MORPHOLOGICAL HOMOGENEITY OF A POPULATION OF ALASKA WILLOW PTARMIGAN

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Willow Ptarmigan (*Lagopus lagopus*) are a large component of the avian life of the tundra of North America and Eurasia. They are abundant near and above the margins of woodlands in Alaska. Since their elected habitats are not continuous over the state, populations of these birds are not always contiguous, and there are extensive areas where no Willow Ptarmigan occur. However, ptarmigan move long distances in migration (Irving 1960; Irving, West, Peyton, and Paneak 1967), and contact between usually disjunct populations of birds is clearly possible.

We have been studying Willow Ptarmigan (*L. lagopus alascensis* Swarth) that breed along the Colville River Valley and migrate south through passes in the Brooks Range to winter from the Colville River south for 200 miles to the Koyukuk River. In the course of studies on the migrations of these ptarmigan (Irving, West, Peyton, and Paneak 1967), food habits (West and Meng 1966), and feeding behavior (Irving, West, and Peyton 1967), we have found regularity in their annual activities that made it interesting to define the population under study in order to provide a basis for determining if the Brooks Range population was dimensionally homogeneous and for subsequent examination of whether it differed morphologically from other populations ascribed to the same subspecies elsewhere in the state. Since the Bergerud, Peters, and McGrath (1963) study of the Newfoundland Willow Ptarmigan (*L. lagopus alleni* Stejneger) and the present investigation both demonstrated variations in morphology based on sex and age, we separated ages and sexes and treated them as separate categories of the population. By so doing, it was also possible to establish criteria useful for determining age and sex of live-caught Willow Ptarmigan in the field.

Drying of wings and tails, as in the preparation of museum specimens, possibly results in shrinkage which would influence comparative tests of measurements among populations. However in order to test for the amount of shrinkage due to drying, it was necessary to eliminate the obvious errors in measurement. The frequency of gross errors in length measurement, the variation between measurers, and the variation among all of the measurements of one person were also determined. From this, it was possible to determine the change in length due to drying.

METHODS

COLLECTION AND MEASUREMENTS

Willow Ptarmigan were collected throughout the year in the Brooks Range. Summer birds were collected on their breeding grounds at Umiat on the Colville River; spring, fall, and winter collections were made at Umiat, at Anaktuvuk Pass, 100 miles south of Umiat at the summit of the Brooks Range, and along the John River draining south from Anaktuvuk to the Koyukuk River, with concentrated collections at Crevice Creek and Bettles Field (fig. 1, table 1).

Birds were either examined in the field after shooting during the months of June through September, or were immediately frozen in plastic bags and shipped back to the Laboratory of Zoophysiology for examination.

Three measurements were taken and two pigment differences were observed on each bird examined. Body weight less crop weight, length of wing, and length of tail were utilized in the study of population homogeneity and also in an attempt to determine the sex of birds caught for banding. The pigmentation of the primaries and rectrices was observed to see if they could be utilized as a criterion for estimating age and sex, respectively. These characters were utilized by Bergerud *et al.* (1963) with varying success in determining age and sex of Willow Ptarmigan in Newfoundland.

Birds were weighed to the nearest 0.1g. The crop was removed and weighed and weight of the crop contents, less crop membrane, was subtracted from the gross body weight. The

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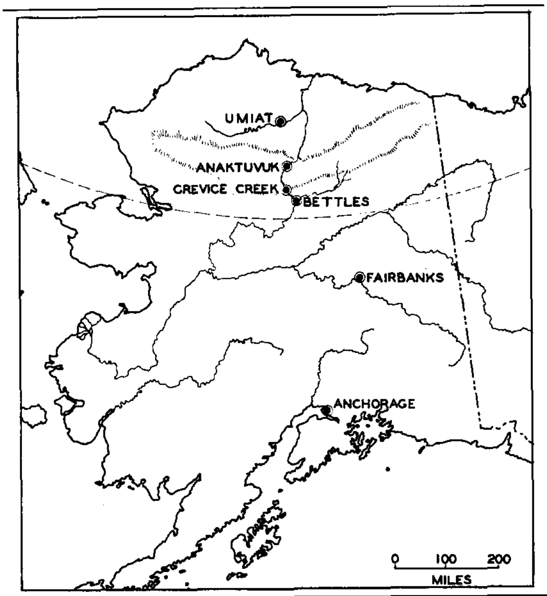

FIGURE 1. Map showing four of the collecting localities in the Brooks Range. Umiat is on the Colville River, Anaktuvuk is at the headwaters of the Anaktuvuk River which flows northward and the John River which flows southward. Crevice Creek is located on the John River and Bettles on the Koyukuk River.

weights of crop contents varied from 0 to 132 g wet weight (Irving, West, and Peyton, 1967).

The length of the wing (we used the left wing) of fresh or previously frozen birds was measured by flattening the wing along a ruler and measuring from the bend of the wrist to the tip of the longest primary (number 8). For dry opened wings, the wing was again flattened along a ruler and the length taken from the notch at the carpal-metacarpal joint to the tip of the longest primary. Anatomically, the bend of the wrist is equivalent to the proximal end of the metacarpus.

The length of the outer tail feather (usually the right) was measured by inserting a millimeter ruler between the sixth and seventh (outer) rectrix and measuring to the tip of the flattened seventh rectrix. Birds with incompletely grown remiges or rectrices were not used. The same technique was used for both fresh and dry tails.

The bird was then opened and sex determined by gonad examination and age determined by presence or absence of the bursa of Fabricius. Since the bursa is present only in juvenile birds and disappears during midwinter (usually by January), age could not be determined by internal examination after December.

The tips of primaries eight and nine were examined for presence or absence of pigment. If primary nine had more dark pigment than eight, the bird was marked as "J" (for suspected juvenile). If primary nine was lighter or equal in pigmentation to eight, then the bird was marked "A" (for suspected adult). These assumptions were made following results obtained by Bergerud *et al.* (1963) on Newfoundland Willow Ptarmigan.

The presence of brown pigment on the tail was recorded to see if brown tail pigment was an indicator of femaleness while lack of brown indicated maleness.

ANALYSIS

The data were coded and punched on IBM cards for analysis. Cards were sorted for locality and for age and sex within each locality. Frequency plots of the distribution of tail length and wing length were made for each category from each location, and means and standard deviations were computed for each category.

In order to ascertain if greater pigmentation on the ninth primary was an indicator of a juvenile bird, the percentage of known adults (no bursa prior to January) with a light ninth primary was determined as was the percentage of known juveniles (with bursa prior to January) with a dark ninth primary. An interval for the discrimination of age categories of the population was thus obtained.

TABLE 1. Location of collecting stations in the Brooks Range and numbers of each age and sex of Willow Ptarmigan collected.

Location	Latitude and longitude		Number collected			
			A♂	A♀	J♂	J♀
Umiat	69°24′N	152°07′W	168	18	49	19
Anaktuvuk	68°09′N	151°46′W	230	81	235	102
John River	68°09′N	152°07′W	35	12	6	3
Crevice Creek	67°22′N	152°04′W	10	31	11	35
Bettles Field	66°55′N	151°28′W	10	36	39	76
Totals			453	178	340	235
Total, all birds			1206			

The same method just described for determining juvenile status by wing pigmentation was used for estimating sex by the presence or absence of brown pigment on the tail.

Each sex and age group (adult male, adult female, juvenile male, juvenile female) was compared with the corresponding group in all four localities by the use of Duncan's multiple range test for unequal sample sizes and heteroscedastic means (Duncan 1957) modified by using Newman and Keul's tables of critical values (Miller 1966). A significance level of 0.05 was used in hypothesis testing. Since no statistically significant differences were found in mean length among localities ($P < 0.01$), frequency distributions were plotted, crossover points were determined, and the means and standard deviations calculated for the four age-sex classes for all the data from the Brooks Range. Crossover points between sexes were designated from the frequency distributions of the original sample data in figures 2–7. Error in designating whether a correct determination of sex was made above or below the crossover point was calculated by determining the per cent of birds that would be incorrectly judged in our sample by using the designated crossover points.

In order to assess the variability in measuring wing and tail lengths, three technicians measured 48 dried wings and 37 dried tails of birds which had previously been measured while still wet (fresh). A total of 12 measurements on each wing and tail was made by the three technicians, each on separate days and with no reference to each other's or their own prior measurements. Analysis of variance was carried out on the dry wing and tail measurements, partitioning the variance among measurers (S. S., M. M., and D. K.), wing (or tail) lengths, and individual measurements of each wing (or tail). The results revealed that the differences among the three measurers were not significantly different at the 5 per cent level for either wings ($F_{[2,6]} = 2.76$, $P > 0.10$) or tails ($F_{[2,10]} = 2.04$, $P > 0.10$). Therefore we concluded that the three measurers did not differ in measuring wings and tails. The amount of variation accounted for by individual variation in wing or tail length was significant (wings: $F_{[47,141]} = 684.70$, $P < 0.001$; tails: $F_{[36,108]} = 1063.86$, $P < 0.001$), which is to be expected owing to the large variation in lengths of individual wings and tails.

There was no statistically significant effect of measurement within any one wing (each wing measured 4 times by 3 people) ($F_{[3,141]} = 0.01$, $P > 0.10$). Therefore, each measurer maintained a reasonable degree of consistency from one measurement to the next on successive days on the same wing.

However, there was a statistically significant effect of measurements on any one tail (each tail measured 4 times by 3 people) ($F_{[3,108]} = 3.86$, $P < 0.02$). Therefore, there was a greater variation in measuring of tails than of wings. Apparently tail lengths are more difficult to determine accurately, perhaps because of the greater flexibility of rectrix compared with remex feathers of ptarmigan, or because technicians use varying pressure in inserting the ruler against the tail between the feathers.

Since the above analysis of variance indicated that the differences among measurers were not significant at the 5 per cent level, each of the measurements made by two of the measurers (S. S. and M. M., who had made the original fresh measurements) of the dry wings and tails was compared with the corresponding fresh (wet) length. Most of the dry measurements did not vary more than one or two millimeters, and usually any larger variation was a multiple of five millimeters and was assumed to be due to misreading the ruler. These misreading errors were eliminated so as to minimize error before making comparisons with the wet measurement. The frequency of measurements discarded as misreadings of the ruler was only 1.8 per cent of the 720 measurements.

Following this minimization of error, each set of dry measurements (1st, 2nd, 3rd . . . 8th) was compared with the one wet (fresh) measurement for wings and again for tails (Simpson 1960).

RESULTS

AGE DETERMINATION

Using 287 ptarmigan of known age (by presence or absence of the bursa of Fabricius from October–December; 104 adults, 183 juveniles) it was found that 97 per cent of the juvenile birds (with bursa) of both sexes had more dark pigment on the ninth primary than on the eighth. Similarly 97 per cent of the adult birds (without bursa) had less pigment on the ninth than on the eighth primary, while 3 per cent of the adults had more pigment on the ninth than on the eighth primary. Therefore, a bird that has less pigment on the eighth primary than on the ninth was considered juvenile with 97 per cent accuracy in our sample. Primary pigmentation was used

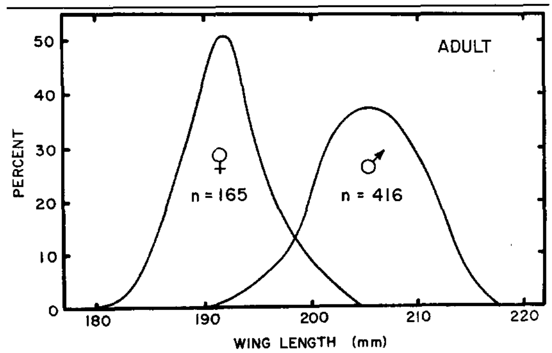

FIGURE 2. Frequency distribution curves for the observed sample of adult Willow Ptarmigan wings collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

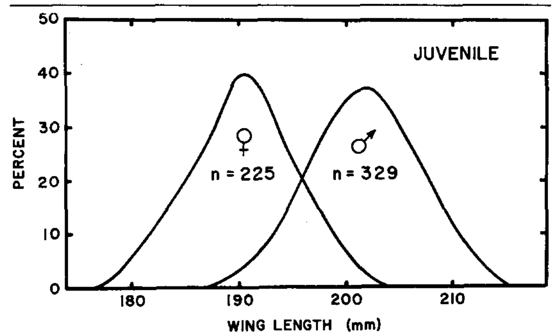

FIGURE 3. Frequency distribution curves for the observed sample of juvenile Willow Ptarmigan wings collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

as a determinant of age for birds collected after the bursa had disappeared in midwinter. The primaries of true juveniles which appear in the birds' first summer are retained for a full 11 months and are not molted until the following August. Ninety-seven per cent of the birds classed as juveniles, therefore, are at least three months old, but less than 14 months old, with the other 3 per cent being over 14 months old. Projecting the above estimate of age to the Brooks Range population, age could be judged correctly by wing pigmentation with an accuracy of 97 per cent (± 2 per cent at the 95 per cent confidence level) for any sample flock.

TAIL PIGMENTATION

It was hypothesized that birds having any brown pigment on the tail were females. Of 947 birds examined, 59 per cent of the adult females and 76 per cent of the juvenile females had brown pigment on the tail. However, 10 per cent of the adult males and 20 per cent of the juvenile males also had brown pigment on the tail. Therefore, sex could be judged by tail pigmentation with an accuracy of only 78 per cent for juveniles (74.0–81.8, at the 95 per cent confidence level) and with an accuracy of only 81 per cent (76.9–84.1) for adults.

WING LENGTH

Frequency distributions of length of left wings of Willow Ptarmigan from the Brooks Range were plotted separately for each age-sex class (adult male, adult female; juvenile male, juvenile female—figs. 2 and 3). It was not possible to combine any of the age-sex classes since the differences in wing length among them were statistically significant (table 2).

The differences in length of wing between sexes enabled us to distinguish sex by wing

TABLE 2. Wing, tail, and wing plus tail lengths of Willow Ptarmigan from the Brooks Range, Alaska.

	n	Mean ± SD	Test	Calculated *t* value	Probability[a]
Wing					
Adult male	416	205.6 ± 4.7	A♂ vs A♀	34.87	< 0.001
Adult female	165	192.0 ± 4.1	A♂ vs J♂	10.56	< 0.001
Juvenile male	329	201.8 ± 5.2	J♂ vs J♀	26.00	< 0.001
Juvenile female	225	190.1 ± 5.1	A♀ vs J♀	4.04	< 0.001
Tail					
Adult male	387	122.6 ± 5.3	A♂ vs A♀	25.53	< 0.001
Adult female	157	110.6 ± 4.8	A♂ vs J♂	13.10	< 0.001
Juvenile male	264	117.1 ± 5.3	J♂ vs J♀	21.28	< 0.001
Juvenile female	201	107.1 ± 4.6	A♀ vs J♀	6.86	< 0.001
Wing plus Tail					
Adult male	380	328.4 ± 8.7	A♂ vs A♀	33.55	< 0.001
Adult female	148	309.2 ± 7.5	A♂ vs J♂	13.24	< 0.001
Juvenile male	255	318.6 ± 9.5	J♂ vs J♀	24.77	< 0.001
Juvenile female	192	297.3 ± 8.7	A♀ vs J♀	6.36	< 0.001

[a] Probability of obtaining a greater or equal difference between the two means if the null hypothesis is true.

TABLE 3. Crossover points and frequency of incorrect sex determination in the observed sample of Brooks Range Willow Ptarmigan.

	Crossover point (mm)		Frequency of incorrect determination
	male	female	(%)
Wing			
adult	⩾ 199	< 199	6.1
juvenile	⩾ 196	< 196	13.1
Tail			
adult	⩾ 117	< 117	10.2
juvenile	⩾ 113	< 113	14.5
Wing plus Tail			
adult	⩾ 315	< 315	5.6
juvenile	⩾ 307	< 307	13.4

length in most adult and juvenile birds. The crossover point for adult wings was 198.5 mm (fig. 2), and the frequency of incorrectly determining the sex of birds in this sample was 6.1 per cent (table 3). For juvenile wings, the crossover point was 196 mm (fig. 3), and the frequency of incorrect classification was 13.1 per cent (table 3).

TAIL LENGTH

Frequency distributions of the length of the outer rectrix of Willow Ptarmigan from the Brooks Range were plotted separately for each age-sex class (fig. 4 and 5). Again it was not possible to combine any of the age-sex classes since the differences among all groups were statistically significant (table 2).

The crossover point for adult tails was 117 mm (fig. 4), and the frequency of incorrectly determining sex in this sample was 10.2 per cent (table 3). For juvenile tails, the crossover point was 113 mm (fig. 5), and the frequency of incorrect classification was 14.5 per cent (table 3).

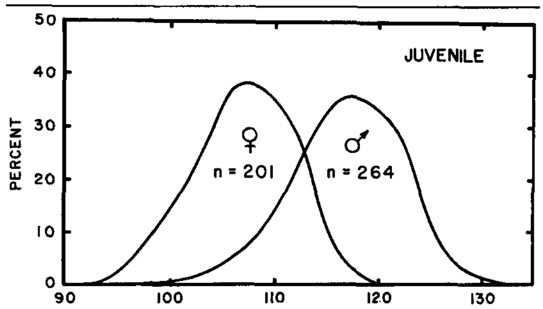

FIGURE 5. Frequency distribution curves for the observed sample of juvenile Willow Ptarmigan tails collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

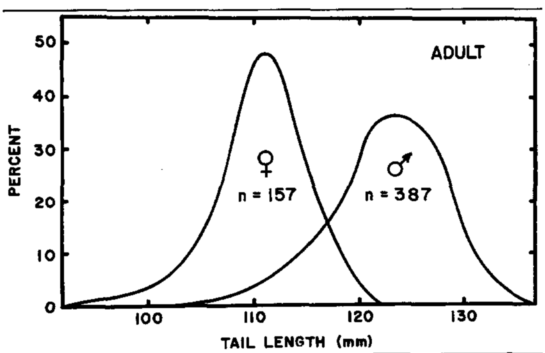

FIGURE 4. Frequency distribution curves for the observed sample of adult Willow Ptarmigan tails collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

WING PLUS TAIL LENGTH

Since there was suspected correlation between wing and tail length, the two measurements were summed for each individual in the hope of increasing the accuracy of sex determination based on length measurements. Frequency distributions of wing plus tail length for adult and juvenile birds are given in figures 6 and 7. For adults, the crossover point was 314 mm (fig. 6), and the frequency of incorrectly determining sex in this sample was 5.6 per cent (table 3). For juveniles, the crossover point was 307 mm (fig. 7), and the frequency of incorrect classification was 13.4 per cent (table 3).

BODY WEIGHT

There were marked variations in mean net body weight among categories and with time of year, but the lack of data for certain months

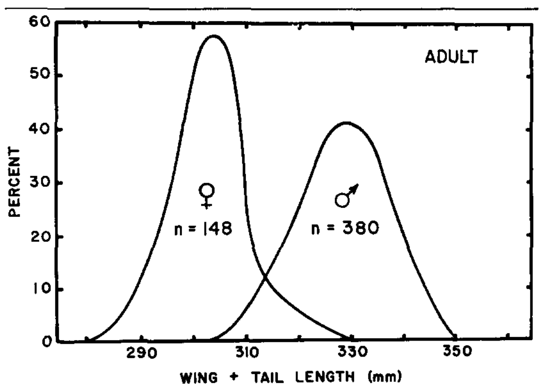

FIGURE 6. Frequency distribution curves for the observed sample of adult Willow Ptarmigan wing plus tail measurement collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

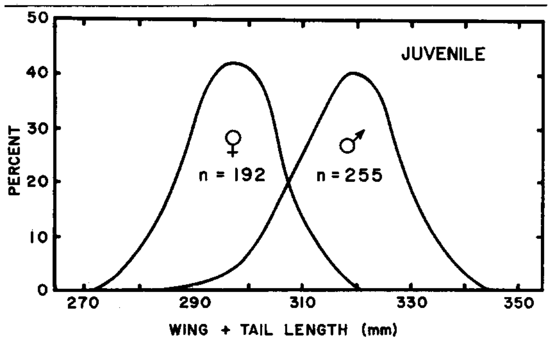

FIGURE 7. Frequency distribution curves for the observed sample of juvenile Willow Ptarmigan wing plus tail measurements collected from the Brooks Range. The breaking point between male and female is indicated by the crossover point between the two curves.

prohibited an analysis of seasonal changes in weight. Therefore we did not consider it appropriate to average body weights over the year in order to use weight as a criterion for estimating sex. Further data on weight in relation to fat content are included in another publication (West and Meng 1968).

EFFECT OF DRYING ON LENGTH

The dry measurements for wings and tails were statistically different than the wet measurements ($P < 0.05$; table 4). The average dry wing measurement was 0.7 mm shorter than the wet measurement, and the average dry tail measurement was 0.8 mm shorter than the wet measurement.

DISCUSSION

The monophasic frequency distribution of wing and tail lengths for each age-sex class of Willow Ptarmigan from the Brooks Range indicates that we are dealing with a population composed of four homogeneous but distinct categories.

TABLE 4. Student's *t*-test for the difference between wet and dry measurements of wings and tails of Brooks Range Willow Ptarmigan.

Measurer	Mean Diff. of wet-dry	n	*t* value	Probability[a]
Wings				
M_1	0.61	33	4.69	< 0.001
M_2	0.69	35	4.54	< 0.001
M_3	0.60	35	4.14	< 0.001
M_4	0.74	35	5.00	< 0.001
S_1	0.57	35	3.93	< 0.001
S_2	0.76	34	6.03	< 0.001
S_3	0.71	34	5.46	< 0.001
S_4	0.76	34	5.14	< 0.001
Tails				
M_1	0.80	30	4.00	< 0.001
M_2	0.90	30	3.80	< 0.001
M_3	0.50	30	2.36	< 0.025
M_4	1.07	30	4.07	< 0.001
S_1	0.93	30	3.54	< 0.001
S_2	1.03	30	4.24	< 0.001
S_3	0.83	29	3.18	< 0.005
S_4	0.67	30	2.71	< 0.010

[a] Probability of obtaining a greater or equal difference between the wet and dry measurements if the null hypothesis is true.

Because of the differences among the four categories, comparison of the Brooks Range population with other populations of Willow Ptarmigan must be done between age-sex classes. We have preliminary data on Willow Ptarmigan collected in several localities throughout Alaska that show differences when compared with the Brooks Range population. Results of this study will be published elsewhere. However, the data on wing length in the study by Bergerud *et al.* (1963) allowed us to compare the Newfoundland Willow Ptarmigan with the Brooks Range population (table 5). In all age-sex classes, the differences were significant at the 5 per cent

TABLE 5. Comparison of wing length between Willow Ptarmigan from the Brooks Range, Alaska, and Willow Ptarmigan from Newfoundland. Newfoundland data from Bergerud, Peters, and McGrath 1963.

Age	Sex	Location	n	Wing length mean ± SD (mm)	P
Adult	M	Brooks Range	416	205.6 ± 4.7	< 0.001
		Newfoundland	64	201.5 ± 4.0	
Adult	F	Brooks Range	165	192.0 ± 4.1	< 0.02
		Newfoundland	77	188.9 ± 8.3	
Juvenile	M	Brooks Range	329	201.8 ± 5.2	< 0.001
		Newfoundland	64	199.4 ± 2.9	
Juvenile	F	Brooks Range	225	190.1 ± 5.1	< 0.01
		Newfoundland	57	187.4 ± 4.8	

level, with the means for the Brooks Range birds always longer. A significant difference, although expected because of the large geographical disparity in the range of the two subspecies, indicates the potential of these comparisons in distinguishing large samples of related populations of birds. Tail lengths could not be compared since Bergerud (personal communication) measured plucked feathers while we measured only to the point where the feather left the skin.

The best method of sex determination by dimension for Brooks Range adults was the addition of wing and tail lengths, which determined sex correctly in 94.4 per cent of our sample of the Brooks Range population. For juveniles, however, the large variation in tail length made the wing-plus-tail measurement less reliable than wing length alone, and therefore wing length was the best method for determining sex of juveniles. This classified birds according to sex correctly in 86.9 per cent of our sample of the Brooks Range population.

The ability to distinguish sex by wing and tail length in adult and juvenile birds is helpful in sexing birds during winter in the field. It must be noted that the criteria established for distinguishing sex by wing and tail length measurements are the least accurate at the crossover point. Wings or tails differing greatly from the crossover point values permit very reliable sex determinations. This fact can easily be seen from observation of the areas under the curves above and below the crossover points in figures 2–7.

The frequency distributions of dimensions of wing and tail show an obvious sex difference in that wing and tail length measurements of females exhibit smaller variances than those of the males. This difference is more pronounced for adults than for juveniles. Although not as clearly shown, Bergerud *et al.* (1963:709) demonstrated the same tendency in their figures of wing and tail distribution. However, their differences in variation are partially obscured by the fact that both adult and juvenile birds are included in the same figure. We cannot recall any previous similar observation on large samples.

The live capture and marking program which we initiated in 1963 now can give us more nearly complete information on the sex distribution of birds moving through Anaktuvuk Pass. Irving, West, Peyton, and Paneak (1967) have discussed the sex-age distribution in the migrating and wintering population where the migratory motion could only be inferred by the collection of birds at a few points of occurrence. A better picture can now be obtained by capturing and recovering live marked birds. Similarly, the 97 per cent association between presence of the bursa of Fabricius and darker primary pigmentation allows us to distinguish age of most live Willow Ptarmigan at any season.

The variation due to different people in measuring wing and tail lengths has not previously been evaluated to our knowledge, and therefore no comparisons can be made with other samples. It is clear from the analysis of variance that practiced individual measurers are consistent in their measurements of one individual wing and tail, that there is reasonable uniformity among measurers, and that the frequency of gross errors in measurement is relatively low.

The significant amount of shrinkage of ptarmigan wings and tails due to drying, although less than one millimeter in either case, points out that comparative measurements between populations must be done on either a wet (fresh) or a dry basis and not a combination of the two. If this is not done, any statistically significant differences encountered could be due to either the differences between the wet and dry lengths or the actual differences in lengths between the two populations.

The amount of error introduced by utilizing wet instead of dry measurements for comparisons (or vice versa) would be only 0.39 per cent for our sample of Willow Ptarmigan wings and 0.69 per cent for tails. However, Barth (1967) in comparing lengths of wing of two species of gulls (*Larus argentatus* and *L. fuscus*) when measured fresh and again after drying for six months found a shrinkage of 5.2 ± 1.08 mm in wings that averaged 431.7 mm when fresh. In that case, the error that could be introduced would be 1.24 per cent.

SUMMARY

The frequency distributions of wing length and tail length of 1200 Alaskan Willow Ptarmigan (*Lagopus lagopus alascensis*) were determined for each of the four sex-age classes collected from four localities in the Brooks Range of northern Alaska. None of the differences in any measurement within any sex-age class was statistically significant among the four localities within the Brooks Range. The monophasic frequency distribution and the lack of statistically significant differences in mean length within sex-age classes regardless of locality indicate that the sample is

from a single homogeneous population. The four sex-age classes, however, have statistically significant different wing and tail lengths. Adult females exhibit less variation in length measurements than do the other age-sex groups.

Sex was determined by a combination of wing and tail length measurements in our sample of adult Brooks Range Willow Ptarmigan with an accuracy of 94.4 per cent. For juveniles, sex was determined by wing length alone with an accuracy of 86.9 per cent in our sample, but the presence of brown pigment on the tail was not an accurate indicator of sex.

Age can be estimated with 97 per cent accuracy using primary pigmentation. Juvenile birds (from three months to fourteen months of age) have the ninth primary tip darker than the eighth while adults (15 months and older) have the ninth lighter or equal to the eighth in pigmentation.

The frequency of human error in measuring a series of wing and tail lengths was only 1.8 per cent, and there were no statistically significant differences in measurements made by three measurers. The amount of shrinkage due to drying of wings and tails averaged 0.7 and 0.8 mm, respectively. Therefore, when making comparisons with other populations, either fresh or dry material must be measured on both samples and not a combination of the two, or else the appropriate wet-dry correction factor must be applied to one set of data.

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