ADAPTATION OF HEART AND LUNG WEIGHT TO HIGH ALTITUDE IN THE ROBIN

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Adaptation of heart and lung weight to high altitudes has not been conclusively studied in bird populations of one species. Rensch (1931) concluded that the ratio of heart weight to body weight increases with altitude in certain tropical passerines. Moreau (1944), while agreeing that such a trend would be expected, maintained that Rensch's data were unsatisfactory. Altitudinal differences in the ratio of heart weight to body weight claimed by Strohl (1910) for ptarmigan have since been shown to be interspecific differences (Johnston, 1963). Hartman (1954, 1955), Norris and Williamson (1955) and Williamson and Norris (1958) have presented data on relative heart size in high and low altitude bird populations. Only Norris and Williamson (*op. cit.*) have attempted to show that adaptation in heart weight to high altitude occurs within different populations of the same species. Their data suggest but do not prove that relative heart weight varies directly with altitude. The present study was undertaken to provide a rigorous analysis of variation in weight of the heart and lungs in subspecifically distinct populations of American Robins (*Turdus migratorius*) from montane and lowland situations.

MATERIALS AND METHODS

All montane robins were collected between June 27 and August 2, 1961, at 9500 to 9800 feet near Gothic, Colorado. They were in breeding condition. These birds are referable to the subspecies *Turdus migratorius propinquus*. Lowland robins were collected at approximately sea level near New Haven, Connecticut. These birds were obtained between September 27 and October 25, 1961, and are referable to the nominate subspecies *Turdus m. migratorius*. Many of these lowland birds were collected in migrating flocks. The total body weights of the montane and lowland subspecies cannot be directly compared due to seasonal and physiological differences associated with breeding and migration. Therefore the length of the tarsometatarsus was taken as an indicator of total size.

All of the birds were collected by shooting. Only specimens in which the heart and lungs were undamaged were subjected to the measurements described subsequently. The specimens were placed in plastic bags immediately after collection to prevent drying, and they were weighed within three hours. The total body weights were taken on a triple beam balance accurate to 0.1 gm. The heart, lungs, and tarsometatarsus were removed from the bird and preserved in 10 per cent formaldehyde. The organs were later removed from the formaldehyde, blotted, trimmed, and then weighed on a balance accurate to 0.1 mgm. Blood clots were removed from the heart after it was partly opened. The length of the tarsometatarsus was determined with a vernier caliper accurate to 0.01 mm. The sex of each bird was ascertained by examination of the gonads. Immature birds were not separated on the basis of sex. At the times of collection all birds were either in adult or juvenal plumage, enabling easy separation of adults and immatures. Immature birds, as defined here, are birds less than one year old.

For statistical purposes the t test was used except when the variances of two means were significantly different (at 5 per cent level). In this case an approximation described by Bailey (1959), in which d is treated as being distributed like Student's

TABLE 1

TOTAL WEIGHT, HEART WEIGHT, LUNG WEIGHT AND TARSOMETATARSUS LENGTH OF MONTANE AND LOWLAND ROBINS*

	Total weight	Heart weight	Right lung weight	Left lung weight	Total lung weight	Tarsometatarsus length	$\frac{\text{Heart weight}}{\text{Total weight}} \times 100$	$\frac{\text{Total lung weight}}{\text{Total weight}} \times 100$
Montane adult males	78.58	0.9392	0.7791	0.7858	1.5645	3.248	1.20	1.99
	6.40	0.1246	0.1485	0.1652		0.117	0.18	
	(37)	(37)	(27)	(23)	(25)	(34)		
Lowland adult males	83.68	0.7593	0.5895	0.6078	1.1959	3.242	0.91	1.43
	5.32	0.0836	0.1427	0.1074		0.099	0.11	
	(7)	(7)	(7)	(6)	(6.5)	(7)		
Montane adult females	80.40	0.9360	0.7338	0.7678	1.5031	3.241	1.16	1.87
	6.54	0.1145	0.1150	0.1317		0.120	0.16	
	(23)	(20)	(11)	(12)	(11.5)	(21)		
Lowland adult females	82.28	0.8411	0.5096	0.4724	0.9820	3.155	1.02	1.19
	4.37	0.0746	0.0295	0.0161		0.055	0.10	
	(4)	(4)	(4)	(4)	(4)	(4)		
Montane immatures	74.96	0.8380	0.7192	0.7123	1.4313	3.280	1.12	1.91
	5.76	0.2980	0.1855	0.1281		0.123	0.48	
	(32)	(28)	(16)	(17)	(16.5)	(30)		
Lowland immatures	81.56	0.7157	0.5151	0.5246	1.0397	3.152	0.88	1.27
	4.93	0.1006	0.0778	0.1030		0.145	0.13	
	(15)	(15)	(14)	(14)	(14)	(15)		
Montane group	77.75	0.8355	0.7521	0.7577	1.5097	3.257	1.16	1.94
	(93)	(85)	(54)	(52)	(53)	(85)		
Lowland group	82.24	0.7467	0.5350	0.5367	1.0717	3.177	0.91	1.30
	(26)	(26)	(25)	(24)	(24.5)	(26)		

* From top to bottom, respectively, mean, standard deviation, and sample size in parentheses. Weights are means expressed in grams; lengths are means expressed in centimeters.

t with f degrees of freedom, was used. Differences between means at the 5 per cent level were considered significant.

The standard deviation of the ratio of heart weight to total weight in table 1 was derived from the standard deviations of the means of heart weight and total weight according to the method outlined by Worthing and Geffner (1943).

RESULTS

Total weight, heart weight, lung weight, tarsometatarsus length, and heart and lung weight to total weight ratios for montane and lowland robins are given in table 1. Tables 2 and 3 show that there is a high probability that the tarsometatarsus lengths of montane and lowland adult birds are in the same distribution of values. Heart and lung weights of the two adult populations were compared using the tarsometatarsus length as an index of body size. The heart and lung weights of montane adult males and females were significantly higher than those of lowland adult males and females (tables 2 and 3).

TABLE 2

A COMPARISON OF MEANS OF ADULT MALE ROBINS FROM MONTANE AND LOWLAND SITUATIONS

	Variance ratio (F)	Variance ratio at 0.95 probability level ($F_{.95}$)	Standard deviation	Student's t value	Degrees of freedom	Probability
Total weight	1.45	3.77	3.66	3.39	42	< 0.01
Heart weight	2.221	3.78	0.0735	5.94	42	< 0.01
Right lung weight	1.083	3.83	0.0896	4.99	32	< 0.01
Left lung weight	2.366	4.54	0.0739	5.26	27	< 0.01
Tarsometatarsus length	1.395	3.79	0.0847	0.166	39	> 0.85

TABLE 3

A COMPARISON OF MEANS OF ADULT FEMALE ROBINS FROM MONTANE AND LOWLAND SITUATIONS

	Variance ratio (F)	Variance ratio at 0.95 probability level ($F_{.95}$)	Standard deviation	Student's t value	Degrees of freedom	Probability
Total weight	2.24	8.65	3.31	1.05	25	~ 0.30
Heart weight	2.36	8.67	0.071	2.43	22	< 0.025
Tarsometatarsus length	4.76	8.66	0.076	0.206	23	> 0.85
Right lung weight[1]	15.20	8.79		5.96[2]	12.58	< 0.001
Left lung weight[1]	66.97	8.77		7.60[2]	11.91	$\ll 0.001$

[1] When $F > F_{.95}$ a modified d test is used rather than the Student's t test (Bailey, 1959).
[2] Normal variable with zero mean and unit standard deviation.

The tarsometatarsus lengths of the montane and lowland immatures were significantly different (table 4). This may be due to the young being of different ages. There is also the possibility that the montane immature birds have a faster relative growth rate. This is suggested by a comparison of mean total weight, heart weight, and lung weight for immature birds from montane and lowland situations with the corresponding values for adults (table 5). These percentages show that the heart weight of the montane immature birds was much closer to the adult heart weight than was the heart weight of the lowland immature birds. This occurred in spite of the fact that montane immature birds were not as near the adult weight as the

TABLE 4

A COMPARISON OF MEANS OF IMMATURE ROBINS FROM MONTANE AND LOWLAND SITUATIONS

	Variance ratio (F)	Variance ratio at 0.95 probability level ($F_{.95}$)	Standard deviation	Student's t value	Degrees of freedom	Probability
Total weight	1.36	2.31	3.29	6.45	45	$\ll 0.001$
Left lung weight	1.55	2.53	0.061	8.47	29	$\ll 0.001$
Tarsometatarsus length	1.39	2.01	0.093	4.32	43	< 0.001
Heart weight[1]	8.79	2.32		1.97[2]	38.4	< 0.03
Right lung weight[1]	5.64	2.53		4.03[2]	20.9	$\ll 0.001$

[1] When $F > F_{.95}$ a modified d test is used rather than the Student's t test (Bailey, 1959).
[2] Normal variable with zero mean and unit standard deviation.

TABLE 5
RELATIVE GROWTH RATES OF IMMATURE ROBINS

	Per cent of mean adult value		
	Total weight	Heart weight	Lung weight
Montane immatures	95.0	89.5	93.5
Lowland immatures	98.5	81.0	95.5

lowland immature birds. The heart and lung weights of the two immature populations could not be statistically compared due to the differences in tarsometatarsus length. However, the raw data (table 1) suggest that heart and lung weights are higher in the montane immature birds.

DISCUSSION

The function of the increased relative heart and lung weight demonstrated here in high-altitude robins is still unknown. At high altitudes the partial pressure of oxygen is much less than at low altitudes. At 9500 feet, the altitude at which most of the montane birds were collected, the air pressure and the oxygen pressure are 71 per cent of the pressure at sea level (Dill, 1938). The barometric pressure at 9500 feet is about 535 mm. Hg as compared with approximately 760 mm. Hg at sea level. Thus the difference in oxygen pressure between the two environments is 45 mm. Hg. For an animal living at high altitudes, either the tissues must be supplied with ample oxygen for active metabolic processes or an oxygen debt will be incurred to be paid back in a subsequent rest period. Increased heart and lung weight probably represent mechanisms serving to provide adequate oxygen for the tissues in an environment low in oxygen. Increased lung weight may indicate the development of extra surfaces for gaseous transfer. An enlarged heart may be capable of a greater work output. Blood hemoglobin content and cardiac output increase in man at high altitudes (Dill, 1938). The former appears to be a factor in long term adaptation whereas the latter is a very short term response. The heavier heart of robins at high altitudes may indicate long term adaptation in cardiac output.

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SUMMARY

Data from 60 adult montane robins (*Turdus migratorius propinquus*) and 11 adult lowland robins (*Turdus m. migratorius*) show that heart weight and right and left lung weight are significantly higher in the montane populations. Tarsometatarsus length of adult montane birds is not significantly different from that of adult lowland birds.

Data from 32 immature montane robins (*T. m. propinquus*) and 15 immature lowland robins (*T. m. migratorius*) suggest that heart weight and right and left lung weight are higher in the high-altitude populations. The problem of relative growth in robin populations at different altitudes needs further investigation.

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