RELATIVE HEART SIZE IN ALASKAN TETRAONIDAE

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ABSTRACT.—Heart:body size ratios were measured in over 1,900 specimens of seven species of Alaskan Tetraonidae. Blue Grouse (*Dendragapus obscurus*) and Ruffed Grouse (*Bonasa umbellus*) have hearts averaging only 0.4 to 0.5% of body weight. At the other extreme, Rock Ptarmigan (*Lagopus mutus*) have hearts averaging 2.0% of body weight. Between these extremes are White-tailed Ptarmigan (*L. leucurus*), 1.1%; Spruce Grouse (*Canachites canadensis*), 1.2%; Sharp-tailed Grouse (*Pedioecetes phasianellus*), 1.4%; and Willow Ptarmigan (*L. lagopus*), 1.4%. Intraspecific variations related to sex, age, body size, season, and locality were found in some but not all species. The members of this family seem to have evolved diverse strategies for meeting cardiovascular requirements, and heart size alone does not reveal the nature of these systems. *Received 18 April 1978, accepted 29 November 1978.*

FOR at least 80 years ornithologists have been intrigued by the wide range in relative heart size or "heart ratio" (heart weight divided by whole body weight) exhibited in the class Aves. Some species have hearts as small as 0.3 or 0.4% of body weight, while at the other extreme a few species have hearts comprising 2.5% of body mass.

Early authors brought out many hypotheses about patterns in heart size related to climate, altitude, body size, season, muscle activity levels, and other factors. Firm conclusions were hampered by extremely small sample sizes and other methodological problems, as mentioned by Moreau (1944). This early literature was reviewed by Brush (1966), who showed that, in fact, heart:body weight ratios are poorly correlated with altitude and general activity. He concluded "that heart rate is at least as important in adjustments to increased metabolic demands, as is heart size, that the mechanism of adjustment cannot be predicted from heart size alone, and that birds of similar size may employ different combinations of capacity and intensity in making these adjustments."

Since Brush's publication there have been few papers reporting heart ratios for extensive collections of birds. Köster's (1976) work on Tyrant Kingbirds (*Tyrannus melancholicus*) and Smooth-billed Anis (*Crotophaga ani*) in the Colombian Andes is an exception. His data on 114 kingbirds and 138 anis showed that mean heart ratios increased as altitude of collection increased from sea level to 2,300 m, the difference being most pronounced in *Crotophaga*. Köster commented that the two species have invaded the higher elevations recently and that the increase in heart size probably is not a genetic response.

I became interested in avian heart size in 1962 when I first observed differences in heart ratios among the seven species of Tetraonidae living in Alaska (Ruffed Grouse, *Bonasa umbellus*; Sharp-tailed Grouse, *Pedioecetes phasianellus*; Spruce Grouse, *Canachites canadensis*; Blue Grouse, *Dendragapus obscurus*; White-tailed Ptarmigan, *Lagopus leucurus*; Willow Ptarmigan, *L. lagopus,* and Rock Ptarmigan, *L. mutus*). Specimens examined from 1962–1969 while I was employed by the Alaska Department of Fish and Game yielded enough data for quantitative analysis of both intraspecific and interspecific variation in this group of birds.

MATERIALS AND METHODS

I compiled heart and body weights of 1,951 grouse and ptarmigan in this study. Willow and Rock ptarmigan comprise 1,414 of this total. Most specimens were birds that had reached adult body size, but

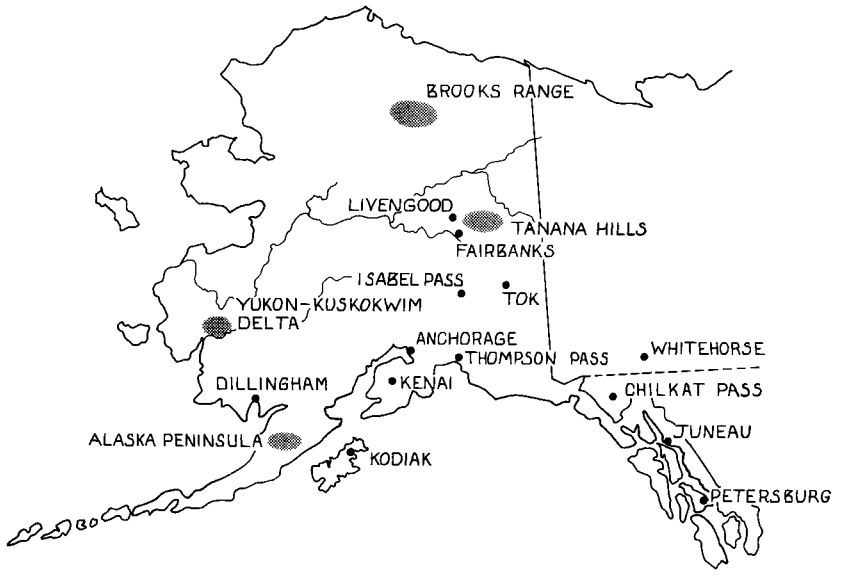

Fig. 1. Collection localities of grouse and ptarmigan.

some young birds were collected to check for differences related to age. All birds were collected by shooting except for chicks, which were killed by heart pressure after capture.

The sex of each specimen was determined by examining gonads or plumage. The Bursa of Fabricius, wing molt pattern, and date of collection were used, as appropriate, to place a specimen in an age class. Birds were classed as "adult" (any bird collected after 19 October of its first year of life), "immature" (first-year birds from 1 September to 19 October), or "chick" (young of the year in June, July, and August). These arbitrary groupings reflect age-related variations in heart ratio, as will be discussed.

Body weights (gross weight minus the crop and its contents) were measured with balances sensitive to ± 0.1 g. Heart weights were measured with the same balance before 1965, but most hearts were weighed on balances sensitive to ± 0.01 g. The heart weights were from fresh or recently thawed hearts, minus pericardium, with blood blotted from the chambers and with blood vessels cut off at the top of the atrium. (Hearts stored in formalin had to be discarded because of weight losses, and are not included in this study.) Fat, commonly found around the top of the ventricles in tetraonids, was removed with scissors. Heart ratios calculated with and without this fat usually differed by only 0.02 to 0.04%, although in exceptionally fat birds (especially Ruffed Grouse, which have very small hearts) the difference might range to 0.10%.

Grouse and ptarmigan were collected from dozens of localities in Alaska and adjacent Canada. Localities were considered as one collection area if they were in the same valley or mountain system. Ptarmigan move considerable distances in interior and northern Alaska between breeding and wintering areas, and it seems unjustified to consider each locality where these birds were shot as having distinct "populations" of ptarmigan (see West et al. 1968, Weeden 1964). Locations of major collections are shown in Fig. 1.

When extensive comparisons of subsamples were necessary, as with data from Spruce Grouse, Rock Ptarmigan, and Willow Ptarmigan, the data were programmed for computation in the University of Alaska's IBM 360-40 computer. Duncan's Multiple Range Test was applied to these subsamples (Duncan 1957). The tables of Newman-Keul were used instead of those of Duncan, as in the Newman-Keul tables the chance for wrongly deciding that two means are different remains constant at 0.05 regardless of the number of means being compared, whereas with Duncan's method the chance for error increases progressively with the number of means (Miller 1966).

Most subsamples are described in this paper by the mean, range, standard deviation (SD), and coefficient of variation (CV, calculated as $SD/\bar{x}$).

RESULTS

Blue Grouse.—Sixteen adult male and five adult female Blue Grouse were shot near Juneau and Petersburg, Alaska at elevations from sea level to 350 m. Mean body weight for cocks was 1,318 g (range 1,176–1,457 g, SD = 81, CV = 6.1%); mean heart ratio was 0.48% (range 0.36–0.58%, SD = 0.06, CV = 12.5%). Body weights of hens varied so much (due mainly to seasonal reproductive changes) that a mean was not calculated; the range was 776 to 1,172 g. Heart ratios averaged 0.40% among the five females, and ranged from 0.31 to 0.49%. There is no discernible relationship between body size and heart ratio within one sex in this sample of Blue Grouse. Collections were too few to test for altitudinal or seasonal variations.

Sharp-tailed Grouse.—This species ranges in Alaska from latitude 62° to 68°N and from the Yukon border nearly to the Bering Sea coast. My collections are from Tok, Livengood, and the Fairbanks area at elevations of 150 to 500 m. Fourteen males averaged 734 g (range 678–802 g, SD = 33, CV = 4.5%). Their hearts averaged 1.38% of their total weight (range 1.14–1.53%, SD = 0.11, CV = 7.9%). Twelve hens weighed 645 g on the average (range 613–680 g, SD = 23, CV = 3.6%), and had heart ratios averaging 1.39% (range 1.14–1.56%, SD = 0.13, CV = 9.4%).

Two immature male Sharp-tailed Grouse weighed 659 and 687 g, with heart ratios of 1.09 and 1.22%, respectively. Body weights and heart ratios of five immature females were 649 g (1.15%), 547 g (1.19%), 652 g (1.24%), 611 g (1.28%), and 522 g (1.39%). This sample, although small, suggests that immature Sharp-tailed Grouse in autumn have not yet achieved mature body weight, and have relatively smaller hearts than adults.

Ruffed Grouse.—D. Boag donated data from 15 adult male Ruffed Grouse taken in May near the Alberta Biological Station at Gorge Creek, southwest Alberta, at an elevation of about 1,500 m, and one each from June and July from the same area. These cocks had a mean body weight of 549 g (range 501–589 g, SD = 27, CV = 4.9%), and their heart ratios averaged 0.41% (range 0.34–0.50%, SD = 0.05, CV = 12.2%).

I collected 11 male and 19 female Ruffed Grouse during October through April at elevations of 150 to 350 m in the Tanana Valley of central Alaska, mainly within 30 km of Fairbanks. The males ranged in size from 578 to 681 g (mean 632 g) with hearts ranging from 0.37 to 0.53% of body weight (average 0.43%). Hens were slightly smaller (range 454–681 g, average 590 g) but had the same mean heart ratio (range 0.34–0.55%). The heart ratios of big hens were smaller than those of small hens; the mean ratio of the 10 heaviest females (average 641 g) was 0.40%, whereas nine smaller females (average 534 g) had a mean ratio of 0.46% ($P < 0.05$). The Alberta males showed no size-related trend in heart ratio, but these birds were remarkably homogeneous in body weight. Alaskan cocks seemed to show a reverse trend, with big birds having big hearts, but the sample was small.

One might question whether a very small (454 g) female Ruffed Grouse in this collection with a very large heart relative to its size (0.55%), should be included in the analysis. However, there seems to be no basis for excluding it. It acted normally before being shot, was not emaciated, and looked healthy when examined internally. Furthermore, a female Ruffed Grouse found dead of starvation 7 February 1968, weighing 432 g, had a typical heart ratio of 0.41%. This suggests that heart mass and body mass decrease at similar rates during slow starvation.

TABLE 1. Major collections of adult Spruce Grouse by sex, area, and month.

		Body weight (g)				Heart ratio (%)			
	N	Mean	Range	SD	CV	Mean	Range	SD	CV
Males									
Fairbanks									
September	12	637	575–775	54	8.5	1.18	0.95–1.45	0.13	11.3
Kenai									
June	5	574	543–592	19	3.3	1.19	1.01–1.39	0.14	11.4
October	13	573	544–605	17	3.0	1.12	0.82–1.29	0.15	13.4
Dillingham									
April	6	605	537–643	44	7.2	1.24	1.06–1.41	0.13	10.7
May	8	605	482–672	68	11.2	1.25	1.03–1.48	0.17	13.6
June	8	543	541–638	40	7.4	1.24	1.05–1.40	0.10	8.4
July	8	554	521–578	21	3.8	0.86	0.77–0.96	0.07	8.1
September	5	579	555–610	27	4.7	1.32	1.26–1.43	0.06	4.7
Females									
Fairbanks									
September	16	612	558–665	30	4.9	1.15	0.98–1.36	0.11	9.9
October	7	617	466–723	78	12.6	1.21	0.79–1.53	0.23	18.5
Kenai									
October	6	567	519–595	27	4.7	1.12	0.96–1.35	0.16	14.3
Dillingham									
April	5	528	479–580	41	7.6	1.19	1.00–1.27	0.11	10.1
May	8	561	468–629	66	11.7	1.14	0.83–1.38	0.20	17.7

Eleven immature male Ruffed Grouse were significantly heavier (mean 593 g, range 526–677 g, SD = 43.2, CV = 7.3%) than 10 immature females (mean 502 g, range 450–542 g, SD = 30.4, CV = 6.0%). Heart ratios of the two sexes were similar (males: mean 0.43%, range 0.34–0.48%, SD = 0.04, CV = 9.3%; females: mean 0.44%, range 0.39–0.54%, SD = 0.05, CV = 11.4%).

Spruce Grouse.—The Spruce Grouse I examined came from Dillingham, Kenai, and the general Fairbanks area. Collections with more than four individuals of one sex for a given month and area are in Table 1. Most samples are not statistically distinguishable, in part because of small sample sizes and high individual variation. The only sample that clearly differs from all others is the group of eight males shot in July in Dillingham, with a very low mean heart ratio and low variability in the sample. Inspection of other collections suggests that the low heart ratio is a function of season, not location, because other collections of Dillingham males show rather high heart-to-body weight ratios. The data on body weight for males in this area from April through September indicate that heart and body size were stable in April and May, declined proportionately in June (resulting in the same heart ratio as earlier in spring), but diverged in July when body size stabilized or increased slightly while heart size continued to decline. Heart weight "caught up" with body weight in September.

Spruce Grouse at Dillingham may have proportionately bigger hearts in fall than members of the same species collected elsewhere at the same time. A Duncan's Multiple Range Test using pooled September and October samples showed significant differences ($P < 0.05$) in mean heart ratio between 12 Dillingham Spruce Grouse (mean 1.29%) and 19 birds from Kenai (mean 1.12%) and 38 grouse from the Fairbanks area (mean 1.18%). The difference persisted when data were adjusted to correct for different sex ratios in the collections from the three areas.

TABLE 2. Heart weight and heart ratio of Spruce Grouse chicks from Kenai, Alaska, in relation to body weight.

Weight class (g)	N	Body weight (g)			Heart weight (g)			Heart Ratio (%)		
		Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
0–99	13	22.6–90.8	58	25.9	0.2–0.8	0.52	0.22	0.67–1.26	0.93	0.18
100–199	9	101–197	136	30.1	0.7–1.2	0.89	0.14	0.56–0.79	0.66	0.05
200–299	3	220–292	248	—	1.2–1.5	1.40	—	0.51–0.68	0.57	—
300–399	9	302–395	331	31.2	1.6–2.1	1.90	0.16	0.51–0.63	0.57	0.03
400–499	0	—	—	—	—	—	—	—	—	—
500–599[a]	8	519–599	563	26.8	5.0–7.4	6.36	0.88	0.96–1.31	1.13	0.12
500–605[b]	13	519–605	570	20.0	4.6–7.8	6.46	0.99	0.82–1.35	1.13	0.15

[a] Collected before 20 October. Separated from next collection to show stabilization in body and heart size in October, after period of rapid change in July–September.
[b] Collected 20–31 October.

Female Spruce Grouse may have lower heart ratios in June–August than in fall and winter. Pooled data from small collections (not in Table 1) showed that 10 hens collected from June through August had a mean heart ratio of 0.88% (range 0.81–1.03%), compared with means varying from 1.12 to 1.21% in other months (Table 1). The data also suggest a small but persistent difference between the sexes, with cocks having proportionately larger hearts.

Spruce Grouse chicks have different heart:body ratios from adults. The Department of Fish and Game's studies near Kenai provided the chance to find out how this characteristic changed as chicks approached maturity. There was a very definite indication (Table 2) that the whole body grew at a different rate from the heart, first faster and then more slowly, resulting in decreasing, then increasing, heart ratios. The data only give a rough approximation of a true time series, because the actual ages of chicks were not known. Hatching occurs usually during the third week in June in the area where the grouse were collected. Chicks in the first weight class were collected 23 June to 7 July; chicks 100–199 g were collected 7 July to 23 July; chicks 200–299 g were collected late in July; and birds weighing 300–399 g were shot 3 to 11 August. There is a 2-month gap in the data, from early August to early October (8–14 October) when young Spruce Grouse in the 500–599 g class were collected. During this time, mean heart weight increased from 1.9 to 6.4 g, a much faster growth rate than the whole body, which rose from 330 to 560 g.

Because adult Spruce Grouse from Kenai had mean heart ratios of 1.12% in September and October, it seems that young-of-the-year achieve the adult heart:body ratio by early October in that area. Fifty first-year birds from Fairbanks in September had smaller bodies (581 vs. 623 g for adults), smaller hearts (5.58 vs. 7.23 g), and lower ratios (0.97 vs. 1.16%) than 28 adults from the same area and month (see Table 1). All differences are significant at the 0.01% level. Later in the fall (1–19 October), 34 immature Spruce Grouse from the Fairbanks area did not differ significantly in body weight (mean 607 g) or heart ratio (mean 1.18%) from adults. Thus, the timing of attainment of the adult heart-ratio characteristic appears to be the same in Kenai and Fairbanks.

White-tailed Ptarmigan.—Main collections of this species were made in the Alaska Range (Isabel Pass), Chugach Mountains (Thompson Pass), Anchorage area, and Kenai Mountains at altitudes of 550 to 1,200 m. Twenty-five males and 30 females were taken in October–April, mostly at elevations 175 to 300 m lower than normal summer ranges.

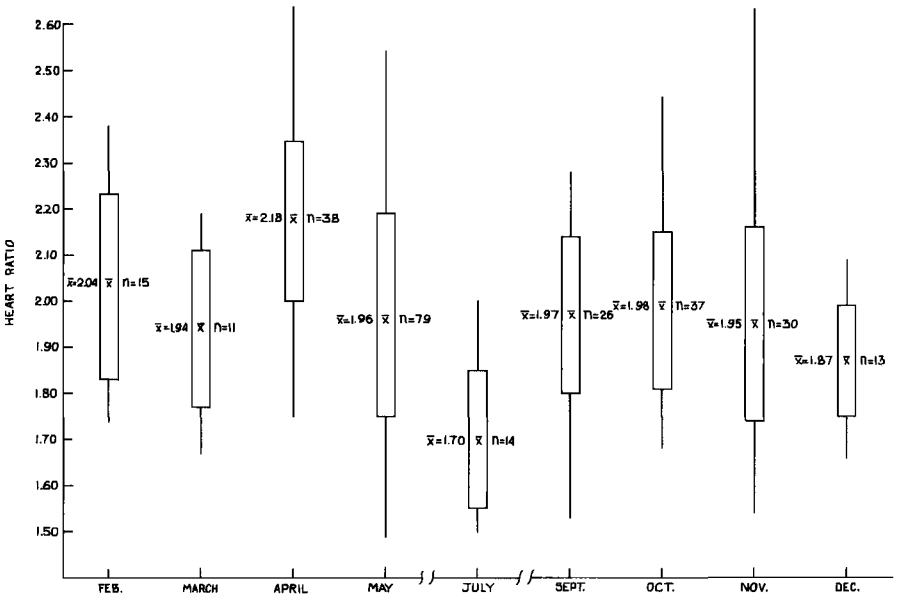

Fig. 2. Ranges, standard deviations (boxes), and mean monthly heart ratios ($\bar{x}$) of adult female Rock Ptarmigan from the Tanana Hills, central Alaska.

The body weights and heart ratios in the male White-tailed Ptarmigan (mean body weight 359 g, range 298–416 g; mean heart ratio 1.04%, range 0.82–1.19%) did not differ significantly from those of females (mean body weight 351 g, range 279–381; mean heart ratio 1.07%, range 0.87–1.34%) when all collections of one sex were pooled. That this could be an accident of sampling is suggested by the fact that eight males from Thompson Pass in November had significantly larger heart ratios (1.07%; $P < 0.01$) than 11 males from the Alaska Range in February and March (0.97%). Whether season, body condition, or some attribute of location was the main source of variation is not known.

Four adult females shot in summer and early fall had body weights and heart ratios as follows: 5 June, Chilkat Pass, British Columbia, 432 g and 0.96%; 12 August, Alaska Range, 360 g and 0.86%; 12 August, Alaska Range, 330 g and 0.97%; and 14 September, Thompson Pass, 355 g and 1.15%.

An adult male shot 5 June in Chilkat Pass at 1,000 m elevation had a larger relative heart size (1.51%, body 310 g) than any other White-tailed Ptarmigan I examined. Nothing unusual about the bird's external or internal appearance gave a clue as to cause of the high heart-to-body ratio. An adult female collected 26 July near Gorge Creek, Alberta (2,400 m elevation) had an extraordinarily big heart (2.61%, body 288 g). According to D. Boag, the specimen appeared normal.

Seven chicks collected 12 August 1963 near Isabel Pass had smaller heart ratios than adults. Four males weighing 253, 243, 264, and 229 g had heart ratios of 0.59, 0.62, 0.68, and 0.72% respectively; three females weighing 244, 244, and 243 g had heart ratios of 0.45, 0.66, and 0.82%. The chicks were about 7 weeks old.

Rock Ptarmigan.—Most Rock Ptarmigan were collected in the Tanana Hills north and east of Fairbanks. This series includes birds from all months except January. Other large collections are from the central Alaska and Brooks Ranges in late winter.

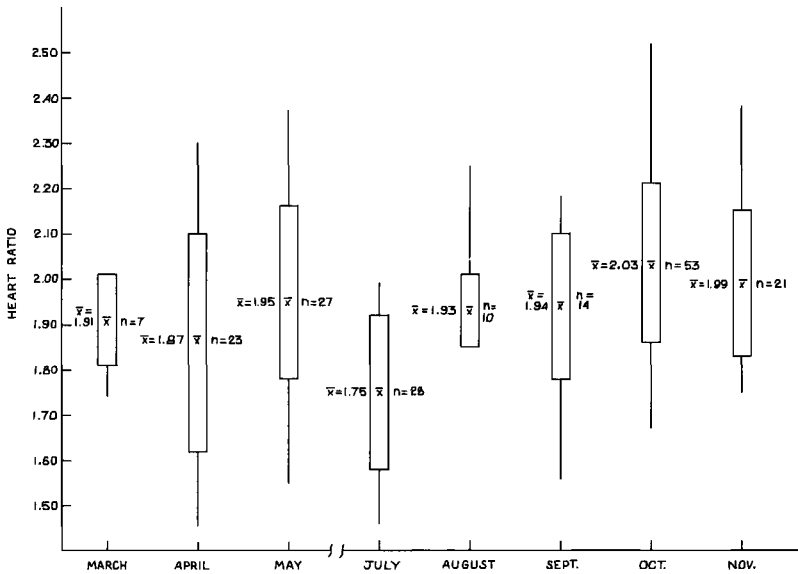

Fig. 3. Ranges, standard deviations (boxes), and mean monthly heart ratios ($\bar{x}$) of adult male Rock Ptarmigan from the Tanana Hills, central Alaska.

Considering just the Tanana Hills collection (Figs. 2 and 3), most monthly means are not significantly different from each other according to the Duncan Multiple Range Test. However, males had relatively smaller hearts in April and July ($P < 0.05$) than in May or August through November. Hens had significantly smaller hearts in July ($P < 0.01$) than in any other months tested (February, March, April, May, and September through December). Males and females did not differ in their average heart ratios in March, May, July, September, October, or November, but hens had bigger heart ratios in April ($P < 0.01$). This may result from hearts getting bigger during the annual spring movement of hens back to breeding grounds. Males usually do not make this migration (Weeden 1964).

Individual variation within months, coupled with small samples, almost certainly masks changes in heart ratios occurring throughout the year. Hens in May, for example, show high variation in heart ratio (CV = 11.2%) associated with reproduction. At this time of year heart size does not change as rapidly as body weight does when oviducts thicken and ova enlarge.

As mentioned earlier, female Rock Ptarmigan had lower heart ratios in July than other months. This was because heart size decreased at a relatively faster rate than body size in midsummer, although both body and heart decreased to their annual low point at that time. Males also showed low heart ratios in July, although the mean body weight in my sample was slightly higher in July (433 g) than in April (424 g) or May (416 g). Heart size was smallest in July.

Data from Rock Ptarmigan collected in February through April in the Alaska Range, Tanana Hills, and Brooks Range are summarized in Table 3. The collections are quite homogenous with respect to mean body size and heart ratios except for the March samples. In that series, Brooks Range birds had smaller bodies than birds from the other areas, but this was mainly due to the preponderance of hens in the Brooks Range sample. There is a slight overall tendency for heart ratios to decrease from February through April.

TABLE 3. Body weights and heart ratios of Rock Ptarmigan from three areas in Alaska in late winter.

Month and area	N (♂, ♀)	Body weight (g)				Heart Ratio (%)			
		$\bar{x}$	Range	SD	CV	$\bar{x}$	Range	SD	CV
February									
Alaska Range	16, 8	426	371–468	24.9	5.8	2.08	1.81–2.47	0.13	6.2
Tanana	2, 15	423	380–471	26.3	6.2	2.02	1.74–2.38	0.19	9.4
March									
Alaska Range	34, 38	421	365–482	32.0	7.6	1.97	1.60–2.44	0.16	8.1
Tanana	7, 11	423	378–485	35.8	8.5	1.93	1.67–2.19	0.12	6.2
Brooks Range	4, 16	398[a]	344–460	29.6	7.4	1.93	1.70–2.58	0.20	10.4
April									
Tanana	19, 7	421	359–479	30.1	7.1	1.92	1.68–2.42	0.16	7.6
Brooks Range	4, 10	427	384–475	25.3	5.9	1.80	1.58–1.95	0.13	7.0

[a] Significantly different from other means for March at $P < 0.05$.

Young Rock Ptarmigan (Table 4) had relatively small hearts in July with a progressive rise in heart ratio through early October, when young birds had heart ratios approaching those of adults. Although samples were smaller for Rock Ptarmigan chicks than for Spruce Grouse, the former did not seem to have the same decline in heart ratios in July and August observed among young Spruce Grouse. The high variability in samples of immature Rock Ptarmigan is due mainly to the pooling of individuals of different age and body weights within months.

Willow Ptarmigan.—Large samples of this species were obtained in November through April from many parts of Alaska, providing a chance to test for regional variations in heart ratio (Table 5). Preliminary tests showed no month-to-month variations during November to April, so months were pooled. Heart ratios of males and females were similar within each area, but because males had bigger bodies than females, the sexes were analyzed separately.

West et al. (1970) suggested that the relatively large Willow Ptarmigan in the Brooks Range and Yukon-Kuskokwim delta areas are *L. l. alascensis* whereas Whitehorse, Alaska Range, and upper Tanana populations are *L. l. albus,* a smaller race. Heart ratios reflect these body size trends, with mean heart ratios being smaller ($P < 0.01$) in *alascensis*.

TABLE 4. Body weights and heart ratios of young Rock Ptarmigan in autumn in central Alaska.

Month and sex	N	Body weight (g)				Heart ratio (%)			
		Mean	Range	SD	CV	Mean	Range	SD	CV
July									
Sexes combined	18	137	56–256	42.3	30.9	1.10	0.81–1.48	0.16	13.8
August									
Males	22	371	287–430	40.4	10.8	1.65	1.32–2.16	0.22	13.3
Females	24	335	286–375	21.0	6.3	1.55	1.13–1.83	0.17	10.7
September									
Males	15	429	377–465	26.0	6.0	1.73	1.51–2.02	0.15	8.5
Females	30	411	340–456	27.3	6.6	1.83	1.53–2.16	0.14	7.6
October									
Males	38	437	401–478	20.1	4.6	1.98	1.76–2.52	0.16	7.9
Females	28	401	333–467	30.9	7.6	1.89	1.59–2.18	0.14	7.6

TABLE 5. Regional comparison of heart and body size of Willow Ptarmigan collected in winter.

Area, sex	N	Mean body weight (g)	Mean heart weight (g)	Mean ratio (%)
Yukon-Kuskokwim Delta				
Males	55	620	7.56	1.22
Females	44	539	7.01	1.30
Kodiak Island				
Males	14	617	7.82	1.27
Females	28	523	6.74	1.29
Brooks Range				
Males	129	603	7.19	1.19
Females	16	514	6.40	1.24
Alaska Peninsula				
Males	18	586	7.79	1.33
Females	23	513	7.03	1.37
Tanana Hills				
Males	13	567	8.10	1.43
Females	62	500	6.89	1.38
Alaska Range				
Males	86	547	7.52	1.37
Females	67	477	6.66	1.40
Whitehorse				
Males	12	521	7.48	1.46
Females	30	458	6.57	1.44

Regressions of heart ratio on body size were run for the two sexes. Regression coefficients ($b = 0.0024$ for males; $b = 0.0020$ for females) were different from 0 at the 99% level according to a standard t-test. Thus, in addition to the regional differences in body size and heart ratio just mentioned, there is a trend for small birds of each sex to have relatively larger hearts than bigger birds.

DISCUSSION

Some of the earliest published observations on avian heart size concerned members of the family Tetraonidae. Strohl (1910) saw that *Lagopus mutus* living at high elevations had relatively bigger hearts than *L. lagopus* from lower elevations. He attributed the difference to the effects of altitude, but Stieve (1934) found that the differences persisted when specimens of the two species were collected at the same altitude, and decided the differences were genetic. Johnston (1963) reaffirmed Stieve's observations but asserted that the interspecific differences should be attributed to body weight differences. Semenov-Tyan-Shanskii (1960) added seasonal considerations to the discussion of ptarmigan heart size by showing that *L. lagopus* hearts were one-fourth larger in midwinter than in May–June. He also showed that female *Lyrurus tetrix* (Black Grouse) and *Tetrao urogallus* (Capercaillie) had relatively larger hearts than males.

The first data about *L. leucurus* heart ratios were published by Johnson and Lockner (1968). They demonstrated that this species has much smaller heart ratios than other *Lagopus,* despite its smaller body size and high-altitude habitat. They suggested two interpretations: heart rate might be faster in *leucurus,* or, alternately, *leucurus* behavior might place less intense demands on its cardiovascular system. In that connection it is worth noting that all three *Lagopus* have higher resting

metabolism rates than would be predicted on the basis of body size, but that *leucurus* (Johnson 1968) could not maintain a high metabolic rate when exposed to temperature stress as well as *lagopus* and *mutus* (West 1972).

My data suggest that one or more of Alaska's seven species of Tetraonidae exhibit intraspecific variation in heart ratio related to sex, age, season, locality, and body size. *Sex-related variation* occurred among Rock Ptarmigan collected in one general location in April, when hens had relatively larger hearts than cocks. This difference resulted from temporary differences in body weight or heart weight trends between the sexes and did not persist over the whole year. No differences in heart ratios between the sexes were found in fall or winter samples from any other Alaskan tetraonid.

Age differences occurred among Spruce Grouse and Rock Ptarmigan. In the former, young chicks had higher heart ratios than somewhat older chicks, and young in the fall did not have hearts as large as those of adults until late October. Rock Ptarmigan chicks had smaller heart ratios than adults until late October. In a limited test, young Ruffed Grouse in September had hearts proportionately as large as those of adults. Hartman (1955) found that immatures of some species had different heart ratios from adults, whereas others did not. My data indicate that heart ratios may change rapidly in young birds, so that age of the young bird at the time of collection will greatly affect the comparison with adults.

Month-to-month differences in heart ratio occurred in July, when both male and female Rock Ptarmigan had relatively small hearts, and in April, when hens had higher ratios than at other times. Other seasonal differences probably occur, but require larger samples to define. Pendergast and Boag (1973) showed seasonal changes in heart ratios of adult Alberta Spruce Grouse. Heart ratios in June, July, and August appear from their graphs to be close to 1.0% in both sexes, whereas in late fall and spring ratios average about 1.3%.

Small female Ruffed Grouse in interior Alaska had higher heart ratios than larger females. The same *size-related difference* was demonstrated among male and female Willow Ptarmigan. In this case, however, the large and small birds were collected in different places, so identification of the source of variation is difficult. *Location* appeared to be the major variant related to differences in fall heart ratios among adult Spruce Grouse.

Occasionally enough birds were collected from one flock to estimate *individual variation.* For example, 33 male Rock Ptarmigan shot in March 1963 near Paxson, Alaska Range, had heart ratios ranging from 1.62 to 2.24% (mean 1.91%); there was no correlation between body size and heart ratio. The Coefficient of Variation was 8.6%. As noted in the section on Spruce Grouse, CV values up to 18.5% have been observed in some subsamples.

My conclusion from these data on intraspecific variation is an echo of Moreau's (1944) cautions about small samples. Samples of 10 to 20 adults collected within a short time (up to a month) are needed for an initial estimate of a species' heart ratio. These collections should be made at a season when no unusual energy demands are imposed on the birds, and when body weight is fairly constant. Additional specimens should be obtained to test for seasonal, geographic, sex, and age variability.

Intraspecific variations in heart ratios should be useful in identifying periods of high or low metabolic demand for a given species because all members of a species have inherited the same basic cardiovascular system. The midsummer low in relative heart size of at least some adult tetraonids, for example, probably indicates a de-

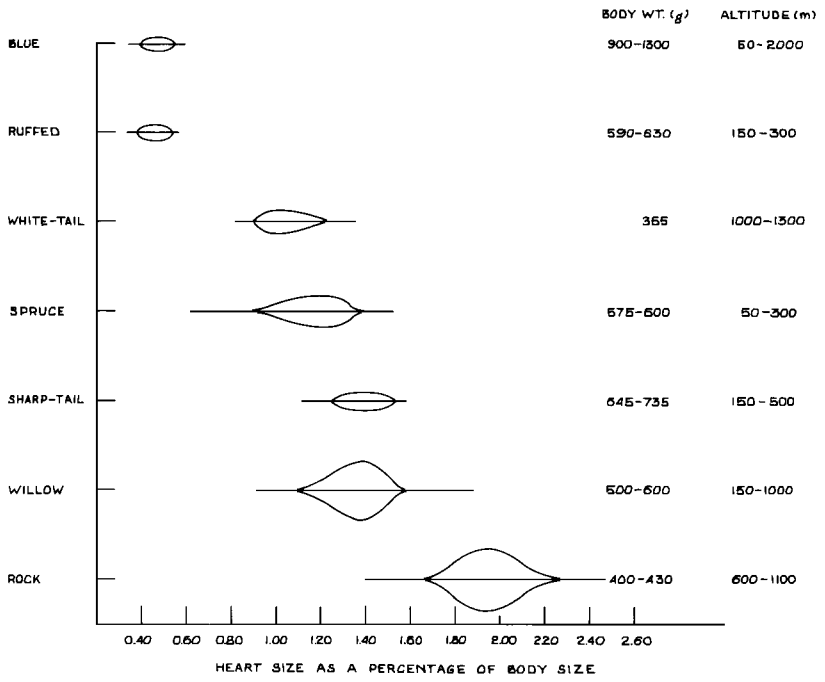

Fig. 4. Comparison of heart ratios of Alaskan tetraonids. The length of each line spans the range of individual variation observed. The thickened portion represents the range of subsample means, and is broadest where subsample means tend to cluster. Where a range of body weights is given, the smaller figure represents the mean for females and the larger the mean for males.

clining total energy demand. Demands of migration or dispersal may be reflected in rising heart ratios.

The rapid changes in heart ratios among Spruce Grouse and Rock Ptarmigan chicks, however, are probably more closely related to major shifts in other aspects of cardiovascular function. As Odum (1941) pointed out, the total cardiac output of blood may decrease in chicks during a particular phase of their growth as heart ratio decreases and heartbeat frequency stays the same. At this time the oxygen exchange capacity of the blood may be doubling or tripling because of increasing hemoglobin content and erythrocyte count. Hence net cardiovascular performance is probably improving even while relative heart size is temporarily decreasing.

This study has demonstrated extreme differences in relative heart size among the seven Tetraonidae found in Alaska (Fig. 4). Blue and Ruffed grouse heart ratios are among the lowest known in birds, whereas Rock Ptarmigan heart ratios are among the highest.

It is obvious that body size, altitude of living quarters, or general body activity levels, taken alone, do not explain the ranking by heart ratios of Alaskan tetraonids. Ruffed Grouse and White-tailed Ptarmigan have much smaller hearts than would be expected on the basis of their size in comparison with other members of the family. White-tailed Ptarmigan have smaller hearts, and Spruce and Sharp-tailed grouse have larger hearts, than would be expected according to altitudinal rankings. And in terms of general body activity there seems no good reason why Willow

Ptarmigan should have heart ratios significantly smaller than Rock Ptarmigan, or why Spruce and Sharp-tailed grouse should have heart ratios two to three times those of Ruffed and Blue grouse.

These anomalies strongly suggest that different tetraonids have evolved very different total cardiovascular strategies to meet what may appear to be fairly similar energy demands. Norris and Williamson (1955) reached the same conclusion about Pygmy Nuthatches (*Sitta pygmaea*) and Brown-headed Nuthatches (*S. pusilla*). As Brush (1966) pointed out, heart rate is the other component of this system that is likely to vary among as well as within species. Other cardiovascular elements cannot be ignored. For example, myoglobin levels must be much lower in Blue and Ruffed grouse than in the ptarmigans and Spruce Grouse, judging from the color of pectoral, wing, and leg muscles in these species. Perhaps erythrocyte or hemoglobin levels vary among tetraonids too. The whole question is an intriguing area for future physiological research.

The collector of gross heart size data has, at least for the time being, contributed as much as he or she is likely to until a second generation of questions comes back from the laboratory.

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