve was similar to the curve for reproductive organ weight and attributed the gain in body weight to maturation of the ovary and oviduct; he did not examine weights of other body component parts.

Data for Rock Ptarmigan (Table 2) indicate that in addition to the reproductive organs (ovary and oviduct), weights of the carcass and internal organs also contribute to the increase in body weights of prelaying females. These data refute Lewin's contention and demonstrate that increases in weight of wild, unconfined prelaying female Rock Ptarmigan, as in pen reared captive Ring-necked Pheasants, are not limited to the ovary and oviduct.

A summary of analysis of variance tests that denotes the specific body components responsible for the increases in weight within the general morphological categories of carcass weight and internal organ weight is presented in Table 2. Measurements of most body components exhibited an increase in weight or size associated with ovarian recrudescence, except the following: weight and length of the large intestine; weight of the ventricular contents; weight of the crop, weight of the ceca, weight of the pectoral muscles; weight of the heart and linear measurements of the femur, the tibiotarsus and the pelvic bone.

Why were the latter measurements not positively correlated with changes in reproductive status? Failure of these data to indicate a period effect on the length and weight of the large intestine is contrary to the findings of Anderson (1972) in Ring-necked Pheasants. Colon weights did not increase, although the cloacal region visually appeared enlarged and distended as birds approached egg laying. However, colon weights presented here included fecal contents. Anderson failed to mention whether these contents were removed from the colon prior to weighing. Perhaps the contents became lighter in weight as birds approached laying and counterbalanced weight increases in the colon itself. Evidence in support of the later contention is a statistically significant decrease in the weights of crops and ceca and an apparent decrease in the weights of the ventricular contents during the same period. Studies by Watson (1964) and Weeden (1969) on Rock Ptarmigan and Irving _et al._ (1967) on Willow Ptarmigan also demonstrated that the weights of crop contents decrease from winter to spring.

The data did not indicate a prelaying accretion of labile protein in the form of pectoral muscle tissue as might be expected considering the findings of Anderson (1972). Anderson found that weights of the sternal muscles in wild Ring-necked Pheasants were greatest following winter and that they decreased in weight during the breeding season; he attributed the loss of muscle tissue mass to mobilization of protein to meet the requirements of egg production.

Other studies indicate a variety of results and hypotheses on this subject. The interpretation of results of data on pectoral muscle (P. major and P. minor) weights as presented by Pendergast and Boag (1973) in a study of Spruce Grouse (Canachites canadensis) is somewhat confusing. They found a significant correlation between total body weight and weight of the pectoral muscles but their data (as interpreted from graphs) illustrate an approximately 10 percent increase in means of total body weight during the prelaying period and an approximately five percent decrease in means of weights for each pectoral muscle during the same period. They alluded to the hypothesis that skeletal musculature makes a major contribution to changes in total body weight and that the change in muscle weight reflected the intramuscular deposition of fat.

Hanson (1962) found that weights of the breast muscles of Canada Geese (Branta canadensis interior) increased during migration and decreased during the postnuptial molt; he attributed the postmigratory hypertrophy to "use" and the loss of pectoral muscle tissue during the molt to mobilization of amino acids for accelerated formation of new feather keratin. Hanson did not find evidence that muscle tissue was depleted to supply protein for production of eggs.

Using the rationale of both Anderson and Hanson and considering the data presented by Pendergast and Boag, one would have expected a decrease in the weights of the breast muscles of prelaying female Rock

Ptarmigan since these birds had just completed migration from wintering areas to the breeding areas, had commenced their prenuptial molt shortly after arrival on the breeding areas and had advanced physiologically to the stage of egg laying.

Since the population of female Rock Ptarmigan studied probably migrate less than 160 km, their breast muscles may not respond to this limited "use" by hypotrophy to a detectable extent as did those of Canada Geese whose migrations are 10 times longer than those of ptarmigan. Perhaps the gradual and partial prenuptial molt is not as demanding on protein metabolism as the postnuptial molt, where in geese all flight feathers are lost simultaneously, and does not influence breast muscle mass. In any event, it appears that female Rock Ptarmigan cope with the protein demands of migration, molt, supplemental regrowth and egg laying in a manner different from species referred to in other studies.

Data presented on heart weights may be misleading because the weight of the deposit of fat encircling the atrial region is included. In general, a decrease was noted in weights of hearts from the time of arrival on the breeding areas to egg laying, with lowest values in period II. Perhaps the high values in period I were due to an increase in muscle mass as a result of the demands of migration on the circulatory system. The low values in period II may be the result of a decrease in muscle mass as females become sedentary and terrestrial and intermediate values in period III may be the result of increased quantities of atrial depot fat as demonstrated in the subcutaneous fat depots (see Table 2, subcutaneous fat index).

Failure of the data to show a period effect on lengths of the femur and the tibiotarsus bones, along with the fact that adults and juveniles had bones of similar length, illustrate that these bones have a relatively high growth priority (Wilson 1952) and reach mature length dimensions before one year of age and that weight increases exhibited by these bones are the result of a change in density, not length. Taylor and Moore (1954) demonstrated that prior to egg laying many individual bones in domestic fowl function as a reservoir of minerals which can be withdrawn for egg shell formation.

Pelvic bone width was not significantly correlated with ovarian follicle size. Had the distance between opposite pubic bones (Breitenbach et al. 1963) been measured, instead of the distance between pelvic acetabuli, there probably would have been a positive correlation. Pubic bones separate prior to egg laying to permit passage of shelled eggs.

The increase in weight and size of parts of the body during the prelaying period is ultimately related to reproduction and associated activities, which include: the production of shelled eggs; behavioral activities and the formation of new feathers. Growth of the ovary and the oviduct is a basic necessity for the formation of shelled eggs. Resumption of growth (regrowth) documented in this study may be a morphological adjustment to satisfy the physiological demands for: growth and maintenance of the basic reproductive structures; formation of a given quantity of shelled eggs; and growth and maintenance of accessory structures that augment all patterns of growth and activities associated with reproduction. The possible functional significance of regrowth patterns exhibited by component parts of the body of prelaying female Rock Ptarmigan documented in this study are summarized in annotated outline form in Table 12.

Although the avian egg contains appreciable amounts of protein (12% fresh weight, Romanoff and Romanoff 1949, p. 312), these data did not indicate that the pectoral muscles serve as a storage site for protein as evidenced by Anderson (1972) in Ring-necked Pheasants. Similarly, Hanson (1962) did not find muscular tissue to be withdrawn for egg production but he suggested that the liver may function as a labile protein store. However, the prelaying increase in size and weight of the liver is usually attributed to its role in intermediary lipid metabolism (Lorenz et al. 1938). I have circumstantial evidence that the protein requirements of egg production may be augmented by a labile protein store in the alimentary tract tissue.

Leopold (1953) demonstrated that intestinal morphology of gallinaceous birds was related to their food habits. He found that browsing galliforms (grouse) had longer ceca and intestines than seed-eating quails, partridges and pheasants and related the differences to quality and bulk of their respective foods; longer guts were an adaptation to low quality bulk foods. More recent studies by Lewin (1963) on California Quail, Moss (1972) on Red Grouse, Moss (1974) on Rock Ptarmigan, Pendergast and Boag (1974) on Spruce Grouse and Miller (1975) on Mallards (Anas platyrhynchos) support Leopold's contention.

In view of these findings, it is difficult to explain the increase in length and size of the alimentary tract documented in the present

Table 12. Possible functional significance of changes in weights and measurements of component parts of the body of prelaying female Rock Ptarmigan collected in Interior Alaska, 1969-71.

I. Growth of primary or basic reproductive structures required for formation and development of ova and production of shelled eggs (the ovary and the oviduct).

II. Growth of secondary or subordinate reproductive structures required for processing of food, storage and mobilization of energy and nutrients or removal of wastes.

   A. Growth of storage sites by accumulation of chemical components required for formation of shelled eggs and for long range maintenance of the organism's structural and functional integrity (the skeletal bones, the subcutaneous fat deposits, the alimentary tract and the liver).

   B. Growth of components of the alimentary tract directly related with digestion (chemical and mechanical) and absorption of nutrients (the proventriculus, the ventriculus muscle, the small intestine and the ceca).

   C. Growth of accessory or supportive organs for growth and maintenance of all parts of the body (the spleen, the kidneys, the pancreas and the liver).

study since the prelaying diet is probably increasing in quality along with gut length and weight. If Rock Ptarmigan increase food consumption by over 39% during the prelaying period like Ring-necked Pheasants (Breitenbach *et al.* 1963), the increase in alimentary tract size may be a morphological adjustment to maintain prior levels of digestive efficiency since an increase in food consumption (hyperphagia) may be associated with a decrease in digestive efficiency. Evidence supporting this concept is furnished by Campbell and Fell (1964) who demonstrated that a daily period of hyperphagia caused alimentary enlargement in lactating rats but when the daily ration of food was divided into three portions, hypertrophy became insignificant. However, the virtual absence of darkness in the alpine arctic in spring enables ptarmigan to feed throughout the daylight hours and perhaps consume more food than in winter, yet not impair digestive efficiency since the amount of food contained in the alimentary tract at a given time does not increase; in fact, data for the crop, ventricular contents and ceca illustrated a decrease in weight as spring progressed (Table 2). These data indicate that the splanchnic hypertrophy exhibited by prelaying Rock Ptarmigan was not induced by hyperphagia.

Breitenbach *et al.* (1963) had evidence that hyperphagia was not the only factor responsible for enlargement of the alimentary tract in prelaying female birds. They demonstrated that weights of the liver and the intestines in Ring-necked Pheasants increased prior to egg laying and that the increase in weights of these organs was greater in birds subjected to limited food intake than in birds fed *ad libitum*.

Fell *et al.* (1963) demonstrated that in lactating rats the alimentary tract increased in weight, size and total nitrogen content up to weaning; epithelium of the lower small intestine and cecum was both hypertrophied and hyperplastic. Though these changes correlated with increased food intake of the lactating rat, they suggested (p. 188) that the results were

> due to an adaptive response of the intestinal mucosa to the increased bodily demands rather than to a direct effect of increased food consumption.

Data from my study indicate this may at least be the case for prelaying female Rock Ptarmigan.

It seems quite probable that the increase in alimentary tract size in prelaying female Rock Ptarmigan was not a response to absolute dietary quality or hyperphagia but could be a morphological adjustment to increased bodily demands during reproduction and could function as a labile protein store to aid in the formation of eggs and/or feathers.

In summary, the increase in weight and/or size exhibited by component parts of the body is a cumulative response to many proximate factors, i.e., photoperiod, temperature, humidity, precipitation, plant phenology and behavior. Ultimately, these changes in morphology during the prelaying period must have evolved because of their adaptive value for production of high quality eggs. These observations emphasize that reproduction requires integrated participation of many component parts of the body; not only those labeled as reproductive organs (the ovary and the oviduct).

Environmental and Morphological Intra- and Interassociations

Correlation coefficients were used to evaluate the relative association of snow cover index, date of collection, cumulative temperature, molt index, femur length, tibiotarsus length, pelvic bone width, ovarian follicle size, reproductive organ weight and body weight to each other in two age classes of female Rock Ptarmigan sampled in two periods. Results of correlation analyses on these variables are summarized in Tables 4 and 5.

Snow Cover

Watson (1963) found that in winter and early spring, flocks of Rock Ptarmigan utilized wind blown, snow free areas for feeding. Data for period I failed to indicate a significant association between snow cover index and date of collection. As date of collection advanced, it was expected that birds would be collected from sites with less snow cover because of either a decrease in snow cover or a shift of birds to snow free sites.

There are several explanations for the apparent failure of ptarmigan to react to local snow conditions. Perhaps gross snow cover did not change significantly during this period of time and if it did, changes were only temporary because of occasional snow flurries. It is unlikely that snow cover in alpine areas did not decrease between April 19 and May 1. A more plausible explanation is that female ptarmigan were not readily responding to the availability of snow free patches of ground as reported by Watson (1963) for Rock Ptarmigan in Scotland.

Female ptarmigan may have actively responded in a negative way to decreasing snow cover. Although the prenuptial molt of females may be initiated during period I, their plumage is predominatly white and there may be survival value in their remaining in and on snow covered areas for visual "concealment" from predators. A secondary benefit of remaining on the snow pack is that it enables them to easily feed on vegetation in an elevational strata which will be essentially unavailable to them when snow cover is absent. Moss (1974), while studying interspecific competition in Alaskan ptarmigan, reported that Rock Ptarmigan rarely leave the substrate to feed; my field observations concur with his findings. Ultimately, this type of behavior promotes more complete utilization of the food resources available during the prelaying period and may secondarily function to conserve food in lower elevational strata for consumption during later phases of reproductive recrudescence.

In period II', both age classes exhibited a statistically significant affinity for areas relatively free of snow cover. These data are not in contrast with either of the previously stated hypotheses ("predation" and "food resource") concerning use of snow covered areas by ptarmigan nor do they contradict the fact that snow cover decreased with date of collection. During period II', the prenuptial molt has advanced to a stage where the birds are noticeably brown; in this plumage the birds would be less visible to predators if they avoided areas completely covered by snow.

Perhaps the warmer temperatures and melting snow pack, characteristic of period II', yield a new supply of vegetation frozen from the previous year and initiate a resurgence of plant growth and invertebrate activity; all of which make the periphery of melting snow banks nutritiously attractive to female Rock Ptarmigan during the physiologically demanding prelaying period.

Date of Collection

The correlation of both ovarian follicle size and reproductive organ weight with date of collection in period I, indicated that ovarian recrudescence had commenced at least as early as this time period. Failure of the data to indicate a similar association with body weight indicated that the increase in weight was not great enough to affect that variable and perhaps was not yet manifested in body components other than the reproductive organs.

It is interesting that for juveniles in period I variation in date of collection was more intensely correlated with variation in reproductive organ weight than with variation in ovarian follicle size. This lesser degree of correlation may be because initial increases in reproductive organ weight are primarily the result of increases in the size of the oviduct, not the ovary. Evidence in support of this contention is furnished by Anthony (1970) who reported that in California Quail recrudescence of the oviduct was more rapid and reached completion earlier than that of the ovary.

It is possible that reproductive organ growth commenced at some time prior to arrival on the breeding areas. Mackie and Buechner (1963) found in Chuckar (Alectoris graeca) that initial recrudescent development commenced seven to 10 weeks prior to egg laying. Anthony (1970) found that reproductive organ development in California Quail required 10 to 12 weeks. Likewise, Payne (1969) reported that the ovaries in female Redwinged Blackbirds (Agelaius phoeniceus californicus) and Tricolored Blackbirds (Agelaius tricolor) became active three months prior to ovulation. In a sample of female Rock Ptarmigan collected on the breeding areas in March, Robert Weeden (pers. comm.) found that the ovaries were noticeably active. Evidence in this study indicated that ovarian recrudescence occurred as early as late April and considering the findings in other research, it is possible that development of the reproductive organs in female Rock Ptarmigan is initiated several months prior to this on the wintering areas.

As expected, ovarian follicle size, body weight, molt index, reproductive organ weight and snow cover index all showed highly significant correlations with date of collection in period II'. These data indicated that although reproductive organs were developing in period I, other components of the body did not become involved until period II' during which time the rate of change of the reproductive organs was greatly accelerated.

Ovarian Follicle Size

In period I, ovarian follicle size and date of collection, because of interrelationships, were correlated with the same variables, except for the statistically significant association between molt index and ovarian follicle size. One interpretation of this discrepancy is that initiation of the prenuptial molt in female Rock Ptarmigan is influenced more directly by ovarian recrudescence and associated sex hormones than by photoperiod. In a study of Rock Ptarmigan in Scotland, Watson (1956) indicated the relative importance of the sex hormones in modifying the prenuptial molt. It is likely that annual variations in temperature during the present study influenced the association of photoperiod with the molt. Watson (1973) and Hewson (1973) have shown that temperature effects the timing and extent of the prenuptial molt in Scottish Rock Ptarmigan.

In period II', molt index exhibited a more intense correlation with date of collection than with ovarian follicle size. These findings and the previous correlations indicate that the molt was associated with ovarian recrudescence and influenced proximately by levels of circulating sex hormones and ultimately by air temperatures; it later became more directly influenced by photoperiod.

An interpretation of the association between the molt index and temperature and/or photoperiod would include the following: the prenuptial molt is keyed to annual variations in air temperature but if the temperature stimulus is insufficient, molt will be initiated by photoperiod, in either case later stages of the molt are controlled by photoperiod.

Body Weight

In period I, variation in skeletal measurements was associated with approximately 45 and 60% of the variation in body weight of juveniles and adults, respectively. Variation in measurements of each of the three bones was more intensely correlated with variation in body weights in adults than in juveniles. Apparently body weight of juveniles was more variable with respect to skeletal size than was body weight of adults. One would expect body weights of older age groups (a product of at least two years of environmental stress) to be less variable than body weights of the juvenile age class which has not yet been subjected to a complete year of selective pressures. It is also probable that the variation in ecological niches within the adult age class and between years is considerably less than variation in ecological niches occupied by juveniles; the resulting relative homogeneity in ecological niches yields less variation in body weight relative to skeletal size in adults than in juveniles.

The negative correlations between body weight and both cumulative temperature and date of collection in period I, indicated that each age class may have lost body weight after arriving on the breeding areas. These findings are not unreasonable since females have moved from wintering areas at lower elevations to alpine tundra areas where in period I inclement weather and deeper snow may have affected food availability and caused a loss in body weight. Perhaps the flocking behavior of birds that occurs for a short period after arrival on the breeding areas is an adaptation to alleviate food shortages by giving all birds the opportunity to utilize any local feeding areas. If territories were set up promptly after arrival, this opportunity might not be possible. I have observed this behavior to be influenced by local weather conditions. Birds spaced over a hillside on clear sunny mornings tend to gather for feeding into loose flocks in the afternoon following increasing cloud cover and snow flurries.

It is possible that food is relatively unavailable in early spring and although flocking behavior is an adaptation to give each bird the opportunity to utilize all available food resources, slight decreases in body weight may still be expected until appreciable quantities of food become available with melting of the snow cover and the resurgence of plant growth.

During period II', many variables are as intensely correlated with body weight as skeletal parameters. In period II', as in period I, associations between body weights and other variables are more intense for adults than for juveniles.

Cumulative Temperature

As expected cumulative temperature and date of collection exhibited similarly intense associations with ovarian follicle size since in reality the cumulative figure had an inherent date factor plus a temperature component. In each age class and in each period cumulative temperature demonstrated a more intense association with ovarian follicle size than did date of collection. Likewise, in period II', date of collection was not as intensely correlated with reproductive organ weight as was cumulative temperature.

Effects of Year and Area on Morphology and Reproduction

An original objective of this study was to characterize, with morphological variables, the condition of individual females during the prelaying period and to compare these within year characteristics between years of increasing and decreasing ptarmigan populations. Though my research terminated prior to evidence of a change in the trend of the study population, *post facto* evaluations of data on annual winter and spring weather patterns and local topography made comparisons of morphological characteristics between years and between areas, respectively of particular interest.

The general patterns of weather in Interior Alaska in the winter preceding each spring of this study were quite dissimilar: (1) the winter of 1968-69 and the spring of 1969 were relatively warm with little snowfall; (2) the winter of 1969-70 and the spring of 1970 were extremely cold and with moderate snowfall; and (3) the winter of 1970-71 and the spring of 1971 had moderate temperatures and extremely heavy snowfall.

Likewise, temperatures recorded at the field camp on the breeding area during the prelaying period exhibited considerable annual variation (Fig. 2): (1) the spring of 1969 was relatively cold for a week, then warmed and remained warm through the prelaying period; (2) the spring of 1970 was warm for a week and moderate in temperature thereafter; and (3) the spring of 1971 was moderate in temperature early in the spring, then turned cold and remained relatively cold through the prelaying period. These contrasting patterns of weather enabled me to evaluate the effects of both winter and spring weather on morphology and reproduction in female Rock Ptarmigan.

Slope exposure has a profound local ecological effect on plants and animals in the alpine arctic (Bliss 1956). Because the study area was transected by a creek (Porcupine Creek) that roughly divided the area into a series of south-facing slopes and an opposite series of north-facing slopes (Fig. 1), the data were examined for an area effect, which was predominately a slope exposure effect, on prelaying female ptarmigan.

Data for snow cover index, body weight, reproductive organ weight, ovarian follicle size and adrenal gland size were tested for year and area effects.

In an attempt to distinguish between effects carried over from the previous winter and effects incurred on the breeding areas, the data were separated into two periods: (I) to assess the effects of the previous winter's environment; and (II') to assess the effects of the current spring's environment.

Data gathered in period I was not examined for area effects for the following reasons: (1) inadequate sample size; (2) during this period female ptarmigan are probably still strongly under the influence of the winter environment and data would not be indicative of a local spring environmental effect; and (3) female ptarmigan are still quite mobile during this period and unattached to a specific local area.

Though primarily interested in testing for year and area effects, age class and date of collection effects could not be ignored. If the latter two effects were not taken into account in a test situation, a disproportionate sampling distribution of either would yield biased results. To test for year and area effects on snow cover index, body weight, reproductive organ weight, ovarian follicle size and adrenal gland size, an analysis of covariance technique, testing simultaneously for year, age class and area effects with date of collection as a covariate, was utilized.

Snow Cover

Data for snow cover index recorded in period I reflected the general winter weather patterns of Interior Alaska (Table 6); snow cover was least in 1969, intermediate in 1970 and greatest in 1971 (Table 7). With the exception of snow cover in 1970 being less than in either of the other two years, these trends continued on through period II'. The decrease in snow cover in period II' of 1970 is not unexplainable; it was paralleled by relatively warm temperatures in the last two weeks of April and the first week of May.

Although it was not demonstrated statistically that adults were collected from locations with less snow cover than juveniles, the data indicated that in the majority of cases adults were found on areas with less snow cover than areas on which juveniles were found. One would expect that being experienced breeders, adults would take priority over juveniles in selecting areas relatively free of snow cover on which to settle, nest and lay eggs.

The failure of the snow cover index to indicate an area effect (difference in snow cover between south-facing slopes and north-facing slopes) may also be explained. Prevailing northerly winds in winter blow the snow off north-facing slopes and deposit it in drifts on the south-facing slopes. This amount of snow cover added onto the south-facing slopes may override the effects of increased solar radiation on the southern exposures in spring, and both north- and south-facing slopes may become free of snow cover at nearly the same time.

It is also possible that there was a difference in snow cover between north- and south-facing slopes and that ptarmigan on the north-facing slopes had a less suitable proportion of area to select from.

Body Weight

In all cases, except period I in 1971, the data indicated that when juveniles arrived on the breeding areas they weighed less than the adults and that throughout period II' juveniles remained lighter in weight than adults. Failure of the data for period I in 1971 to indicate a statistical difference between body weights of juveniles and adults may be the result of a small sample. This seems probable since data in period II' indicated that each age class in 1971 was lighter in weight than those in 1969 and 1970; suggesting that in 1971 adults failed to gain weight and juveniles lost weight relative to the respective age classes in 1969 and 1970. It seems more likely that age class differences were not detected in period I in 1971 because of the small sample. Implications of differences in weight by age class have been discussed in a previous section.

Annual differences in body weight were not statistically significant in period I. Juveniles in 1971 may have weighed more than juveniles in other years but this apparent difference is perhaps the result of small sample size. The data for period II' indicated that weights of each age class in 1969 were heavier than in other years and that weights of birds in 1971 were less than those in other years. These differences in body weight correlate with climatological data. It appears that in the warm and relatively snow free spring of 1969 birds gained more weight than in the spring of 1971 which had extensive snow cover and was relatively cold.

The spring weather conditions in 1970 were intermediate to 1969 and 1971 and may explain its intermediate values for body weight.

Although one may expect that birds occupying south-facing slopes would be heavier than birds occupying north-facing slopes because of less extensive snow cover and more advanced reproductive cycles, the data did not substantiate this belief. Slope exposure had no apparent effect on body weight.

Reproductive Organ Weight

Though differences were not statistically significant, the data indicated a close association between weights of the reproductive organs in period I and the previous winter's weather and the current spring's snow cover index. For both age classes the reproductive organs were relatively more developed in 1969 following the mildest of the three winters, least developed in 1971 following the winter of greatest snowfall and relatively small but of intermediate size following the extremely cold winter of 1970. These annual differences in weight of the reproductive organs were present in period II'. These data should not be interpreted to mean that following inclement winter and spring weather reproductive organs fail to reach mature size. It seems more likely that final development of the reproductive organs is temporarily delayed but that final weights achieved were similar in all years. Edwards *et al.* (1964) demonstrated that nesting in Ring-necked Pheasants was delayed following relatively cold and snowy winter and spring weather.

In period I and period II', the reproductive organs of adults were found to be more developed than those of juveniles. Lewin (1963) found that in California Quail the reproductive organs in adults were larger than those in juveniles until several weeks prior to egg laying at which time there was no detectable difference between age classes. In contrast, Mackie and Buechner (1963) failed to find age related differences in either the rate of ovarian recrudescence or the length of the recrudescent period. There was no evidence in this study indicating that when laying commenced reproductive organs of juveniles were not similar in weight to those of adults.

There was some indication that weights of the reproductive organs were greater in birds collected from south-facing slopes than in birds collected from north-facing slopes but the differences were not statistically significant. Variation in reproductive recrudescence related to slope exposure will be discussed in the following section.

Reproductive organ weight varies with year, age class and possibly slope exposure. Evidence indicated that these variations in reproductive organ weight were only temporary and did not exist when laying commenced.

Ovarian Follicle Size

Ovarian follicle size was the only variable that exhibited statistically significant year, age class and area effects.

Data on ovarian follicle size for period I indicated that in each age class follicles in 1970 were larger than those in either 1969 or 1971, even though winter weather conditions were apparently mildest in 1969. However, during the first week of field procedures the spring of

1970 was considerably warmer than the spring in either 1969 or 1971 (Fig. 2). This suggests that ovarian recrudescence responded immediately to the warm spring temperatures in spite of contrasting amount of winter snowfall, winter temperatures and spring snow cover.

The relatively warm spring temperatures in period I of 1970 may have decreased the amount of snow cover to a level similar to that of 1969. Since I did not detect a difference between the snow cover indices in period II' of 1969 and 1970, it seems likely that the much warmer spring temperatures in period II' of 1969 resulted in birds of that year having heavier, more developed reproductive organs than those birds in period II' of either 1970 or 1971. These data indicated that although the amount of winter snowfall and winter temperatures may have affected the weight and size of the reproductive organs of females arriving on the breeding areas, the influence of subsequent spring temperatures was paramount and the response to it was rapid.

The area effect exhibited by ovarian follicle size may have been in response to local temperatures instead of snow cover and the appearance of snow free areas. Since data presented here did not indicate a statistically significant correlation between snow cover and slope exposure, it is unlikely that area differences in follicle size were related to snow cover. The increased solar radiation on south-facing slopes relative to north-facing slopes probably resulted in higher ground surface temperatures which caused its snow cover to begin to thaw and melt sooner than on north-facing slopes. These data indicate that what may affect the rate of ovarian recrudescence is not primarily the appearance of snow free areas or the lack of snow cover but the warmer temperatures associated with the melting of the snow pack.

Siivonen (1957) mentioned the importance of snow free areas to prelaying female tetraonids. He demonstrated that the appearance of snow free areas, associated with warm temperatures in early spring, was an important indirect factor for the release of the reproductive process in the female. Siivonen believed that the relative success of the reproductive process was related to the appearance of snow free spots which freed nesting sites from snow cover and solved the food problem of early spring with the availability of early green plants.

Likewise, it is quite probable that the annual, area and age class differences in the size of ovarian follicles documented in this study were in part related to the appearance of new food supplies associated with warmer temperatures and the disappearance of snow cover.

Adrenal Gland Size

Although variation in adrenal gland size has been associated with age class, state of health, the reproductive cycle and stress stimuli (Sturkie 1965), my data indicated that age class, area, year and date of collection had no statistically significant effect on adrenal gland size. Breitenbach et al. (1963) also failed to show a statistically significant effect of restricted food intake on the weights of adrenal glands in prelaying hen pheasants.

Data for period I indicated that adrenal glands were larger in 1971 (the year of extreme snowfall) than in either 1969 or 1970. This observation may be the result of stresses related to the extensive snow cover in 1971.

Though not statistically significant, the data in essentially all year and age class categories indicated that females from north-facing slopes had larger adrenal glands than females on south-facing slopes (Table 7). This difference in size exhibited by the adrenal glands may in part be the result of stresses related to reproduction, since birds collected from north-facing slopes also had less developed ovarian follicles than birds collected from south-facing slopes.

Perhaps the linear measurement used to evaluate adrenal gland size was relatively insensitive to cellular and/or mass changes that are usually associated with stress stimuli and reproduction. Höhn (1947) found that there was no seasonal trend in weights of adrenal glands from ducks but that the ratio of component tissues (interrenal tissue and chromaffin tissue) was greatly altered.

CONCLUSIONS

In this study of gross morphology in free-living prelaying females, weights and measurements of component parts of the body of 165 juvenile and 144 adult Rock Ptarmigan collected in Interior Alaska during a population decline, 1969-71, were analyzed by season, age class, area and year. Variation in weight and/or size of various components of the body was attributed to the influences of weather, slope exposure, age class, reproductive status and body size.

Seasonal variation in body weight was primarily associated with the reproductive cycle, however the ovary and the oviduct were not the only parts of the body responsible for prelaying increases in body weight. Increases in weight and/or size exhibited by other components of the body are an adaptive response to the increased bodily demands of reproduction and function: (1) to enhance assimilation and processing of food; (2) as material reserves which are withdrawn for egg formation; and/or (3) as accessory or supportive organs for growth and maintenance of all parts of the body. Evidence indicated the accumulation of fats in subcutaneous depots, and the accumulation of minerals in the skeleton, however no protein reserves were found to accumulate in the breast muscles. Increases in weight and/or size of component parts of the alimentary tract were probably an adaptive response to increased bodily demands during reproduction and may subsequently function as a protein reserve to facilitate formation of eggs and/or feathers.

Adults were heavier than juveniles during the prelaying period.

Age class differences in body weight were in part attributable to the adults advanced reproductive cycle, however weights of the breast muscles and the large intestine were not correlated with ovarian recrudescence but exhibited age class differences. Apparently juveniles do not achieve adult body size until their second autumn of life.

Seasonal and annual variations in morphology and the reproductive cycle were attributed to the effects of winter and spring weather and melting of the snow pack on availability of food resources.

APPENDIX A.

Results of analysis of covariance involving body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index with date of collection as a covariate for juvenile (J) and adult (A) female Rock Ptarmigan collected from April 19 to April 30 (period I) in Interior Alaska, 1969-71 (N = 80).

Source of Variation	Degree of Freedom	Analysis of Variance (F)				
		Body Weight	Reproductive Organ Weight	Ovarian Follicle Size	Adrenal Gland Size	Snow Cover Index
Year	2	2.96	1.50	3.73*	2.59	5.86**
Age	1	5.73*	6.87*	21.94**	1.79	1.98
Year x Age	2	2.19	0.07	0.01	0.62	0.53
1969 J vs 1970 J	1	0.88	0.95	1.81	0.85	1.37
1969 J vs 1971 J	1	8.46**	0.84	0.49	2.04	5.54*
1970 J vs 1971 J	1	5.28*	0.04	3.13	0.60	2.38
1969 A vs 1970 A	1	0.45	0.76	1.13	4.06*	0.07
1969 A vs 1971 A	1	0.02	2.14	0.69	1.39	5.24*
1970 A vs 1971 A	1	0.59	0.56	3.50	0.38	7.15**
1969 J vs 1969 A	1	10.06**	3.33	9.18**	0.34	0.12
1970 J vs 1970 A	1	3.20	4.10*	9.85**	3.77	3.42
1971 J vs 1971 A	1	0.05	0.91	4.84*	0.02	0.22
1969 J vs 1970 A	1	6.59*	0.94	17.81**	7.26**	0.38
1969 J vs 1971 A	1	8.76**	0.01	3.39	3.00	4.19*
1969 A vs 1970 J	1	5.73*	8.00**	3.44	0.08	2.19
1969 A vs 1971 J	1	0.12	5.44*	9.41**	0.88	6.61*
1970 J vs 1971 A	1	5.18*	0.91	0.58	1.03	1.28
1970 A vs 1971 J	1	0.91	3.15	17.98**	0.51	9.01**
Covariate[a] -- Date Collection	1	0.11	13.12**	17.93**	1.61	7.90**

*$0.01 < P \leq 0.05$

**$P \leq 0.01$.

[a] Regression coefficient for covariate.

APPENDIX B.

Results of analysis of covariance involving body weight, reproductive organ weight, ovarian follicle size, adrenal gland size and snow cover index with date of collection as a covariate for juvenile and adult female Rock Ptarmigan collected on two areas (differing in slope exposure) from May 1 to May 23 (period II') in Interior Alaska, 1969-71 (N = 229).

Source of Variation	Degree of Freedom	Analysis of Variance (F)				
		Body Weight	Reproductive Organ Weight	Ovarian Follicle Size	Adrenal Gland Size	Snow Cover Index
Year	2	6.20**	3.78*	14.09**	0.24	43.31**
Age	1	30.44**	4.48*	10.24**	1.88	0.18
Area	1	0.02	0.11	10.32**	0.68	0.18
Year x Age	2	0.56	1.60	0.33	0.03	1.39
Year x Area	2	0.87	0.63	2.01	0.89	1.46
Area x Age	1	0.65	0.62	1.08	0.43	4.14*
Year x Area x Age	2	0.49	0.17	3.65*	1.69	0.64
Covariate[a] -- Date of Collection	1	60.41**	228.00**	566.56**	0.18	117.78**

*0.01<P≤0.05.

**P≤0.01.

[a] Regression coefficient for covariate.

APPENDIX C.

Results of analysis of covariance involving body weight, reproductive organ weight, adrenal gland size and snow cover index with date of collection as a covariate for juvenile (J) and adult (A) female Rock Ptarmigan collected from May 1 to May 23 (period II') in Interior Alaska, 1969-71 (N = 229).

Source of Variation	Degree of Freedom	Analysis of Variance (F)			
		Body Weight	Reproductive Organ Weight	Adrenal Gland Size	Snow Cover Index
Year	2	8.74**	6.80**	0.04	42.31**
Age	1	33.63**	7.46**	0.69	0.02
Year x Age	2	0.39	1.44	0.40	1.99
1969 J vs 1970 J	1	0.61	1.21	0.22	4.05*
1969 J vs 1971 J	1	6.55*	10.56**	0.67	24.97**
1970 J vs 1971 J	1	3.01	4.30*	0.08	57.22**
1969 A vs 1970 A	1	4.33*	6.33*	0.23	0.39
1969 A vs 1971 A	1	10.99**	3.72	0.17	28.23**
1970 A vs 1971 A	1	1.75	0.19	0.00	21.43**
1969 J vs 1969 A	1	15.56**	2.52	0.06	1.15
1970 J vs 1970 A	1	8.07**	0.13	0.51	2.70
1971 J vs 1971 A	1	10.55**	8.27**	1.02	0.13
1969 J vs 1970 A	1	3.77	0.60	0.05	0.22
1969 J vs 1971 A	1	0.35	0.10	0.08	15.67**
1969 A vs 1970 J	1	24.13**	7.96**	0.08	1.12
1969 A vs 1971 J	1	57.24**	30.12**	0.38	46.76**
1970 J vs 1971 A	1	1.91	0.59	0.40	36.95**
1970 A vs 1971 J	1	25.55**	6.52*	1.27	34.95**
Covariate[a] -- Date of Collection	1	60.81**	265.11**	0.00	134.89**

*0.01<P≤0.05.

**P≤0.01.

[a] Regression coefficient for covariate.

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