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The *Postilla* series, which ceased publication with Number 232 (2004), was incorporated into the journal *Bulletin of the Peabody Museum of Natural History*, available from BioOne Complete at <https://bioone.org/>.

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Postilla

PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT, U.S.A.

Number 98

April 1, 1966

FURTHER INFORMATION ON THE RELATIVE LENGTH OF THE TARSUS IN LAND BIRDS

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A tendency for island land birds to have a longer tarsus (tarsometatarsus) than their mainland relatives has been discovered recently (Grant, 1965*a*). It has been suggested that this is related to a difference in pattern of foraging between mainland and island birds (Grant, 1965*b*): that the paucity of species on islands has allowed some of those present to extend their range of foraging activities, for which a longer tarsus is presumed to be of advantage.

In functional terms, a long tarsus is mechanically advantageous to birds using firm perches, such as thick branches or the ground, during bipedal locomotion. A short tarsus is advantageous to those using non-rigid perches, where the maintenance of balance during standing or bipedal locomotion poses greater problems than on firm perches. If the interpretation of the significance of long tarsi in island birds is correct, it would imply that a greater range of foraging activities entails a greater use of firm perches, to which the birds have become adapted. There is a little direct evidence in support of this (Grant, 1965*b*). It is the purpose of this paper to present additional, albeit circumstantial, evidence.

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During the last fifteen years several studies have been made of the comparative feeding ecology of two or more closely related species of birds. From the argument presented above, it is to be expected that those birds which make the greatest use of firm perches will have the longest tarsi. To test this, measurements of the relevant species have been assembled. Length of tarsus has been expressed by itself and in relation to two indicators of body-size, wing-length and weight. The Student's *t* test has been applied to the tarsus/wing ratio data where samples contain five individuals or more and standard errors can be calculated.

I. MAINLAND/ISLAND COMPARISONS

1. *Vireo g. griseus* and *V. g. bermudianus*

According to Crowell (1962), the Bermuda vireo feeds lower in the vegetation and more frequently on the ground than does the mainland vireo. There is thus some evidence that Bermuda birds use firm perches more frequently than mainland birds do (Table 1). Correspondingly the tarsus of island birds is larger, both absolutely and relative to the length of the wing.

TABLE 1. Ecological and morphological characteristics of *Vireo griseus* in eastern North America.

	Locality	N	Feeding Stations (percentage use) ¹				
			Ground	Bark	Foliage	Hawk	Hover
<i>V. g. griseus</i>	Mainland	349	0	10.0	82.6	1.1	6.3
<i>V. g. bermudianus</i>	Bermuda	900	3.4	15.6	64.8	2.4	13.8
	Morphological measurements (♂♂ only) ²						
			Weight	Wing	Tarsus	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>V. g. griseus</i>	—		62.4 (10)	19.3 (10)	—	—	0.309
<i>V. g. bermudianus</i>	—		58.7 (3)	20.5 (3)	—	—	0.349

NB Figures in parentheses indicate the sample size: those under the symbol N indicate the total number of observations. The same system is used in subsequent tables.

1 Data from Crowell (1962).

2 Data from Ridgway (1904): measurements in this and all subsequent tables are in millimeters.

2. *Vireo griseus* and *V. bairdi*

Paynter (1955, p. 235) writes "Cozumel Vireos are very common in thickets. During the brief period I observed them I thought that they were more terrestrial and wren-like than other members of the genus." This suggests that they make frequent use of branches, perhaps also the ground. When compared with the most closely related species on the Yucatán peninsula the Cozumel Vireo is found to have an absolutely and relatively longer tarsus (Table 2), although the difference in tarsus/wing ratio is not significant ($P > 0.1$). However, the tarsus/wing ratio of the mainland sample should probably be smaller than that shown in the table, since all mainland specimens were collected in worn plumage in June, whereas island specimens, in unworn plumage, were collected in January and February. An addition of two millimeters to mean wing-length of the mainland sample would alter the tarsus/wing value to 0.350, thereby enlarging the difference between the mainland and island samples and possibly making it significant.

3. *Parus rufescens* populations

Palmgren (1932) showed that a short tarsus was of mechanical advantage to a bird feeding in a hanging position. In British Columbia, Canada, an island and mainland population of Chestnut-backed Chickadee were studied, and they were found to differ very little in the frequency of feeding in a hanging position (Table 3). However, a clear difference in the dimension of the perches used was found, the island birds using thicker perches. Measurements of specimens made later showed that the tarsus/wing ratio of island birds was greater than that of mainland birds (Table 3), although the difference is not significant ($P > 0.1$). It is possible that the foraging differences are related to the presence of *Parus atricapillus* on the mainland and its absence from the island.

II. MAINLAND/MAINLAND COMPARISONS

1. *Parus rufescens* and *P. inornatus*

P. inornatus feeds on the ground, unlike *P. rufescens* (Dixon, 1954). It also has a longer tarsus, both absolutely and relative to wing length and body weight (Table 4).

TABLE 2. Morphology of *Vireo griseus* and *Vireo bairdi* in the Yucatán region of Mexico
Measurements (♂♂ only)¹

	Locality	Weight (g)	Wing	Tarsus	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>V. griseus semiflavus</i>	Quintana Roo	10.24 (17)	53.5 (17)	19.43 (17)	0.896	0.363 ± 0.005
<i>V. bairdi</i>	Cozumel Id.	11.60 (2)	61.2 (5)	22.56 (5)	0.996	0.369 ± 0.003

¹ Measurements of specimens in the Yale Peabody Museum of Natural History made by the author. Weights were taken from the labels of the same specimens.

2. *Parus wollweberi* and *P. bicolor*

There is a clear difference in feeding habits between these two species, *P. bicolor* making greater use of firm perches, including

TABLE 3. Ecological and morphological characteristics of *Parus rufescens* in British Columbia, Canada
Feeding Characteristics¹

		I. Posture (No. of observations)								
	Locality	Hanging in Trees	Standing in Trees	Standing on ground	% Hanging	% Standing				
<i>P. r. rufescens</i>	Mainland	75	25	0	75	25				
<i>P. r. rufescens</i>	Vancouver Id.	67	31	2	67	33				
		II. Estimated perch diameters (No. of observations)								
	Locality	1cm	2cm	3cm	4cm	5cm	6cm	7cm	8cm	Trunk
<i>P. r. rufescens</i>	Mainland	100	0	0	0	0	0	0	0	0
<i>P. r. rufescens</i>	Vancouver Id.	64	11	5	9	3	0	0	1	5
		Morphological measurements (♂♂ only) ²								
	Locality	Weight	Wing	Tarsus	$\sqrt[3]{\text{Weight}}$	$\frac{\text{Tarsus}}{\text{Wing}}$				
<i>P. r. rufescens</i>	Mainland	—	61.7 (30)	15.70 (30)	—	0.254 ± 0.002				
<i>P. r. rufescens</i>	Vancouver Id.	—	61.1 (23)	15.76 (23)	—	0.258 ± 0.002				

1 Observations made by the author, 14 Dec. 1963 - 11 Jan. 1964 (pure flocks only).

2 Measurements made by the author.

TABLE 4. Ecological and morphological characteristics of *Parus rufescens* and *P. inornatus* in eastern North AmericaFeeding Station (percentage use)¹

	N	Ground	Trunk	Branch	Twig*	Foliage/Fruit
<i>P. r. barlowi</i>	736	0	4.7	32.5	20.4	42.4
<i>P. i. inornatus</i>	430	13.3	8.1	8.6	14.6	55.4

Morphological measurements (♂♂ only)

	Weight (g) ²	Wing ³	Tarsus ³	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>P. r. barlowi</i>	9.7 (18)	60.1 (10)	16.3 (10)	0.765	0.271
<i>P. i. inornatus</i>	16.6 (12)	68.7 (10)	21.1 (10)	0.827	0.307

* Twigs were considered to be perches of less than 1/2" in estimated diameter, branches more than 1/2" (this also applies to Tables 5 and 6).

1 Data from Dixon (1954).

2 Data from Dixon (1961).

3 Data from Ridgway (1904).

TABLE 5. Ecological and morphological characteristics of *Parus wollweberi* and *P. bicolor* in southern North AmericaFeeding Station (percentage use)¹

	N	Ground	Trunk	Branch	Twig	Foliage/Fruit
<i>P. w. wollweberi</i>	271	0	6.3	22.5	29.9	41.3
<i>P. b. atricristatus</i>	150	6.7	10.7	37.9	22.0	22.7

Morphological measurements (♂♂ only)

	Weight (g) ¹	Wing ²	Tarsus ²	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>P. w. wollweberi</i>	10.1 (7)	67.0 (10)	17.0 (10)	0.786	0.254
<i>P. b. atricristatus</i>	15.8 (13)	72.7 (8)	19.4 (8)	0.773	0.267

1 Data from Dixon (1961).

2 Data from Ridgway (1904).

the ground, than *P. wollweberi* (Table 5). Similarly, the tarsus and tarsus/wing values are greater in *P. bicolor*. However, the heavier species has the smaller tarsus/weight ratio.

3. *Parus palustris*, *P. coeruleus*, *P. major* and *P. ater*

Several ecological studies of these four species have been made in England (Betts, 1955; Gibb, 1954, 1960; Hartley, 1953), although the data are difficult to analyse for present purposes. All results indicate a substantial difference between the first two and last two species, the former using non-rigid perches predominantly, the last two using firm perches (Table 6). Similarly the first two have a distinctly smaller tarsus/wing ratio than the last two. *P. palustris* has a significantly smaller ratio than *P. major* (< 0.01) and *P. ater* (< 0.01), and *P. coeruleus* has a significantly smaller ratio than *P. ater* (< 0.01). However, the dif-

TABLE 6. Ecological and morphological characteristics of *Parus palustris*, *P. coeruleus*, *P. major* and *P. ater* in England

Feeding Station¹

	Ground	Trunk/Branch	Twig/Bud/Leaf
<i>P. palustris</i>	*	*	***
<i>P. coeruleus</i>	*	*	***
<i>P. major</i>	**	*	**
<i>P. ater</i>	*	**	**

Morphological measurements (sexes combined)

	Weight (g) ²	Wing ³	Tarsus ³	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>P. palustris</i>	10.5	63.0 (10)	15.70 (10)	0.722	0.249 ± 0.002
<i>P. coeruleus</i>	10.5	62.8 (13)	16.10 (13)	0.729	0.256 ± 0.003
<i>P. major</i>	18.0	72.4 (8)	19.46 (8)	0.745	0.268 ± 0.004
<i>P. ater</i>	8.5	59.3 (12)	16.45 (12)	0.800	0.276 ± 0.002

1 Data from Betts (1955): the asterisks indicate the relative frequency of each feeding station used.

2 Data from Gibb (1954).

3 Measurements made by the author.

TABLE 7. Ecological and morphological characteristics of *Dendroica tigrina*, *D. fusca*, *D. virens*, *D. castanea* and *D. coronata* in eastern North America

	Descending order of feeding height ¹	Weight	Wing ²	Tarsus ²	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>D. tigrina</i>	1	—	67.3 (13)	17.56 (13)	—	0.257 ±0.002
<i>D. fusca</i>	2	—	68.8 (25)	16.85 (25)	—	0.244 ±0.001
<i>D. virens</i>	3	—	63.8 (25)	16.41 (25)	—	0.265 ±0.002
<i>D. castanea</i>	4	—	74.9 (17)	17.84 (17)	—	0.238 ±0.003
<i>D. coronata</i>	5	—	73.0 (19)	18.03 (19)	—	0.247 ±0.002

1 Data from MacArthur (1958).

2 Measurements of ♂♂ only, made by the author.

ference between *P. coeruleus* and *P. major* is not significant ($P < 0.1 > 0.05$). Failure to demonstrate a significant difference between these two is perhaps due to the large variation in the small *P. major* sample. The sequence of increasing tarsus/weight ratios parallels the sequence of tarsus/wing ratios. The feeding data available do not permit a meaningful comparison of *P. palustris* and *P. coeruleus*, and of *P. major* and *P. ater*.

4. *Dendroica tigrina*, *D. fusca*, *D. virens*, *D. castanea* and *D. coronata*.

As listed, these five species of sympatric warblers show a descending order of preferential feeding height (Table 7). In similar sequence, the first named feeds most frequently in peripheral parts of a tree, and the last named feeds most frequently in central parts close to the trunk (see MacArthur, 1958). From this it may be deduced that the first species uses rigid perches least, the last species uses them most, etc. In contrast to this sequence of perch use there is no such sequence of tarsus/wing ratios. Thus, although *D. fusca* has a smaller ratio than *D. virens* ($P < 0.01$), and *D. castanea* has a smaller ratio than *D. coronata* ($P < 0.1 > 0.05$), *D. virens* has a larger ratio than both *D. castanea* ($P < 0.01$) and *D. coronata* ($P < 0.01$) (see Table 7). Also the species which is considered to feed least from firm perches, *D. tigrina*, has a larger ratio than *D. fusca* ($P < 0.05$) and *D. castanea* ($P < 0.01$).

5. *Regulus satrapa* and *R. calendula*

There is some evidence that *R. calendula* feeds in an upright position more frequently than *R. satrapa* (Table 8). It also has a longer tarsus and greater tarsus/wing ratio than its congener ($P < 0.01$). A similar correlation between length of tarsus and posture was found by Palmgren (1932) in his comparative study of *Parus atricapillus* and *Regulus regulus*.

CONCLUSIONS AND DISCUSSION

In seven of the eight groups analysed the species making greatest use of firm perches also had the greatest relative tarsus length (tarsus/wing), in accordance with expectation. The excep-

TABLE 8. Ecological and morphological characteristics of *Regulus satrapa* and *R. calendula* in western North AmericaFeeding Method¹

	Hanging	Standing/Hawking			
<i>R. satrapa</i>	**	*			
<i>R. calendula</i>	*	**			
Morphological measurements (♂♂ only)					
	Weight	Wing ²	Tarsus	$\sqrt[3]{\frac{\text{Tarsus}}{\text{Weight}}}$	$\frac{\text{Tarsus}}{\text{Wing}}$
<i>R. satrapa</i>	—	55.6 (17)	16.90 (17)	—	0.303 ± 0.002
<i>R. calendula</i>	—	58.6 (31)	18.35 (31)	—	0.313 ± 0.001

1 Original data involved approximately 100 observations, which were made at the University of British Columbia, Vancouver, Canada, in September, 1963. A single * indicates the use of a feeding method, ** indicates a more frequent use.

2 Measurements made by the author.

tional group, the *Dendroica* warblers, is discussed later. The difference in tarsus/wing ratios between pairs of species was not tested statistically in three instances, but in each of these it is quite substantial. Statistically acceptable differences were demonstrated in four instances and were not demonstrated in three others. Even these latter three differences might be shown to be significant if better material was available. For instance the difference between *Vireo griseus* and *V. bairdi* would undoubtedly be greater if specimens collected in the same months of the year were to be compared. It is possible also that the differences between *Parus coeruleus* and *P. major*, and between Vancouver Island and mainland *P. rufescens*, are significant, and that samples twice as large as those used here would demonstrate this.

In contrast to the other seven groups, the *Dendroica* warblers do not show correlation between relative tarsus length and foraging position. For instance *D. tigrina*, the species which feeds highest and most peripherally in the foliage and therefore may use rigid perches least has the second largest tarsus/wing ratio instead of the expected smallest. However in bad weather it does feed low in the vegetation (MacArthur, 1958), and in the West Indies

in winter it feeds close to the ground (reports quoted by MacArthur), hence its representation as the species using rigid perches least may be incorrect. Analysis of the remaining species should take into account the variety of selective forces acting upon tarsus length and wing length. Selection can act directly upon each structure for several functions, such as for heat exchange; the capacity for wings (Eliassen, 1963) and tarsi (Brush, 1965) to gain or lose heat has been demonstrated. Selection can also have an indirect effect upon them; the direct effect of selection upon body size can be expected to have an allometric consequence upon the size of exposed parts (Hamilton, 1961). Thus, with these effects properly understood, it may be possible to do what cannot be done at present, to reconcile the lack of correlation between relative tarsus length and perch characteristics of some of the *Dendroica* species with the established correlation in other groups.

These results are subject to the qualification that a difference in relative tarsus length is as much dependent upon a difference in wing length, which may be the more important, as upon a difference in tarsus length. Indeed selection may have favored long wings and short tarsi in birds foraging on twigs and thin branches, and short wings and long tarsi in forms using rigid perches (Dilger, 1956). However, in six out of seven instances the tarsus is also larger relative to body weight in those species making greatest use of rigid perches; in the seventh example an allometric effect of a body size differential appears to be of overriding importance (cf. Dilger, 1956), since the species using firm perches most is more than 50 per cent heavier than the other (Table 5). A second qualification is that, of the three bone elements of the leg, only the tarsus has been considered (measurements are available for this one only), whereas changes in the length of femur and tibiotarsus may be more important than changes in the length of tarsus. However, when proportions of these three bones change, it is usually the distal bones which change the most (Engels, 1938*a*; Grant, 1965*b*; Miller, 1937). The time is now ready for a functional analysis of all muscles and bones of the hind limb in relation to the body it supports and transports. This has been done already with aquatic birds (Engels, 1938*b*; Miller, 1937; Stolpe, 1932), cursorial birds (Davis, 1957;

Engels, 1938a, 1940; Kunkel, 1962; Stolpe, *loc. cit.*), and arboreal birds which feed in a hanging position from rigid or non-rigid perches (Palmgren, 1932; Richardson, 1942; Stolpe, *loc. cit.*), but not with those which feed predominantly in an upright position.

SUMMARY

Several comparisons of closely related species of land birds have been made. In most instances it was found that the species which made the greatest use of rigid perches in foraging also had the greatest relative tarsus length (tarsus/wing ratio). This evidence supports a theory of the significance of long tarsi in land birds, which was deduced from a study of island birds.

ACKNOWLEDGMENTS

This study was undertaken at the Zoology Department of the University of British Columbia, at the Yale Peabody Museum, and at the Zoology Department of McGill University. I am grateful to I. McT. Cowan, N. P. Ashmole and D. M. Steven respectively for the provision of working facilities. I am also grateful to J. S. Barlow (Royal Ontario Museum), W. E. Godfrey (National Museum of Canada) and Mrs. A. Stickney, Jr. (Peabody Museum) for the loan of specimens.

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