HEART WEIGHT IN BIRDS

By FRANK A. HARTMAN

Since the heart is the source of power for the circulation, its relative size indicates the capacity to move the blood. Determinations of heart weights in relation to body weights have been made in vertebrates, especially birds, by a number of investigators over the years. Many of the values reported have been based on single specimens and a majority are Old World species.

In collecting material for other studies we have accumulated a considerable amount of data on the heart weights of birds taken in the United States and Panamá. Our material confirms some of the old ideas and suggests problems for further research. Moreover, data on many birds not published hitherto are recorded.

METHODS

All except small birds were weighed in the field soon after shooting, on one of the following Chatillon spring balances, the most sensitive one for the weight involved being used: 6000 grams capacity with 24 grams sensitivity; 2000 grams capacity with 25 grams sensitivity; 500 grams capacity with 10 grams sensitivity; 100 grams capacity with 0.25 grams sensitivity (a very long balance, made for the purpose). Small birds were weighed at camp on a torsion balance of 120 grams capacity and 2 mgm. sensitivity.

While in the field, immediately after weighing, the birds were enclosed in plastic bags to prevent drying. In camp the hearts were removed after cutting the blood vessels close to the organ. Blood was expressed by gentle pressure on cotton or filter paper through slits in the ventricles. Weighings were made immediately either on the torsion balance or, in the case of hearts little more than a gram in weight, on a Roller-Smith balance with a capacity of 1500 mg. and sensitivity to 0.02 mg. All weights are from adult birds unless otherwise stated. None but healthy, well nourished birds were used.

Nomenclature is based largely on Peters' check-list (1931–1951) and on the check-list of the American Ornithologists' Union (1931) for North American passerine species.

All Panamanian birds were collected during the dry season, January through March, at the following stations: Juan Mina on the Chagres River; La Jagua River east of Panama City; Mount Copete (7000 feet) above Boquete; Palo Santa near the village of El Volcán (4000 feet); and Santa Clara, 15 miles from the Costa Rican border on the Pan-American highway (4500 feet). Florida birds were collected in January and February or June and July on Lake Okeechobee, in the Everglades, around islands off the Gulf coast, and on the prairies of the peninsula. Birds from Maine were obtained at Lake Kezar in June, July, August and September. Birds from Ohio were collected at various times throughout the year. Most specimens were obtained in the morning before 11 a.m. or in the late afternoon.

ACKNOWLEDGMENTS

First we wish to thank Dr. Michael M. Clay for calculating many of the data. We are very much indebted to Mr. Richard Archbold of the Archbold Biological Station, Florida, for his personal assistance in the collection of material and for the use of the facilities of the Archbold Biological Station. In Panamá our studies in the Canal Zone were based at the Juan Mina Field Station of the Gorgas Memorial Institute through the good offices of Dr. H. C. Clark. Mr. Pablo Brackney kindly granted us the use of a cottage at El Volcán and Mr. Toliffe Mönniche aided us on our expedition on Mount

Copete above Boquete. Mr. James Zetek at the Barro Colorado Island Laboratory was very helpful at all times with invaluable advice. Above all we wish to thank Dr. Alexander Wetmore for the identification of most of the Panamanian birds. This study was aided by grants from the Comly Fund and the Graduate School of the Ohio State University.

RESULTS

More than 1340 hearts were weighed among 291 species and subspecies in 64 families. The percentage of heart weights were calculated using body weights from the respective individuals from which the hearts were obtained. The list (p. 227 ff.) shows the number of individuals in each species, the mean values, standard errors of the means, or the individual values if the series is small. Sexes are separated for body weights but not for hearts. Representative members of each family are plotted in figure 1, the scales being logarithmic, the heart weights being in milligrams and the body weights being in grams. The species starred in the list are shown in figure 1.

It can be noted in the figure that the values tend to follow a straight line down to a body weight of about 200 grams and then follow another less steep line below this value.

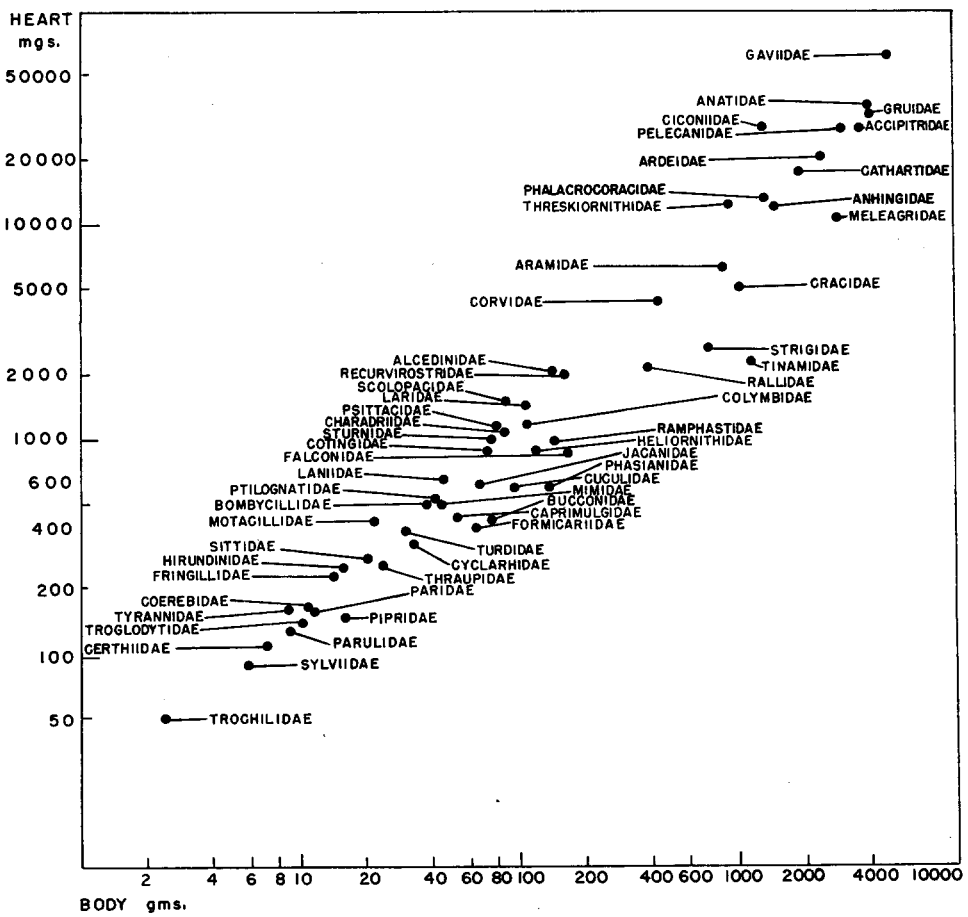

Fig. 1. Selected plottings of heart weights against body weights (log scales).

In other words, smaller birds have relatively larger hearts than do larger birds. With exceptions to be discussed, the bird heart seems to follow a logarithmic relationship to body size. Deviations from this can best be noted in the list.

Among the families there are great differences, the heart weight ranging from a little more than 0.2 per cent to 2.4 per cent of the body. Wide differences may be found between species in the same family. Differences between closely related species may appear to be significant but further data and analysis may prove them not to be.

The tinamous have relatively the smallest hearts of all birds, 0.2 per cent or slightly above. Following down the list, the pelican appears to have a smaller heart than the cormorant but the difference is questionably significant ($P<0.05$). Anhinga hearts are significantly larger than those of the pelican ($P<0.01$). Among the herons there was a significant difference between hearts of the Great Blue Heron of Florida and those of the Louisiana Heron, the latter being larger ($P<0.01$). These last were about the same percentage weight as those of the Anhinga. Among the anatids the heart of *Nomonyx* is much larger than that of other ducks weighed, even *Aythya* ($P<0.01$). There was a significant difference between the hearts of two vultures, those of the Black Vulture being larger than those of the Turkey Vulture ($P<0.01$).

Specimens of the Bald Eagle taken in Florida were young birds which had never been permitted to fly although they were fully feathered. They were but a few months old. The hearts of the Bob-white and Wild Turkey collected in Florida were among the smallest of all birds studied (0.40 per cent of the body). Shore-birds had hearts that were among the largest; especially was this true of the Ruddy Turnstone and the Short-billed Dowitcher. Among the larids the heart of the Roseate Tern is significantly larger than that of the Common Tern ($P<0.01$). Although our data are limited, hearts of columbids showed a considerable range in size, some being among the smallest. In the psittacids the parakeet *Pyrrhura* possessed the largest heart although two specimens of *Brotogeris* had hearts just as large. The cuculids had small hearts as did the large strigids while the Burrowing Owl of Florida possessed a larger heart. The trochilids possessed the largest hearts of all birds. The hearts of kingfishers were fairly large, being 1.25 to 1.39 per cent of the body. Toucans with hearts 0.65 to 0.74 per cent of the body were among those with small hearts. Picid hearts varied greatly in size, those of the smaller species being relatively larger.

The range of heart size was great among the formicarids, being from about 0.57 (*Taraba major*) to 1.16 per cent (*Dysithamnus*) of the body. The range among the dendrocolaptids was still greater, being from 0.78 per cent to 1.61 per cent. The hearts of the swallows were among the largest. The hearts of the Cedar Waxwing and Red-eyed Vireo were especially large (1.55 per cent). The larger heart of the Red-eyed Vireo compared with that of the White-eyed Vireo was of questionable significance since $P<0.05$. The largest parulid, the Chat, possessed one of the smallest hearts in this family (1.01 per cent). In the tanagers the heart values tended to be low, few being more than 1.30 per cent and half of them less than 1.0 per cent. These differences may be too great to be explained by body size.

Obviously there are factors other than body size that influence the relative size of the heart. These may be sex, age, activity, season, climate and altitude. We shall consider these in turn and in the terminal discussion.

Sex.—Heart percentages were separated as to sex in all preliminary calculations, but since no significant differences were found all values were combined. Even in those species which show considerable sexual difference in the body weight, the heart is of the same relative size. For example, among the icterids we have the following data:

	Sex	Body weights in grams	Number	Heart percentage
Sturnella magna	♀	76.0±3.2	4	1.09±0.071
	♂	101.5±2.5	14	1.16±0.026
Cassidix mexicanus	♀	98.0±3.3	3	0.97
	♂	185.8±7.7	6	1.02
Agelaius phoeniceus	♀	30.3	2	1.13
	♂	48.7	2	1.06

Age.—Heart weights were determined in nestlings of a few species. A large series of Brown Pelicans only a few weeks of age and ranging in weight from 1100 to 3600 grams had the same relative heart weight as the adults (see list, p. 227). Even the hearts of very young pelicans, 1100 to 1500 grams in weight, had practically the same range (mean, 0.84 per cent) as the remaining 64 weighing from 1600 to 3600 grams (mean, 0.81 per cent). Furthermore, there was no difference between sexes. Also a considerable series of young Double-crested Cormorants was weighed, ranging in size between 675 and 1500 grams. The relatively larger value for the hearts in the adult birds was of questionable significance since $P<0.05$.

In addition to the adult Great Blue Herons three very young birds from the same nest were weighed. Their body weights and heart percentages were: 575 grams, 0.76 per cent; 1300 grams, 0.78 per cent; and 1550 grams, 0.85 per cent. The first two were appreciably smaller than the mean for the eight adults ($P<0.01$).

Four young Common Terns not included in the list gave a greater range in relative size of the hearts than did the adults. Their bodies weighed 63, 73, 86, and 87 grams while their hearts were, respectively, 0.79, 1.26, 1.16, and 0.89 per cent. One half-grown pigeon (*Columba albilinea*; 140 gm.) possessed a smaller heart (0.52 per cent) relatively than the adults (1.09 per cent).

Two nestling Striped Horned Owls possessed hearts approximately the same relative size as the adult. Three young specimens (160, 190, and 200 grams, body weight) of the Pileated Woodpecker of Florida from the same nest had relatively smaller hearts than did the adult (0.67, 0.76, and 0.79 per cent as against 0.98 per cent, respectively).

One young Red-eyed Towhee (38.1 grams) possessed a much smaller heart (0.60 per cent) than the adult. Two young Swamp Sparrows (15.9 and 16.5 grams) that could fly had hearts somewhat smaller (0.95 and 0.99 per cent) than the adults (1.19 per cent) whereas a young Song Sparrow weighing 20.2 grams possessed a heart 1.04 per cent of the body compared to 1.18 per cent for the adults. However, birds not nearly grown sometimes possessed hearts of almost the same relative size as adults. The heart of a female Mourning Dove weighing only 47 grams was 1.08 per cent of the body. One young Cowbird weighing 31.5 grams possessed a heart only 1.07 per cent of the body weight. Occasionally fully fledged birds of the year (cranial bones still soft) have been weighed, and their hearts have been found to be adult in size relative to the body.

More information is needed as to the relative size of the heart at different ages in the growth of the young birds for different species. The magnitude of the difference may be expected to vary in different species.

Activity.—Activity may have an important influence on heart size. Thus, trochilids, among the most active of birds, have by far the largest hearts (Hartman, 1954, and list). Likewise many other small birds are more active than larger birds. Among the relatively large hearts are those of the parulids, certhiids, parids, vireonids, and hirundinids. Equally large in relation to size were the hearts of some charadriids, scolopacids and recurvirostrids. These are rather active birds and not very large.

Among the parulids the heart ranges extended from a little more than 1 per cent to 1.58 per cent, being lowest in the Chat. This low value may be of questionable signifi-

cance, however, P for the difference between the Chat and the Redstart being <0.05. The latter species is smaller and more active than the former. In the icterids the heart range is great, varying from 0.62 to 1.49 per cent. The Cowbird has a relatively larger heart than does the Meadowlark (P<0.01) or the Boat-tailed Grackle (P<0.01). Fringillids show differences that might be attributed to activity and size. The Indigo Bunting possesses a larger heart in relation to the body weight than does the Towhee (P<0.01). The heart of the Savannah Sparrow is significantly larger than that of the Towhee (P<0.01), but the heart of the Savannah Sparrow is not larger than that of the Swamp Sparrow, according to our data, t being 2.0 (5 per cent = 2.20).

The smaller woodpeckers possess somewhat larger hearts than do the large ones. The hearts of the Yellow-bellied Sapsucker and Downy Woodpecker were among the largest. The hearts of kingfishers were fairly large, being 1.25 to 1.39 per cent of the body. These birds are quite active.

Seasonal variation.—Although we do not have enough data on any one species for adequate proof, the combined data from several species strongly indicate that the hearts are relatively lighter during the colder months of the year in some species. This is shown in table 1.

In nine species the difference was too small to indicate a definite trend or there was no difference, as the following examples show. Green Herons taken in Florida showed an average of 0.916 per cent for the heart in six specimens collected in January, February, and March whereas the average of the heart in five specimens collected in April, May, and June was 0.956 per cent. Turkey Vultures from Florida showed an average of 0.68 per cent for the heart in seven specimens collected in December, January, and February, whereas five specimens collected in April and May had hearts averaging 0.75 per cent of the body weight. Six specimens of Killdeer collected during February in Florida had hearts averaging 1.31 per cent of the body weight, whereas two specimens collected during June in Ohio had hearts averaging 1.49 per cent. The difference is not significant since the range is too great for the small number of individuals. Four specimens of the Red-bellied Woodpecker obtained in January had hearts averaging 1.09 per cent of the body weight whereas five collected in March, April, and October had hearts averaging 1.29 per cent. However, the range in each group is so great that the difference is not significant.

Table 1
Comparison of Heart/Body Ratio

Species	Cool season, November through March			Warm season, April through October		
	Body no.	Av. gm.	Heart Avge. per cent	Body no.	Av. gm.	Heart Avge. per cent
Fulica americana	2	594	0.59	1	485	0.80
Aramus pictus	1	89	0.65	1	85	0.82
Actitis macularia	1	38	0.95	1	45	1.16
Archilochus colubris	2	3.2	2.13	1	3.05	2.62
Dendrocopos borealis	5	39.8±0.62	1.21±0.05	3	52	1.38
Parus bicolor	1	22.2	1.31	4	22.4±0.6	1.65±0.15
Sitta carolinensis	4	20.48±0.69	1.22±0.004	3	20.3	1.47
Troglodytes aëdon	1	9.8	1.10	2	11.05	1.47
Dumetella carolinensis	1	37	0.73	1	42.4	1.18
Toxostoma rufum	1	59.5	0.87	2	70.4	1.08
Sialia sialis	9	31.11±3.17	1.18±0.04	2	30.5	1.36
Polioptila caerulea	1	5.5	1.14	2	5.5	1.48
Lanius ludovicianus	4	45.5±1.9	1.26±0.07	3	49	1.47
Richmondena c. cardinalis	3	43.3	1.16	3	41.4	1.53
Richmondena c. floridana	2	39	0.81	3	35.3	1.00
Spizella passerina	1	11.0	1.18	1	14	1.32

Four species possessed hearts of about the same percentage in cold and warm weather. In the Yellow-bellied Sapsucker one specimen collected in January had a heart that was 1.40 per cent of the body weight whereas three obtained in August and September also had an average of 1.40 per cent. Six winter specimens of Scrub Jay (January, February) had hearts averaging 1.04 per cent, and seven spring specimens (March and April) had hearts averaging 1.08 per cent. Two January specimens of Red-eyed Vireo had hearts that were 1.51 per cent of the body weight, and nine summer specimens (August, September) had hearts averaging 1.55 per cent of the body weight. The Towhees of Florida showed little difference in the winter (January, February) as compared with spring (March, April) specimens. Seven birds obtained in the first period possessed hearts that were 0.84 per cent of the body weight and six specimens collected in the latter period had hearts averaging 0.80 per cent. Ten January and February specimens of Eastern Meadowlark possessed hearts 1.18 per cent of the body weight, whereas eight April specimens had hearts 1.11 per cent of the body. The difference was not significant.

Thus, of 25 species for which we have seasonal data, 16 indicated relatively smaller hearts in cold weather and 9 showed insignficant or no differences. In general, when there is a difference, our data suggest that warm seasons are associated with larger hearts in the same species.

Climate.—A factor which might influence heart size is climate. However, this is difficult to evaluate because of complex inherent differences between species which obscure possible correlations with climate. However, there are a few subspecies or closely related species for which we have data. There is a significant difference in heart size between the Double-crested Cormorant of Florida and the Olivaceus Cormorant, the percentage values being 0.839 and 0.70, respectively ($P<0.01$). There may be a difference between the hearts of the northern and Floridan races of the Pileated Woodpecker. An average of 1.20 per cent for the former and 0.98 per cent for the latter indicates as much, but more data are needed. The difference between the hearts of the Black-capped Chickadee and the Carolina Chickadee may be significant ($P<0.05$). Likewise, hearts of *Vireo carmioli* are smaller (1.0 per cent) than those of all of the northern vireos (1.32 to 1.68 per cent). Two of the tropical wrens shown (*Thryothorus and Henicorhina*) have smaller hearts (0.72 to 0.93 per cent) than the northern members of the family (*Troglodytes* and *Telmatodytes,* 1.10 to 1.53 per cent). The Red-eyed Towhee has a questionably larger heart than that of the white-eyed race of the species in Florida (1.24 ± 0.14, compared to 0.843 ± 0.03 per cent; $P<0.05$). The hearts of the Florida race of the Cardinal are significantly smaller than hearts of the nominate race of Ohio ($P<0.01$). Thus, we see that our limited data indicate that the hearts of some species in warm climates are relatively smaller than those of related northern species.

Altitude.—In species which live at high altitudes the hearts may be larger than related forms found at lower levels. This may account for the larger heart (1.32 per cent) of the Quetzal as compared with other trogons. The heart of the former is questionably larger ($P<0.05$) than that of *T. massena* and significantly larger than that of *T. collaris* ($P<0.01$). The Quetzal rarely goes below 5000 feet whereas the others are found lower.

LIST OF BODY WEIGHTS AND RELATIVE WEIGHTS OF HEARTS

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
TINAMOUS			
Tinamus major (Pan.)	*2 ♀, 1140, 1175	2	0.195, 0.219
Nothocercus bonapartei (Pan.)	1 ♀, 455; 1 ♂, 500	2	0.21, 0.23
LOONS			
Gavia immer (Maine)	1 ♀, 2544; *1 ♂, 4880	2	1.10, 1.33
GREBES			
Poliocephalus dominicus (Pan.)	*6 ♀, 113.3±3.9; 8 ♂, 129.8±4.6	8	1.09±0.06
Podilymbus podiceps (Fla.)	2 ♀, 312, 375; 2 ♂, 375, 500	1	1.18
PELICANS			
Pelecanus occidentalis (Fla.)	*42 ♀, 3148±41.5; 53 ♂, 3636±42.5	12	0.815±0.022
	76 (young, 1100–3600	76	0.816±0.008
CORMORANTS			
Phalacrocorax auritus (Fla.)	*36 ♀, 1541±1.1; 30 ♂, 1810±5.4	7	0.893±0.039
	41 (young), 675–1500	41	0.824±0.017
Phalacrocorax olivaceus (Pan.)	1 ♀, 1000; 4 ♂, 1100, 1180, 1320, 1500	2	0.67, 0.72
SNAKEBIRDS			
Anhinga anhinga (Fla.)	6 ♀, 1257±41.2; *6 ♂, 1249.5±58	8	1.018±0.035
HERONS			
Ardea herodias herodias (Ohio)	1 ♀; 2040	1	1.00
Ardea herodias wardi (Fla.)	*4 ♀, 2213, 2300, 2385, 2950; 7 ♂, 2646±134	8	0.88±0.03
Casmerodius albus (Pan.)	2 ♀, 825, 952; 9 ♂, 937.4±36	5	0.82±0.04
Hydranassa tricolor (Fla.)	2 ♀, 325, 360; 18 ♂, 444±10.2	13	0.99±0.04
Florida caerulea (Fla.)	8 ♀, 315±10.4; 11 ♂, 364±14.2	3	0.67, 0.68, 0.69
Butorides virescens (Fla.)	11 ♀, 215.2±5.0; 7 ♂, 212.0±7.4	11	0.94±0.02
Agamia agami (Pan.)	1 ♀, 475; 2 ♂, 525, 550	1	0.72
Nycticorax nycticorax (Fla.)	4 ♀, 675, 795, 800, 850; 6 ♂, 810±34	6	0.90±0.05
Nyctanassa violacea (Fla.)	7 ♀, 649±16.3; 8 ♂, 716±18.3	13	0.86±0.037
Tigrisoma lineatum (Pan.)	1 ♂, 930	1	0.73
Heterocnus cabanisi (Pan.)	1 ♂, 1025	1	0.75
Ixobrychus exilis (Ohio)	3 ♀, 73, 80, 95; 8 ♂, 78.2±5.25	2	0.81, 0.85
STORKS			
Mycteria americana (Fla.)	*4 ♂, 3050, 3150, 3220, 3300	4	0.79, 0.95, 0.97, 1.01
IBISES			
Guara alba (Fla.)	9 ♀, 715±24.3; *10 ♂, 952±27.9	13	1.12±0.03
DUCKS			
Cairina moschata (domestic)	*9 ♂, 4026±241	9	0.95±0.05
Anas fulvigula (Fla.)	1 ♀, 880; 2 ♂, 1100, 1122	2	0.89, 1.00
Aythya affinis (Fla.)	2 ♀, 500, 511; 5 ♂, 601±39.5	4	0.82, 0.82, 0.88, 0.92
Nomonyx dominicus (Pan.)	1 ♀, 360; 1 ♂, 410	2	1.24, 1.36
VULTURES			
Sarcorhamphus papa (Pan.)	2 ♂, 3100, 3350	2	0.77, 0.84
Coragyps atratus (Fla.)	*6 ♀, 2172±48; 6 ♂, 1989±32.4	6	0.90±0.05
Coragyps atratus (Pan.)	1 ♀, 2000; 2 ♂, 1400, 1675	3	0.64, 0.73, 0.86
Cathartes aura (Fla.)	4 ♀, 1662±118; 10 ♂, 1479±60	12	0.71±0.03
Cathartes aura (Pan.)	2 ♀, 1275, 1800; 3 ♂, 1140, 1175, 1175	5	0.67±0.04
HAWKS			
Buteo jamaicensis (Pan.)	1 ♀, 1100	1	0.55
Buteo lineatus (Fla.)	8 ♀, 638±35.5; 5 ♂, 522±38.7	7	0.73±0.05
Buteo platypterus (Pan.)	3 ♀, 365, 398, 398; 7 ♂, 324±17.7	2	0.57, 0.61

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
Hypomorphnus urubitinga (Pan.)	1 ♀, 1250	1	0.50
Haliaeetus leucocephalus (Fla.)	*2 ♀, 3630, 3812	2	0.76, 0.84
FALCONS			
Micrastur ruficollis (Pan.)	*1 ♀, 170; 1 ♂, 165	2	0.57, 0.59
Polyborus cheriway (Pan.)	5 ♀, 930±18; 8 ♂, 882±55	1	0.90
Falco columbarius (Fla.)	1 ♀, 185	1	1.66
Falco sparverius (Fla.)	5 ♀, 114.7±6.6	1	1.27
CURASSOWS AND GUANS			
Chamaepetes unicolor (Pan.)	4 ♀, 1150, 1205, 1226, 1325; *5 ♂, 1095±63	5	0.49±0.02
QUAILS			
Colinus virginianus (Fla.)	1 ♀, 150; *5 ♂, 142±4.8	6	0.39±0.02
Odontophorus guttatus (Pan.)	3 ♀, 250, 280, 280; 6 ♂, 312±8.4	2	0.345, 0.375
TURKEYS			
Meleagris gallopavo (Fla.)	*2 ♀, 2900, 3000	2	0.39, 0.40
CRANES			
Grus canadensis (Fla.)	*1 ♀, 4110; 1 ♂, 5375	2	0.70, 0.86
LIMPKINS			
Aramus scolopaceus (Fla.)	*2 ♀, 851, 890; 2 ♂, 1000, 1225	4	0.65, 0.65, 0.76, 0.82
RAILS, GALLINULES, COOTS			
Aramides cajanea (Pan.)	*5 ♀, 355±32.8; 2 ♂, 350, 420	3	0.50, 0.51, 0.61
Laterallus albigularis (Pan.)	1 ♀, 44; 1 ♂, 58.5	2	0.57, 0.64
Gallinula chloropus (Fla.)	2 ♀, 275, 300; 4 ♂, 275, 275, 300, 400	1	1.07
Porphyrula martinica (Fla.)	7 ♀, 216±6.6; 5 ♂, 259.6±11.6	3	0.47, 0.57, 0.61
Fulica americana (Ohio)	7 ♀, 443±24.7; 8 ♂, 543.6±26.2	3	0.56, 0.62, 0.82
SUN GREBES			
Heliornis fulica (Pan.)	*1 ♀, 125; 1 ♂, 143	1	0.72
JACANAS			
Jacana spinosa (Pan.)	6 ♀, 107±8.6; *11 ♂, 77±0.8	8	0.82±0.01
PLOVERS			
Charadrius vociferus (Ohio)	6 ♀, 83.3±2.2; 6 ♂, 81.6±4.8	8	1.35±0.05
Charadrius wilsonia (Pan.)	*6 ♀, 87.4±2.8; 5 ♂, 89.5±3.9	11	1.27±0.03
SANDPIPERS			
Tringa flavipes (Fla.)	3 ♀, 100, 105, 136; 4 ♂, 70, 80, 85, 110	2	1.24, 1.45
Tringa melanoleuca (Fla.)	2 ♀, 186, 250; 5 ♂, 200.8±5.9	1	1.21
Actitis macularia (Fla.)	2 ♀, 38, 45	2	0.95, 1.16
Arenaria interpres (Fla.)	*8 ♀, 107±4.5; 12 ♂, 118±5.8	7	1.55±0.05
Limnodromus griseus (Fla.)	3 ♀, 105, 105, 110; 6 ♂, 98±2.3	7	1.53±0.07
Capella gallinago (Fla.)	1 ♀, 100; 1 ♂, 88	2	1.33, 1.34
Erolia minutilla (Fla.)	2 ♂, 18.5, 20.2	2	1.34, 1.46
Erolia melanotos (Fla.)	1 ♂, 74	1	1.70
STILTS AND AVOCETS			
Himantopus himantopus (Fla.)	4 ♀, 155±7.4; *7 ♂, 169±2.5	10	1.27±0.04
GULLS AND TERNS			
Larus atricilla	8 ♀, 306±24.4; 19 ♂, 294±5.7	3	0.73, 0.93, 0.98
Gelochelidon nilotica (Fla.)	1 ♂, 150	1	0.94
Chlidonias nigra (Fla.)	3 ♂, 54, 55, 55	2	1.16, 1.20
Sterna hirundo (Fla.)	5 ♀, 102±2.2; 7 ♂, 108±3.6	10	1.04±0.05
Sterna forsteri (Fla.)	3 ♀, 115, 120, 123; 1 ♂, 128	1	1.22
Sterna dougallii (Fla.)	7 ♀, 106.7±1.9; *4 ♂, 100, 110, 110, 112	4	1.34±0.04
Thalasseus maximus (Fla.)	9 ♀, 451±19.7; 6 ♂, 440±11.3	6	1.13±0.09

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
PIGEONS AND DOVES			
Columba albilinea (Pan.)	2 ♀, 300, 300; 5 ♂, 304±12.6	7	1.09±0.04
Zenaidura macroura (Ohio)	6 ♀, 109±1.0; 4 ♂, 131±6.3	3	1.11, 1.15, 1.37
Columbigallina passerini (Fla.)	1 ♀, 38.0; 1 ♂, 39.8	2	1.22, 1.22
Leptotila verreauxi (Pan.)	10 ♀, 149.3±4; 10 ♂, 156.3±4.6	5	0.88±0.02
Leptotila cassini (Pan.)	1 ♀, 155; 1 ♂, 175	2	0.54, 0.59
Oreopelia chiriquensis (Pan.)	3 ♀, 300, 305, 325; 5 ♂, 273±24	3	0.33, 0.42, 0.42
PARROTS			
Pyrrhura hoffmanni (Pan.)	14 ♀, 80.8±0.5; *10 ♂, 82.7±1.3	7	1.48±0.01
Brotogeris jugularis (Pan.)	3 ♀, 62.8, 64, 71; 7 ♂, 60.4±2.3	4	1.18, 1.26, 1.50, 1.53
Pionus senilis (Pan.)	1 ♀, 212; 2 ♂, 210, 220	1	1.12
Amazona autumnalis (Pan.)	2 ♀, 370, 390; 1 ♂, 425	1	1.16
CUCKOOS			
Coccyzus americanus (Ohio)	2 ♀, 56.69; 3 ♂, 44, 62, 63	4	1.0, 1.08, 1.17, 1.24
Piaya cayana (Pan.)	8 ♀, 111±2.3; 8 ♂, 104.6±3.2	9	0.61±0.02
Crotophaga major (Pan.)	3 ♀, 132, 140, 141; 5 ♂, 151.4±5.6	4	0.62, 0.66, 0.71, 0.80
Crotophaga ani (Pan.)	9 ♀, 87.7±3.4; *13 ♂, 102±2.1	11	0.57±0.03
Tapera naevia (Pan.)	1 ♀, 35.5; 5 ♂, 55±1.1	2	0.72, 0.80
OWLS			
Otus choliba (Pan.)	1 ♀, 180	1	0.52
Bubo virginianus (Ohio)	1 ♀, 1248; 1 ♂, 1040	2	0.46, 0.51
Pulsatrix perspicillata (Pan.)	*1 ♂, 800	1	0.34
Speotyto cunicularia (Fla.)	4 ♀, 130, 150, 157, 170; 4 ♂, 130, 150, 170, 170	6	0.89±0.01
Strix varia (Ohio)	2 ♀, 681, 771; 1 ♂, 642	1	0.53
Strix varia (Fla.)	1 ♀, 875; 3 ♂, 681, 750, 800	3	0.60, 0.61, 0.68
Rhinoptynx clamator	2 ♀, 400, 475; 2 ♂, young 305, 335	1	0.39
		2	0.42, 0.44 (young)
POTOOS			
Nyctibius griseus (Pan.)	3 ♀, 180, 183, 187; 3 ♂, 150, 167, 190	5	0.58±0.08
GOATSUCKERS			
Nyctidromus albicollis (Pan.)	6 ♀, 49.4±0.8; *9 ♂, 52.5±2.1	6	0.73±0.06
HUMMINGBIRDS			
Campylopterus hemileucurus (Pan.)	3 ♂, 11.2, 11.3, 13.3	3	1.87, 1.96, 2.01
Selasphorus scintilla (Pan.)	*9 ♀, 2.23±0.07; 3 ♂, 2.1, 2.15, 2.75	11	2.40±0.12
TROGONS			
Pharomachrus mocino (Pan.)	3 ♀, 170, 186, 210; 3 ♂, 188, 190, 200	4	1.32±0.06
Trogon massena (Pan.)	4 ♀, 127, 128, 130, 140; 5 ♂, 137±7.6	4	1.07±0.09
Trogon collaris (Pan.)	6 ♀, 65±2; 13 ♂, 66±1.3	12	1.02±0.03
Trogon violaceus (Pan.)	1 ♀, 69.8; 3 ♂, 56.3, 61.3, 68	2	1.00, 1.10
KINGFISHERS			
Megaceryle alcyon (Ohio)	*8 ♀, 146±3.7; 9 ♂, 191±3.3	11	1.39±0.04
Chloroceryle americana (Pan.)	3 ♂, 36.1, 36.8, 38.7	1	1.25
Chloroceryle aenea (Pan.)	1 ♀, 15.1	1	1.32
PUFFBIRDS			
Notharchus macrorhynchos (Pan.)	1 ♀, 80; *3 ♂, 89, 96, 103	1	0.56
TOUCANS			
Aulacorhynchus prasinus (Pan.)	*9 ♀, 145.4±5.5; 6 ♂, 153.7±6.1	10	0.65±0.03
Pteroglossus torquatus (Pan.)	8 ♀, 256.6±5.4; 11 ♂, 262±9.4	7	0.74±0.02
Ramphastos swainsonii (Pan.)	4 ♀, 600±10.6; 1 ♂, 680	2	0.68, 0.70

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
WOODPECKERS			
Colaptes auratus (Fla.)	4 ♀, 92, 95, 99, 120; 2 ♂, 108, 120	6	1.22±0.08
Dryocopus pileatus abieticola (Maine)	3 ♀, 239, 260, 289	2	1.15, 1.24
Dryocopus pileatus floridanus (Fla.)	1 ♂, 250	1	0.98
Dryocopus lineatus (Pan.)	2 ♀, 187, 200; 2 ♂, 165, 167	1	1.18
Melanerpes formicivorus (Pan.)	3 ♀, 74.5, 75, 78.2; 4 ♂, 69, 77, 78, 80	3	0.92, 1.11, 1.22
Centurus carolinus (Ohio)	10 ♀, 61.4±1.7; 9 ♂, 76±2.4	9	1.20±0.05
Centurus rubricapillus (Pan.)	8 ♀, 48.7±0.8; 17 ♂, 55±0.7	8	1.21±0.02
Sphyrapicus varius (Ohio)	3 ♀, 45, 47, 48; 14 ♀, 41±1.1	4	1.42±0.04
Dendrocopos villosus (Maine)	12 ♀, 63±1.4; 11 ♂, 73±1.1	9	1.23±0.03
Dendrocopos pubescens (Ohio)	19 ♀, 28±0.05; 23 ♂, 26±0.04	3	1.33, 1.34, 1.44
Dendrocopos borealis (Fla.)	4 ♀, 45.3±3.5; 5 ♂, 42.4±3.2	8	1.27±0.05
Phloeoceastes guatamalensis (Pan.)	6 ♀, 233.3±4.9; 3 ♂, 222, 255, 260	2	0.97, 1.00
WOODHEWERS			
Xiphorhynchus erythropygius (Pan.)	5 ♀, 45.5±1.0; 1 ♂, 47	2	0.87, 0.96
Xiphorhynchus nanus (Pan.)	3 ♀, 44, 45, 46; 3 ♂, 46, 49, 49	3	0.70, 0.81, 0.82
Lepidocolaptes affinis (Pan.)	3 ♀, 33.2, 33.5, 33.6; 3 ♂, 33.5, 35.5, 38	6	0.92±0.05
Sittasomus griseicapillus (Pan.)	3 ♀, 12.2, 12.5, 13.0; 6 ♂, 14.2±0.25	2	1.24, 1.43
Dendrocincla homochroa (Pan.)	3 ♀, 35.7, 36.2, 43.5; 1 ♂, 49	2	1.52, 1.71
OVENBIRDS			
Synallaxis brachyura (Pan.)	1 ♂, 21.1	1	1.02
Margarornis rubiginosus (Pan.)	1 ♂, 16.1	1	0.97
Pseudocolaptes lawrencei (Pan.)	1 ♀, 50.7; 1 ♂, 55	2	1.13, 1.22
Premnoplex brunnescens (Pan.)	2 ♂, 15, 15.3	2	0.97, 1.01
Anabacerthia striaticeps (Pan.)	1 ♀, 22; 1 ♂, 22.1	2	1.30, 1.34
ANTBIRDS			
Taraba major (Pan.)	*4 ♀, 62, 65.7, 66.7, 73.8; 1 ♂, 69	4	0.50, 0.52, 0.58, 0.67
Thamnophilus doliatus (Pan.)	5 ♀, 28.1±0.5; 7 ♂, 28.2±0.5	5	0.63±0.05
Dysithamnus mentalis (Pan.)	4 ♀, 13.9, 14.3, 14.9, 15; 5 ♂, 14.4±0.2	6	1.16±0.05
Myrmotherula schisticolor (Pan.)	4 ♀, 8.9, 9, 9, 10; 2 ♂, 9, 9.7	1	1.10
Cercomacra nigricans (Pan.)	2 ♀, 15.2, 16.2; 3 ♂, 16.9, 17, 17.8	4	0.68, 0.73, 0.74, 0.87
Myrmeciza longipes (Pan.)	1 ♀, 27.8; 4 ♂, 29, 29.2, 30.5, 32	2	0.57, 0.59
Gymnopithys bicolor (Pan.)	3 ♀, 27.8, 28.5, 29.5; 1 ♂, 29	2	1.03, 1.17
MANAKINS			
Manacus vitellinus (Pan.)	*7 ♀, 17.5±0.3; 6 ♂, 20.1±0.7	7	0.93±0.02
Schiffornis turdinus (Pan.)	1 ♀, 34.1	1	1.49
COTINGAS			
Cotinga ridgwayi (Pan.)	1 ♀, 60.5; 6 ♂, 52.8±1.8	1	1.14
Laniocera rufescens (Pan.)	2 ♀, 41, 52.2; 1 ♂, 38.6	1	1.59
Pachyramphus polychopterus (Pan.)	1 ♀, 20.8	1	1.15
Tityra semifasciata (Pan.)	*1 ♀, 73.2; 1 ♂, 73	2	1.16, 1.23
TYRANT FLYCATCHERS			
Sayornis phoebe (Maine)	6 ♀, 18.9±0.5; 6 ♂, 20.3±0.8	2	1.22, 1.23
Myiozetetes cayenensis (Pan.)	5 ♀, 25.0±1.0; 3 ♂, 27, 27.8, 28	4	0.79, 0.84, 0.85, 0.98
Myiarchus ferox (Pan.)	2 ♀, 29, 30.2; 4 ♂, 29.2, 31.8, 32.5, 33.7	1	0.87

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
Myiarchus tuberculifer (Pan.)	6 ♀, 19.3±0.59; 3 ♂, 19.5, 20.5, 21.0	1	0.81
Myiarchus crinitus (Ohio)	1 ♀, 33.8; 2 ♂, 34.1, 34.8	2	1.14, 1.24
Contopus virens (Ohio)	1 ♀, 15.5; 8 ♂, 14.2±0.4	1	1.53
Empidonax flaviventris (Pan.)	2 ♀, 10, 10.5; 3 ♂, 11.1, 11.2, 11.8	2	0.89, 1.30
Empidonax traillii (Ohio)	4 ♀, 11.5, 12.2, 16.5, 17.3; 6 ♂, 13.56±0.36	8	1.23±0.05
Empidonax minimus (Maine)	5 ♀, 9.22±0.68; 7 ♂, 10.1±0.25	3	1.27, 1.28, 1.52
Mitrephanes phaeocercus (Pan.)	*3 ♀, 8.0, 8.5, 8.6; 3 ♂, 9.1, 9.1, 12.5	3	1.41, 1.60, 2.00
Terenotriccus erythrurus (Pan.)	1 ♀, 8.32; 2 ♂, 16.0, 16.3	1	1.08
Platyrinchus mystaceus (Pan.)	1 ♂, 12.5	1	1.40
Todirostrum cinereum (Pan.)	8 ♀, 6.35±0.13; 5 ♂, 6.37±0.30	4	0.99, 1.00, 1.14, 1.22
Lophotriccus pileatus (Pan.)	2 ♀, 7.0, 7.2; 4 ♂, 7.5, 8.1, 8.4, 8.4	2	0.94, 0.96
Serpophaga cinerea (Pan.)	1 ♀, 7.7	1	1.38
Elaenia flavogaster (Pan.)	4 ♀, 21, 25, 25.8, 26.2; 6 ♂, 23.7±0.56	1	1.27
Pipromorpha oleaginea (Pan.)	2 ♀, 9.6, 9.8	2	1.01, 1.08
SWALLOWS			
Riparia riparia (Maine)	*4 ♀, 12.0, 15.5, 19, 20; 3 ♂, 11, 12.2, 12.8	5	1.42±0.04
Iridoprocne bicolor (Maine)	5 ♀, 22.3±2.3; 10 ♂, 22.9±0.8	4	1.42±0.03
Hirundo rustica (Maine)	6 ♀, 16.5±0.6; 1 ♂, 17.8	4	1.42±0.05
Progne subis (Maine)	6 ♀, 50.7±1.1; 16 ♂, 48.9±1.0	16	1.38±0.04
Pygochelidon cyanoleuca (Pan.)	4 ♀, 9, 9.2, 9.7, 10.1; 6 ♂, 9.8±0.03	5	1.38±0.03
Petrochelidon pyrrhonota (Maine)	4 ♀, 18.5, 19.3, 19.5, 21; 4 ♂, 17.5, 19.3, 23, 23	6	1.42±0.03
Stelgidopteryx ruficollis (Maine)	2 ♀, 13.4, 15.6; 2 ♂, 16.1, 16.2	2	1.49, 1.61
CROWS AND JAYS			
Cyanocitta cristata bromia (Maine)	4 ♀, 85, 88, 90, 98; 1 ♂, 93.6	4	0.90, 0.91, 0.95, 0.96
Cyanocitta cristata cristata (Fla.)	3 ♀, 63, 67, 75; 2 ♂, 72, 78	2	1.00, 1.15
Aphelocoma coerulescens (Fla.)	8 ♀, 70.8±1.4; 8 ♂, 73.9±1.5	13	1.07±0.03
Corvus brachyrhynchos brachyrhynchos (Ohio)	3 ♀, 400, 440, 450; 2 ♂, 340, 445	1	1.20
Corvus brachyrhynchos pascuus (Fla).	*5 ♀, 446±5; 5 ♂, 487±7	10	0.98±0.07
TITMICE			
Parus atricapillus atricapillus (Maine)	21 ♀, 10.9±0.2; *30 ♂, 11.5±0.1	20	1.45±0.02
Parus carolinensis (Ohio)	24 ♀, 9.8±0.1; 13 ♂, 10.6±0.2	4	1.30, 1.30, 1.34, 1.45
Parus bicolor (Ohio)	12 ♀, 20.7±0.4; 17 ♂, 22.4±0.3	5	1.58±0.14
NUTHATCHES			
Sitta carolinensis (Maine)	*21 ♀, 20.8±0.2; 20 ♂, 20.9±0.2	7	1.28±0.06
Sitta canadensis (Maine)	14 ♀, 9.8±0.3; 10 ♂, 10.6±0.3	5	1.47±0.08
CREEPERS			
Certhia familiaris (Ohio)	*4 ♀, 7.3, 8, 8.5, 9.1; 11 ♂, 8.73±0.20	2	1.38, 1.71
WRENS			
Troglodytes aëdon (Ohio)	*4 ♀, 12.2±0.03; 8 ♂, 11.0±0.3	3	1.10, 1.39, 1.53
Troglodytes musculus (Pan.)	1 ♀, 14; 1 ♂, 14.8	2	1.09, 1.24

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
Thryothorus leucotis (Pan.)	3 ♀, 17.2, 18.5, 20.2; 6 ♂, 20.1±0.6	2	0.72, 0.84
Thryothorus modestus (Pan.)	2 ♀, 18, 19	2	0.84, 0.86
Henicorhina leucophrys (Pan.)	1 ♀, 16.8; 4 ♂, 16.7, 17.3, 18.1, 19	1	0.93
Telmatodytes palustris (Ohio)	1 ♀, 11; 2 ♂, 12, 12	3	1.24, 1.27, 1.43
MOCKINGBIRDS			
Mimus polyglottos (Fla.)	*9 ♀, 48±1.6; 9 ♂, 56±1.4	7	1.13±0.03
Dumetella carolinensis (Maine)	8 ♀, 38.9±1.5; 9 ♂, 37.7±1.3	5	1.09±0.05
Toxostoma rufum (Ohio)	2 ♀, 59.5, 71; 7 ♂, 72.2±1.8	3	0.87, 0.99, 1.17
THRUSHES			
Rhodinocichla rosea (Pan.)	1 ♀, 48; 3 ♂, 50, 50.5, 50.8	1	0.62
Turdus migratorius (Ohio)	6 ♀, 81.7±1.8; 12 ♂, 78.7±2.2	1	1.33
Turdus grayi (Pan.)	3 ♀, 70.5, 77, 77.5; 3 ♂, 70, 74, 77.5	3	0.77, 0.87, 1.06
Turdus plebejus (Pan.)	2 ♀, 90, 95; 3 ♂, 66, 79, 89	5	1.18±0.12
Hylocichla guttata (Maine)	*6 ♀, 30.9±2.5; 10 ♂, 31.5±0.5	12	1.21±0.04
Hylocichla fuscescens (Maine)	4 ♀, 29.5, 32.5, 33.5, 34.8; 8 ♂, 32.1±1.1	2	1.21, 1.61
Catharus griseiceps (Pan.)	3 ♀, 30.2, 30.5, 30.8	1	0.83
Sialia sialis (Ohio)	11 ♀, 31.7±0.8; 14 ♂, 30.8±0.6	11	1.21±0.04
GNATCATCHERS AND KINGLETS			
Polioptila caerulea (Ohio)	4 ♀, 5, 5.5, 5.5, 5.5; 8 ♂, 5.74±0.17	3	1.14, 1.48, 1.49
Regulus satrapa (Ohio)	12 ♀, 6.3±0.18; 10 ♂, 6.32±0.18	3	1.26, 1.27, 1.33
Regulus calendula (Maine)	*3 ♀, 5.3, 5.9, 6.3; 9 ♂, 6.6±0.3	3	1.36, 1.42, 1.78
PIPITS			
Anthus spinoletta (Ohio)	*1 ♂, 22	1	1.84
WAXWINGS			
Bombycilla cedrorum (Maine)	12 ♂, 34.25±0.74; *22 ♂, 32.77±0.66	14	1.55±0.01
SILKY FLYCATCHERS			
Ptilogonys caudatus (Pan.)	1 ♀, 33.5; *2 ♂, 38.6, 41.5	3	1.20, 1.37, 1.38
PEPPER SHRIKES			
Cyclarhis gujanensis (Pan.)	*1 ♀, 34.2; 1 ♂, 29.8	1	0.97
SHRIKES			
Lanius ludovicianius (Fla.)	5 ♀, 48.4±0.7; *8 ♂, 47.1±1.1	7	1.35±0.05
STARLINGS			
Sturnus vulgaris (Ohio)	3 ♀, 69.6, 75, 76; *3 ♂, 78.4, 79, 82.4	3	1.15, 1.30, 1.47
VIREOS			
Vireo griseus (Fla.)	1 ♀, 11.5; 8 ♂, 12.2±0.4	5	1.32±0.03
Vireo carmioli (Pan.)	1 ♀, 13.4; 2 ♂, 12.5, 13.5	3	0.97, 1.00, 1.04
Vireo solitarius (Maine)	5 ♀, 16.6±0.6; 5 ♂, 16.3±0.5	1	1.68
Vireo olivaceus (Maine)	14 ♀, 17.36±0.40; 21 ♂, 18.16±0.55	11	1.54±0.06
HONEY CREEPERS			
Dacnis cayana (Pan.)	2 ♀, 14.5, 18; *5 ♂, 12.6±0.5	1	1.50
WOOD WARBLERS			
Mniotilta varia (Maine)	11 ♀, 10.6±0.2; 14 ♂, 10.3±0.2	10	1.15±0.05

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
Vermivora peregrina (Ohio)	7 ♂, 9.78±0.59	1	1.47
Vermivora gutturalis (Pan.)	1 ♀, 9.6; 2 ♂, 9.5, 10.3	3	0.92, 1.05, 1.15
Parula pitiayumi (Pan.)	2 ♂, 6.7, 7	1	1.20
Dendroica aestiva (Ohio)	*11 ♀, 9.82±0.46; 13 ♂, 10.30±0.31	5	1.58±0.09
Dendroica magnolia (Maine)	10 ♀, 8.29±0.21; 17 ♂, 9.09±0.36	9	1.21±0.04
Dendroica caerulescens (Maine)	3 ♀, 9, 9, 9.5; 4 ♂, 9, 9.5, 9.5, 10.3	5	1.33±0.06
Dendroica coronata (Ohio)	19 ♀, 11.83±0.25; 26 ♂, 13.06±0.22	10	1.29±0.04
Dendroica virens (Maine)	16 ♀, 8.75±0.15; 20 ♂, 9.34±0.29	14	1.29±0.08
Dendroica fusca (Maine)	13 ♀, 9.63±0.17; 9 ♂, 9.35±0.30	8	1.17±0.04
Dendroica pensylvanica (Maine)	14 ♀, 9.64±0.17; 20 ♂, 9.59±0.15	11	1.17±0.06
Dendroica castanea (Maine)	7 ♀, 14.13±0.47; 15 ♂, 13.30±0.61	1	1.02
Dendroica striata (Maine)	4 ♀, 6.5, 8.3, 8.8, 11.9; 3 ♂, 13.4, 14.9, 15.2	1	1.28
Dendroica discolor (Fla.)	3 ♀, 8.7, 9, 9; 3 ♂, 7.5, 9, 9.5	6	1.24±0.05
Dendroica palmarum (Fla.)	4 ♀, 8.7, 9, 9, 10; 6 ♂, 9.25±0.42	6	1.24±0.05
Seiurus aurocapillus (Maine)	8 ♀, 19.01±0.53; 11 ♂, 18.04±0.53	12	1.23±0.03
Oporornis philadelphia (Ohio)	2 ♀, 11.5, 12; 6 ♂, 11.8±0.2	5	0.93±0.06
Geothlypis trichas brachydactyla (Maine)	12 ♀, 9.6±0.3; 22 ♂, 10.24±0.11	12	1.30±0.06
Geothlypis trichas ignota (Fla.)	2 ♀, 8.5, 9; 3 ♂, 9, 10.5, 10.5	2	1.24, 1.36
Icteria virens (Ohio)	2 ♀, 25.1, 32.5; 5 ♂, 24.6±0.5	5	1.01±0.09
Wilsonia pusilla (Pan.)	6 ♀, 7.05±0.18; 7 ♂, 7.57±0.13	5	1.05±0.03
Wilsonia canadensis (Maine)	2 ♀, 9.5, 9.8; 9 ♂, 9.94±0.23	1	1.29
Setophaga ruticilla (Maine)	12 ♀, 8.26±0.15; 12 ♂, 7.85±0.18	8	1.25±0.01
Myioborus miniatus (Pan.)	2 ♀, 8.4, 9; 5 ♂, 9.46±0.16	5	1.32±0.14
Basileuterus culcivorus (Pan.)	1 ♀, 10.1; 1 ♂, 11.3	1	1.59
Basileuterus melanogenys (Pan.)	2 ♂, 10.3, 11.2	1	0.87
TROUPIALS			
Zarhynchus wagleri (Pan.)	1 ♀, 110; 3 ♂, 200, 205, 230	1	0.99
Cacicus vitellinus (Pan.)	6 ♂, 115±3.7	2	1.06, 1.16
Amblycercus holosericeus (Pan.)	4 ♀, 55, 56, 56.7, 58; 6 ♂, 70.3±1.5	4	0.79, 0.84, 0.91, 0.96
Dolichonyx oryzivorus (Ohio)	2 ♀, 24.3, 25.1; 6 ♂, 34.5±0.8	6	1.34±0.07
Molothrus ater (Ohio)	10 ♀, 38.67±0.84; 13 ♂, 49.60±0.10	9	1.49±0.04
Sturnella magna (Fla).	9 ♀, 76.0±3.2; 20 ♂, 101.5±2.5	18	1.17±0.09
Icterus galbula (Pan.)	2 ♀, 32.5, 35.3; 8 ♂, 34.0±0.5	6	1.09±0.11
Icterus mesomelas (Pan.)	3 ♀, 52.5, 53, 50.2; 2 ♂, 57.2, 64	2	0.82, 0.87
Cassidix mexicanus (Fla.)	4 ♀, 98±3; 14 ♂, 185.8±7.7	9	1.00±0.04
Agelaius phoeniceus phoeniceus	7 ♀, 43±2.2; 9 ♂, 63±1.3	1	1.20
Agelaius phoeniceus mearnsi (Fla.)	2 ♀, 28.5, 32; 3 ♂, 46, 50, 50	4	1.09±0.10
Euphagus carolinus (Ohio)	4 ♀, 53, 55, 57.2, 58.2; 3 ♂, 65, 66, 76	3	1.18, 1.30, 1.30
Quiscalus quiscula (Fla.)	1 ♀, 77; 2 ♂, 95, 110	3	1.13, 1.13, 1.25
TANAGERS			
Chlorophonia callophrys (Pan.)	1 ♂, 24.1	1	1.37
Tanagra luteicapilla (Pan.)	4 ♂, 11.4, 12.3, 12.7, 14.5	1	1.23
Tangara larvata (Pan.)	1 ♂, 18	1	1.05
Tangara icterocephala (Pan.)	*9 ♀, 22.1±0.4; 14 ♂, 21.7±0.3	10	1.11±0.06

	Body weights in grams	Number of heart weights	Hearts as per cent of body weight
Thraupis episcopus (Pan.)	4 ♀, 33.3±1.1; 7 ♂, 32.9±0.6	3	1.13, 1.32, 1.41
Thraupis palmarum (Pan.)	4 ♀, 37.1, 40, 41.9, 45	1	0.78
Ramphocelus passerinii (Pan.)	3 ♀, 27, 31.9, 33.1; 4 ♂, 30.3, 30.5, 35, 35.4	3	0.80, 0.80, 0.92
Ramphocelus dimidiatus (Pan.)	6 ♂, 29.4±0.9	2	0.64, 0.94
Ramphocelus icteronotus (Pan.)	2 ♀, 33.7, 34	1	0.69
Piranga leucopterus (Pan.)	1 ♀, 37; 2 ♂, 32.4, 32.8	3	0.87, 0.90, 1.04
Habia rubica (Pan.)	1 ♂, 37.3	1	1.45
Tachyphonus rufus (Pan.)	4 ♀, 33.4, 35, 36.5, 37.8; 1 ♂, 31.4	1	0.65
Chlorospingus ophthalmicus (Pan.)	1 ♂, 19.8	1	0.89
Chlorospingus pileatus (Pan.)	1 ♀, 18.2	1	0.66
Phoenicothraupis fuscicauda (Pan.)	1 ♀, 34.7; 3 ♂, 36.8, 39.6, 43	4	0.71, 0.71, 0.74, 1.11
FINCHES			
Saltator atriceps (Pan.)	1 ♂, 77.8	1	1.21
Saltator maximus (Pan.)	5 ♀, 49.5±1.6; 4 ♂, 43.8, 44.8, 44.8, 47.5	2	1.28, 1.30
Saltator striaticeps (Pan.)	4 ♀, 38.3, 39.2, 41, 44.2	3	0.69, 0.75, 0.79
Richmondena cardinalis cardinalis (Ohio)	13 ♀, 42.7±0.7; 16 ♂, 45.7±0.7	6	1.34±0.09
Richmondena cardinalis floridana (Fla.)	1 ♀, 32; 4 ♂, 36, 36.9, 37, 41.2	5	0.92±0.06
Pheucticus ludovicianus (Maine)	2 ♀, 44.3, 45.6; 4 ♂, 41, 42.7, 43, 46.1	1	1.01
Pheucticus tibialis (Pan.)	6 ♀, 61.1±0.8; 3 ♂, 61.3, 63, 66	2	1.05, 1.08
Passerina cyanea (Ohio)	1 ♀, 14; 5 ♂, 15.87±0.62	5	1.44±0.07
Sporophila aurita (Pan.)	7 ♂, 10.6±0.2	2	1.0, 1.2
Tiaris olivacea (Pan.)	4 ♀, 8.5, 9, 9.3, 9.8; 4 ♂, 8.5, 8.6, 9, 10	2	0.97, 1.02
Atlapetes brunnei-nucha (Pan.)	2 ♀, 35.3, 37; 3 ♂, 40, 41, 44.2	2	0.77, 0.97
Atlapetes gutturalis (Pan.)	1 ♀, 35; 2 ♂, 33, 39.2	1	1.11
Pselliophorus tibialis (Pan.)	2 ♂, 32, 33.1	2	0.86, 0.88
Arremonops striaticeps (Pan.)	9 ♀, 37.1±0.7; 5 ♂, 41.9±0.6	5	0.91±0.02
Arremonops conirostris (Pan.)	1 ♂, 41.8	1	0.76
Pipilo erythrophthalmus erythrophthalmus (Ohio)	2 ♀, 36.9, 39; 16 ♂, 42±0.5	3	1.24±0.14
Pipilo erythrophthalmus alleni (Fla.)	4 ♀, 36.3±0.5; 11 ♂, 44.1±0.7	13	0.84±0.03
Passerculus sandwichensis (Ohio)	5 ♀, 13.4±0.8; 5 ♂, 18.4±0.6	5	1.46±0.12
Ammodramus savannarum (Ohio)	1 ♀, 16; 3 ♂, 15.7, 17, 17	4	1.35±0.08
Passerherbulus henslowii (Ohio)	2 ♂, 11.3, 12	2	1.35, 1.37
Spizella passerina (Ohio)	2 ♀, 14, 18.1; 2 ♂, 12, 16.2	4	1.03, 1.17, 1.18, 1.32
Spizella pusilla (Ohio)	3 ♀, 12.2, 12.8, 14.2; 7 ♂, 15±0.9	8	1.29±0.04
Zonotrichia albicollis (Maine)	9 ♀, 25.4±0.7; 9 ♂, 29.6±1.0	1	1.00
Zonotrichia capensis (Pan.)	4 ♀, 20.2±0.8; 7 ♂, 21.0±0.2	6	0.84±0.04
Melospiza georgiana (Maine)	10 ♀, 15.38±0.71; 18 ♂, 18.53±0.45	6	1.19±0.06
Melospiza melodia (Ohio)	11 ♀, 19.89±0.54; 21 ♂, 22.11±0.45	7	1.18±0.05

DISCUSSION

One of the earlier publications on the subject of heart weights is that of Parrot (1893) who lists 97 species represented by 181 specimens. Generally speaking his shorebirds had larger hearts than did our shorebirds. Likewise we differed in many other groups. Hesse (1921) and Rensch (1948) included birds in their study of vertebrate hearts, and Groebbels (1932) compiled a summary of data from other authors. Groebbels found that the data for the same species given by different authors were often contradictory. He attributed this to differences in the method of preparing the heart. He also noted that in some species the heart size differed between the sexes. We have not found such differences in this study.

Sakharova (1946) determined the heart weights in 250 individual birds from the Moscow Zoological Park and compared them with data in the literature. She reported that in some a small difference could be observed which was most often expressed in an increase in the cardiac index of the birds from the Zoological Park. She suggests that this was due to the emaciation resulting from sickness. Therefore those values can hardly be taken as typical. However, in most cases her values agreed with those in the literature which she cites. She notes further that very little change occurs in the cardiac index in birds kept in cages for a long period and that the size of the heart is a more or less constant characteristic for the species.

Crile and Quiring (1940) published heart weights of more than 50 species of birds from North America and Africa, many of them being represented by only one or two individuals. We have values for 14 of the species which they report. If one allows for individual variation, we are in fair agreement except for the Turkey Vulture (their heart value is 2.07 per cent compared with ours of 0.71 per cent), the Great Horned Owl (their value, 0.73 per cent; ours, 0.49 per cent) and the Brown Pelican (their value, 0.66 per cent; ours, 0.815 per cent). Their Turkey Vulture must have been a young bird since it weighed less than one-third as much as an adult.

Stresemann (1927:203) has pointed out that large birds have comparatively smaller hearts than do smaller birds whereas Parrot (1893), Groebbels (1932), Stresemann, and Rensch concluded that birds flying great distances or living in northern latitudes or high altitudes possessed relatively larger hearts than did other birds.

Although size appears to be a factor in the relative proportion of the heart, other influences modify this relationship. Some of these have been indicated but there are differences which are unexplained. For example, the Roseate and Common terns are alike in size but the former possesses the larger heart. On the other hand, species in which the sexes differ in size have hearts which are alike in percentage.

Why do the heart values tend to follow one straight line until about 200 grams body weight and then show slight relative decrease? This question is unanswered. Could it be due to an abrupt change in metabolism? The relative size of the heart must be associated with the rate of metabolism. The latter is raised with increased heat loss and with exercise. Small birds produce more heat to compensate for heat loss through their relatively large surface area and they are more active than large birds. The differences among birds of nearly the same size may be due to differences in activity. Certainly this is true in some species.

Let us examine the data which support this thesis. First of all, the trochilids are probably the most active birds and have, relatively, by far the largest hearts (Hartman, 1954). Many other small birds are very active and have relatively large hearts. The Chat, which is the largest of the parulids, is less active than the smaller members of the family and has apparently the smallest heart. The larger members of the fringillids

possess smaller hearts in proportion to their size and may show less activity. The larger icterids have smaller hearts than the smaller members of the family and may be less active (for example, *Cassidix* and *Sturnella*).

Among the shorebirds, those with relatively larger hearts may be the more active, but the difference in this respect is difficult to evaluate. *Arenaria* and *Limnodromus* possess larger hearts than do others. Birds such as tinamous, quail, and turkeys that rarely fly long distances have very small hearts. Vultures that soar most of the time have smaller hearts than those which flap their wings frequently.

Estimation of the relative amount of physical activity by observation of the birds in the field can be but a crude approximation. A chattering bird or a vigorous songster does not necessarily engage in great muscular exertion. Exact comparison could be made only by measurement.

These limited observations suggest that activity may be a determining factor in heart size in birds. There is evidence that this is true in mammals. Steinhaus, Kirmiz, and Lauritsen (1932) showed that swimming or running caused cardiac hypertrophy in the dog, the former being more effective than the latter. McClintock, Hines, and Jordan (1939) observed that voluntary activity in the female rat in revolving cages for six and one-half months increased dried heart-weight by 10 per cent. Wild hogs possessed hearts 0.638 per cent of the body weight; in domestic hogs they were only 0.38 per cent of the body weight (Geschwend, 1931).

We have calculated the heart weight in terms of per cent of body weight in data published by Crile and Quiring (1940). The greyhound had relatively one of the largest hearts, at 1.26 per cent, and the collie-police dog had a heart only 0.77 per cent of the body weight. Almost all values for mammals were lower than a vast majority of those for birds. Here again, heart-size often was related to activity. The following examples illustrate: grizzly bear, *Ursus horribilis* (zoo specimen)—0.79 per cent; jaguar, *Felis onca* (from zoo)—0.54 per cent; tiger, *Felis tigris* (captive)—0.33 per cent; porpoise, *Phocaena phocaena*—0.52 per cent; anteater, *Tamandua tetradactyla*—0.44 per cent; three-toed sloth, *Bradypus griseus*—0.24 per cent; monkey, *Macacus rhesus*—0.33 per cent; squirrel, *Sciurus hudsonicus*—0.73 per cent; and meadow mouse, *Microtus drummondi*—0.70 per cent. Thus we see that on the whole, mammalian hearts are smaller than avian hearts. This had been shown to be true by Parrot (1893).

Why does climate affect heart size, if it does? Granted that our data are too meager to bear conclusively on this point, they do suggest such an effect. A comparison of subspecies should be most valid (for example, *Richmondena cardinalis cardinalis* and *R. c. floridana*). The northern subspecies has a greater range of stimulation, longer daylight in summer and shorter in winter, together with a greater range in temperature and correspondingly the heart is larger. In the areas corresponding to these races, the mean annual temperature is 54.4°F. (Ohio) and 71.9°F. (Florida).

Does season affect heart size? Our data derived from just a few species are only suggestive. If the difference is valid, it might be explained by difference in activity. In the short daylight of winter in northern climates, birds seek their food, bask briefly in the sun, if at all, and hunt some spot where they can be undisturbed for the long night. This is in contrast to the long summer daylight with prolonged activities of courting, feeding of young, and general reaction to environment.

We have very little data on the effect of altitude, the Quetzal being our sole example. In the tropics the essential difference between low and high altitudes is temperature, especially the cold nights of the latter, the length of daylight being the same. Strohl's observations (1910) on *Lagopus* bear on this point. He found that the hearts of *L. mutus,*

the alpine ptarmigan were relatively much larger than the hearts of *L. lagopus*, the marsh ptarmigan. He attributed this to the differences in altitude to which the birds were subjected.

When does the heart of the developing young bird reach the same proportion to the body as that in the adult? Laura Kaufman (quoted by Groebbels, 1932) has reported the relative heart weight in the domestic pigeon at different ages. From the seventh through the thirteenth day it is much larger (1.8 to 1.6 per cent) than in the adult (1.3 per cent). The time at which the heart percentage becomes the same as in the adult may vary in different species, but more evidence in support of this idea is needed.

In general, it may be said that the smaller, more active birds have relatively larger hearts. In other words the larger hearts are associated with increased metabolism necessitated by heat loss or caused by exercise. Differences between sexes as to heart weight are rare or absent. The inaction brought on by long winter nights is associated in some species with smaller heart weights. Also warm climates may be associated with relatively small hearts. Undoubtedly many factors are involved. A characteristic heart size is inherited. This must be modified by natural selection acting on variations through many generations in response to the circulatory requirements arising from conditions imposed by exercise, heat production and the environment. The heart of each individual may be modified temporarily by any of these influences, but the heart of the average member of the species represents the total response over many generations.

SUMMARY

Percentage heart weights for more than 1340 birds distributed among 291 species and 64 families, are given. These specimens were collected in the eastern United States and Panamá.

When the logarithms of the heart weights are plotted against those of the body weight the values tend to follow a straight line to about 200 grams body weight and then follow another line that is slightly steeper.

Percentage heart weights range from a little more than 0.2 per cent in tinamous to 2.4 per cent in hummingbirds. Relatively small hearts are also found in *Colinus, Meleagris,* and *Chamaepetes*. Somewhat larger are those of some hawks, some rails, some cuckoos, and many owls. Relatively large hearts are found among shorebirds, kingfishers, swallows, titmice, nuthatches, creepers, waxwings, vireos, and warblers.

No evidence of a difference in heart size was found between the sexes.

The age at which heart size attains adult magnitude appears to differ among species.

Heart size is related to activity in many instances, those of birds accustomed to sustained strenuous exertion being the largest in proportion to the body.

Limited data on several species suggest that heart weight decreases in the colder months of the year in some species.

Certain northern subspecies appear to have larger hearts proportionately than do southern subspecies of the same species.

Larger hearts may be associated with permanent residence at high altitude.

Heart weight in birds is relatively greater than in mammals.

LITERATURE CITED

American Ornithologists' Union Committee

1931. Check-list of North American birds. Fourth edition (Lancaster, Pa., Am. Ornith. Union).

Crile, G., and Quiring, D. P.

1940. A record of the body weight and certain organ and gland weights of 3690 animals. Ohio Jour. Sci., 40:219–259.

Geschwind, T.
1931. The heart of the wild hog. Anat. Anz., 72:49–89.
Groebbels, F.
1932. Der Vogel. Erster Band: Atmungswelt und Nahrungswelt (Berlin, Gebrüder Borntraeger).
Hartman, F. A.
1954. Cardiac and pectoral muscles of trochilids. Auk, 71:467–469.
Hesse, R.
1921. Das Herzgewicht der Wirbeltiere. Zool. Jahrb. (Abt. allg. Zool.), 38:243–364.
McClintock, J. T., Hines, H. M., and Jordan, D.P.
1939. Effects of activity upon the tissues of the rat. Proc. Soc. Exp. Biol. Med., 42:139.
Parrot, C.
1893. Ueber die Grössenverhaltnisse der Herzens bei Vögeln. Zool. Jahrb. (system.), 7:496–52.
Peters, J. L.
1931–1951. Check-list of birds of the world (Cambridge, Harvard University Press).
Rensch, B.
1948. Organproportionen und Körpergrösse bei Vögeln und Saügetiere. Zool. Jahrb. Jena (Allg. Zool.), 61:337–412.
Sakharova, T. V.
1946. On the cardiac index in birds. Proc. Moscow Zoological Pk., 3:62–71 (English summary and title, p. 71).
Steinhaus, A. H., Kirmiz, J. P., and Lauritsen, K.
1932. Chronic effects of running and swimming on the hearts of growing dogs revealed by roentgenography. Am. Jour. Physiol., 99:487–502.
Stresemann, E.
1927. Aves. In Kükenthal, Handbuch der Zoologie, Siebenter Band, zweite hälfte: 113–224.
Strohl, J.
1910. Le poids relatif du coeur et l'affect des grand altitude . . . Compt. Rend. Acad. Sci. Paris, 150:1257–1260.

Department of Physiology, The Ohio State University, Columbus, Ohio, November 9, 1954.