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Morphology of the Wings, Legs and Tail of Three Coniferous Forest Tits, The Goldcrest, and the Treecreeper in Relation to Locomotor Pattern and Feeding Station Selection

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MORPHOLOGY OF THE WINGS, LEGS AND TAIL OF THREE CONIFEROUS FOREST TITS, THE GOLDCREST, AND THE TREECREEPER IN RELATION TO LOCOMOTOR PATTERN AND FEEDING STATION SELECTION

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Functional morphology of the wings, legs, and tail of *Parus ater*, *P. montanus*, *P. cristatus*, *Regulus regulus*, and *Certhia familiaris* is analysed and compared, and correlations are sought with locomotion pattern and feeding station selection. These species are treated together because they are sympatric, occur in the same habitat, and partly overlap in feeding station selection, as well as in food selection. Where possible, the selective advantage of a feature is judged in terms of the energy savings that it makes possible with the respective locomotion pattern.

P. ater has relatively low weight, low wing loading and long wing span. It is adapted to slow flight and high manoeuvrability.

P. montanus has high wing loading, relatively short wings and long tail. It is not well adapted to manoeuvrable flight, but more to a clinging and climbing behaviour.

P. cristatus has the highest wing loading of the species. It has short and broad wings, and rather short tail in relation to the body size. It is not adapted to slow manoeuvrable flight. It hops about on the branches or ground to a greater extent than the other species. Further, by its mere size, it is more adapted to low temperatures than the other species.

R. regulus and *C. familiaris* have the lowest wing loadings and shortest arm wings in relation to the total length of the wings. *C. familiaris* also has relatively long span. The longer the span the lower the induced power, which forms a big part of the power consumption in hovering. The induced power per unit body mass is lowest in *C. familiaris* (1.13 W kg^{-1}), and lower in *R. regulus* (1.19 W kg^{-1}) and *P. ater* (1.21 W kg^{-1}) than in *P. montanus* (1.28 W kg^{-1}) and *P. cristatus* (1.31 W kg^{-1}). The ratio (length of hand wing)/(length of arm wing) is 3.0 and 2.9 in *C. familiaris* and *R. regulus*, respectively, and 2.4–2.6 in the other species. The shorter the arm wing is in relation to the total length of the wing, the more proximally the main mass of the wing will be located, and the less the inertial power and inertial loads on the wing skeleton become. The inertial power is another power drain in hovering. Therefore, because of their low wing loading and short arm wings, *R. regulus* and *C. familiaris* are particularly well adapted to slow flight and to hovering.

P. ater and *R. regulus* are partly migratory and, therefore, should benefit more by long wing span than the other species. In fact, *P. ater* has relatively long span while *R. regulus* has not. The relatively short span in *R. regulus* is probably an adaptation for manoeuvrability and practicability in the dense vegetation where it usually forages.

As related to body size, *C. familiaris* has the shortest legs, longest tail and toes, and longest and most curved claws, features that are obvious adaptations to climbing locomotion. The reduction of the leg length in the course of adaptations for climbing has affected the tibiotarsus most and the femur least. It is especially important for the tibiotarsus to be short to minimize the muscle force needed for clinging on a vertical trunk, and also to shorten the legs with least loss of step length. The tail is used as support in climbing (although not during the latter part of the power stroke). The longer the tail is, the less the horizontal force between claw and bark becomes, and, hence, the less the energy expenditure during the power stroke in climbing.

The three tits have almost the same relative leg length. *R. regulus* has the longest legs in relation to body size.

P. ater, *P. montanus* and *C. familiaris* have relatively short tarsometatarsus. Further, *P. ater* and *R. montanus* have long muscle lever arm of the flexor of the tarsometatarsus. Both characters are adaptations for hanging under branches and/or for climbing.

Birds with need of rapid leg movements should have a short lever arm for the flexor muscle of the tarsometatarsus. During foraging *R. regulus*, *P. cristatus* and *C. familiaris* use their legs more for hopping, which requires speed of leg movements, and less for hanging than do *P. ater* and *P. montanus*, and they also have shorter muscle lever arms than the latter two species. In *C. familiaris* the short tarsometatarsus thus is adapted for hanging whereas the short lever arm of the muscle force is not.

When the bird is hanging under a perch with 45° flexion of the tarsometatarsus relative to the tibiotarsus, then the muscle force (of M. tibialis anticus) per unit body mass is about 36, 44, 45 and 54% larger in *R. regulus* than in *P. cristatus*, *P. ater*, *C. familiaris* and *P. montanus*, respectively. The corresponding differences between *P. cristatus* and the three latter species are 6, 7 and 14%.

A clustering process was used to illustrate more clearly the phenetic resemblances among the species regarding the morphology of the locomotor apparatuses. As regards the wing skeleton the tits form a group, and *C. familiaris* is more similar to the tits than to *R. regulus*. The wing-form phenogram shows that *P. montanus* and *P. cristatus* resemble each other most, that *P. ater* is intermediary between these tits and *R. regulus*, and that *C. familiaris* is most similar to *R. regulus*. The phenogram based on the form of the leg and foot shows that the tits resemble each other most and that *R. regulus* and *C. familiaris* are rather unlike the tits and also very unlike each other.

In the tits, the skeleton of the legs is more diverse than that of the wings, and seems to have been subjected to more divergent selection pressures than the wing skeleton. As regards aerial locomotion in the three tits, the adaptation to different niches, and hence to different flight patterns, have led to divergent evolution of the wing feathers rather than of the wing skeleton.

The pattern for all five species together is most diverse in leg characters and wing form and least diverse in the wing skeleton.

1. INTRODUCTION

This paper treats the functional morphology of the wings and legs of the coal tit (*Parus ater*), the crested tit (*P. cristatus*), the willow tit (*P. montanus*), the goldcrest (*Regulus regulus*) and the treecreeper (*Certhia familiaris*). These species occur in Old World coniferous forests and usually gather in mixed-species foraging flocks during the non-breeding season. These species are treated together because they (1) are sympatric, (2) occur in the same habitat, and (3) partly overlap in feeding station selection as well as in food selection. Thereby, they probably influence each other via interspecific competition in an ecological, short time-scale, and, therefore, also in the evolutionary perspective. Their coadaptation may be expected to have involved some divergence as regards feeding behaviour and adaptive morphology. Furthermore, the fact that these species occur together in mixed-species foraging flocks, thus potentially influencing each other's foraging behaviour by watching each other (see, for example, Newton 1967 on cardueline finches; Krebs *et al.* 1972 on the great tit *Parus major*), is another reason for treating these species together.

The birds feed on small spiders, insects, and seeds, and should be classified as 'searchers' rather than 'pursuers' according to the terminology of MacArthur & Pianka (1966). Since 'searchers' spend most of their foraging time searching for food, they cannot afford to reject many kinds of food items, and therefore may be expected to have a generalized diet. The diet of the birds treated here has been investigated by, among others, Palmgren (1932), Haftorn (1954, 1956*a*, *b*, *c*), Gibb (1954, 1960) and Thaler (1973). Coexisting 'searchers' with wide, overlapping, diets may be expected to be ecologically segregated via differences in habitat and/or feeding station selection.

The species treated here differ in feeding station selection, although large overlaps occur (see, for example, Haftorn 1954, 1956*a*, *b*, *c*; Gibb 1954, 1960; Snow 1954). The exploitation of different feeding stations usually requires different structural adaptations of the locomotor apparatus. Therefore, these species can be expected to differ in the adaptive morphology of wings and legs, and the investigation of this possibility is the theme of this paper.

Several investigations have been made on the functional morphology of wings and legs of passerine birds. Palmgren (1932) studied the functional morphology of the hind legs of *R. regulus* and *P. montanus*. Rüggeberg (1960) also made an investigation of the morphology of the hind legs in several passerine birds including *R. regulus* and *C. familiaris*. Partridge (1976) gave some aspects of the morphology of *P. caeruleus* and *P. ater* in relation to their foraging behaviour. The morphology of different tree-trunk foragers has been described by Richardson (1942), who included *C. familiaris*. Winkler & Bock (1976) analysed the mechanics of climbing birds and considered various morphological adaptations for climbing.

The purpose of this investigation is to attempt to answer the following questions:

(i) Which are the quantitative, absolute, morphological differences in the locomotor apparatus among the five species, and what are their adaptive values?

(ii) Which are the relative morphological differences among these species, i.e. differences that are not due to scaling effects? The following example is given to clarify this point. Two birds with different weight, but with similar geometry, do not have the same wing loading, because wing area goes with the square of the linear dimension whereas weight is proportional to the linear dimension cubed. This difference in wing loading is a scaling effect which follows from the difference in size, although geometric similarity prevails. Any deviation from the scaling principles can easily be identified when ratios are taken between pertinent quantities transformed to the same dimension. Furthermore, by curve-fitting for some characters of birds of various sizes there result power functions with exponents that differ from those expected if geometric similarity did obtain. These exponents do not differ much from those for geometric similarity. Therefore, when the power function for a morphological character is not known, the exponent for geometric similarity and that for elastic similarity (McMahon 1975) are used instead in this paper. So, by using empirically found exponents, or the exponents based on geometric or elastic similarity when the exponent is not known, one can identify adaptations involving deviations from the mean trend (of specified kind; i.e. value of exponent) within birds of different size and sort.

(iii) What correlations can be found among differences in absolute and relative sizes and locomotor patterns?

(iv) What correlations can be found between feeding station selection and locomotor pattern during foraging?

2. Materials and methods

The species compared have been collected in the South or middle of Sweden and Norway and hence most likely are referable to the subspecies *Parus a. ater* L., *Parus c. cristatus* L., *Parus montanus borealis* de Selys-Longchamps, *Regulus r. regulus* (L.) and *Certhia f. familiaris* L., although this was not specifically checked.

Measurements on the skeleton of the extremities were taken on museum material, most of which lacked data on weight and sex. Measurements were taken to the nearest 0.1 mm with a slide caliper.

Living birds were caught with mist nets during August and September 1975 in coniferous forests about 50 km east of Göteborg (Gothenburg) and were weighed immediately after capture. All weights reported here are of living specimens. Measuring of toes and wings, including feathers, involved some extension of these structures. Hence, these structures must not be dry and stiff, and, therefore, all these measurements were taken on living or dead, but fresh specimens.

Living *P. cristatus* and *R. regulus* could be sexed whereas living *P. ater*, *P. montanus* and *C. familiaris* were not. The wing areas were measured from photographs on extended wings with the aid of a polar compensating planimeter.

A clustering process was used to illustrate more clearly the phenetic resemblances among the species regarding the morphology of the locomotor apparatuses. The technique applied was the weighted pair-group method with arithmetic averages, which was introduced by Sokal & Michener (1958) and later also explained by Sneath & Sokal (1973). The resemblance matrices (upon which one operates to obtain the phenograms) here contain dissimilarity coefficients based on the percentage differences between mean values of various morphological structures of two species. The dissimilarity coefficient, k, was calculated from the formula

$$k = (1 - X/Y), \tag{1}$$

where X and Y are the mean values of a particular morphological character of two species, Y being the largest value. As can be seen, $X = Y$ gives $k = 0$. Thus, the larger the difference is in a certain character between two species, the larger the coefficient becomes.

2.1. *Definitions*

When wing measurements were taken the wings were adjusted to lie in the positions which they are judged to attain during the middle of the downstroke in flight. Thus, the wings were moderately outstretched laterally on a horizontal plane. The leading edges of the two wings, hand wings included, were adjusted to lie along a straight line normal to the median sagittal plane of the body.

Total wing area, S. When considering aerodynamic characteristics, the total wing area is conventionally measured as the area of both wings, and the portion of body in between, as projected on the wing chord plane.

S_{w} is the area of one wing only, i.e. from the innermost secondary feather, body excluded.

Wing Span, b, is the distance between the two wing tips, when the wings are moderately extended laterally as described above.

Wing length, l_{w}, is the distance from the humero-scapular joint to the wing tip (the tip of the longest primary feather) when the wing is moderately extended.

Arm wing length, l_{aw}, is the distance from the humero-scapular joint to the ulno-carpal joint.

Hand wing length, l_{hw}, is the distance from the ulno-carpal joint to the wing tip (the tip of the longest primary feather).

Aspect ratio is the ratio of the wing span to the mean width of the wing, and is calculated as the ratio of the wing span squared to the total wing area, b^2/S. Long, narrow wings have high aspect ratio, and short, broad wings low aspect ratio.

Foot length, l_{foot}, is the distance between the bases of the claws of toes II and IV, as shown in figure 1.

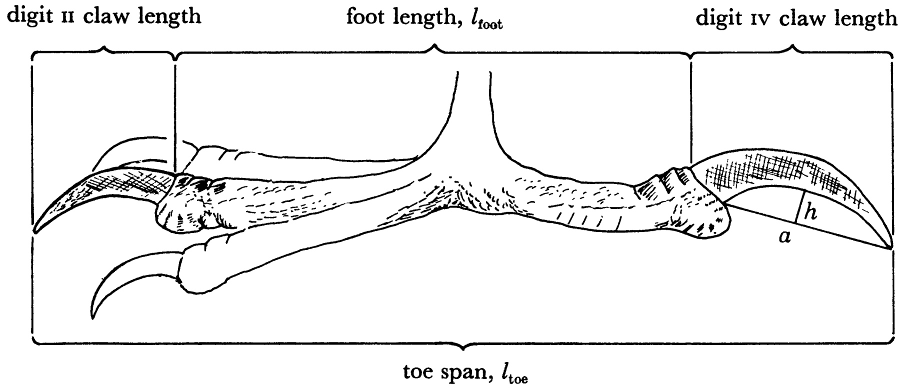


FIGURE 1. Diagram showing how measurements were taken of claws, foot, and toe span.

Toe span, l_{toe}, is the distance between the tips of the claws of toes II and IV, as shown in figure 1.

Claw index, I_c, is the ratio a/h of the length, a, of a claw to height, h, of its curvature, as shown in figure 1.

Relative lengths $\bar{l}$ *and* $\bar{\bar{l}}$. These parameters are defined by the relations

$$\bar{l} = l/M^{\frac{1}{3}} \text{ (in m/kg}^{\frac{1}{3}}\text{)},$$
$$\bar{\bar{l}} = l/M^{\frac{1}{4}} \text{ (in m/kg}^{\frac{1}{4}}\text{)}.$$

2.2. *Measurements*

The mass M and the following direct measurements were used for comparisons: total wing area S, area of one wing S_w, wing span b, and the lengths of the entire wing l_w, arm wing l_{aw}, hand wing l_{hw}, tail l_t, foot l_{foot}, the claws of digits II and IV, humerus l_h, ulna l_u, carpometacarpus l_{cmc}, femur l_f, tibiotarsus l_{tt} and of tarsometatarsus l_{tmt}. These direct measurements give information on the *absolute* differences in these structures among the five bird species.

Greenewalt (1962, 1975) compiled data from different sources on various morphological characters of flying animals. He fitted power functions to the data for various combinations of characters. If geometric similarity were to prevail wing span would be proportional to (body mass)$^{0.33}$ and wing area to (body mass)$^{0.67}$. However, using empirical data Greenewalt (1975) found the following relations for his 'passeriform model', which included species of, among others, the order Passeriformes:

$$(\text{wing span}) \propto (\text{wing area})^{0.5313},$$

and

$$(\text{body mass}) \propto (\text{wing area})^{1.275}.$$

Recalculated and expressed in relation to body mass these became

$$(\text{wing span}) \propto (\text{body mass})^{0.417},$$

and

$$(\text{wing area}) \propto (\text{body mass})^{0.784}.$$

These latter exponents are used in this investigation, i.e. I examined to what extent my birds (all of order Passeriformes) deviated from the general trends specified by these exponents.

Arguments based on elastic stability and flexure underlie the prediction by McMahon (1973) that leg length of animals goes inversely as body mass to the 1/4 power. McMahon (1975) tested his prediction on artiodactyls and the fit was satisfactory. Since it is uncertain whether this power function, or that based on geometric similarity, do apply to birds, the comparison of adaptations among species is carried through with both models, in parallel, for those skeletal elements to which power functions have not been empirically fitted. Therefore, the lengths of the wing and leg bones are compared among the species with reference to expectations based on both geometric and elastic similarities, i.e. with each quantity proportional to (body mass)$^{\frac{1}{3}}$ and to (body mass)$^{\frac{1}{4}}$, respectively.

Empirically-related power function for the bird tail has not been calculated. Therefore, the comparison among the species of the tail length is based on geometric similarity.

The following parameters were calculated: wing loading W/S (where W is body weight in newtons), relative wing area, $S_{\mathrm{w}}/M^{0.784}$, disk loading W/S_{d}, aspect ratio b^2/S, relative wing span $b/M^{0.417}$, and the following ratios: $l_{\mathrm{hw}}/l_{\mathrm{aw}}$, $\bar{l}_{\mathrm{tail}}$, $\bar{l}_{\mathrm{toe}}$, $\bar{\bar{l}}_{\mathrm{toe}}$, $I_{\mathrm{c}}^{\mathrm{II}}$ and ${}_{\mathrm{c}}^{\mathrm{IV}}$ (indices of claws II and IV), $\bar{l}_{\mathrm{h}}$, $\bar{\bar{l}}_{\mathrm{h}}$, $\bar{l}_{\mathrm{u}}$, $\bar{\bar{l}}_{\mathrm{u}}$, $\bar{l}_{\mathrm{cmc}}$, $\bar{\bar{l}}_{\mathrm{cmc}}$, $\bar{l}_{\mathrm{f}}$, $\bar{\bar{l}}_{\mathrm{f}}$, $\bar{l}_{\mathrm{tt}}$, $\bar{\bar{l}}_{\mathrm{tt}}$, $\bar{l}_{\mathrm{tmt}}$, $\bar{\bar{l}}_{\mathrm{tmt}}$, $l_{\mathrm{h}}/l_{\mathrm{u}}$, $l_{\mathrm{f}}/l_{\mathrm{tt}}$ and $l_{\mathrm{tt}}/l_{\mathrm{tmt}}$, where $\bar{l}$ equals $l/M^{\frac{1}{3}}$, and $\bar{\bar{l}}$ equals $l/M^{\frac{1}{4}}$. In all ratios which include the body mass (or weight) the mean mass (or weight) of the birds was used. These different parameters give information about the *relative* differences among the species. These quantities thus can be used to trace morphological dissimilarities in proportions among the species. However, differences in absolute measurements may be equally important from the adaptive point of view and are also considered below.

Each species is compared with each of the other four species. The differences obtained among the species are tested with the Mann–Whitney U test. Three significance levels are indicated in the tables. Since many variables are tested among several species, there is a large risk of obtaining fortuitous significances at low significance levels. Therefore, I base conclusions mostly on differences with significance levels of $P < 0.002$ or less. Further, for the same reason, the number of tests is held at a minimum. Some tests are dependent on each other. Only independent variables contribute to the problem of fortuitous significances. Hence, there are fewer independent tests than listed in the matrices.

S.I. units are used throughout.

3. Feeding station selection and foraging behaviour

As a background for the attempt to relate wing and leg morphologies to feeding station selection and foraging behaviour, a brief account of the latter two aspects of the niches is given here. It is based mainly on Haftorn (1954, 1956*a*, *b*, *c*) and Palmgren (1932), and on my own observations.

3.1. *Feeding stations*

The feeding stations in spruce (*Picea abies* (L.) H. Karst.) of the different species are schematically shown in figure 2.

R. regulus and *P. ater* forage on the needled outer parts of the main-branches, and even on the finest sub-branches. In winter the goldcrest often forages also on the forest ground when this is snow-free.

P. cristatus occupies the main-branches, too, but seldom the tip or base of the branch. It is also often seen on the forest ground.

P. montanus occupies chiefly the base of the main-branches and even the trunk, while *C. familiaris* mainly forages on the trunk.

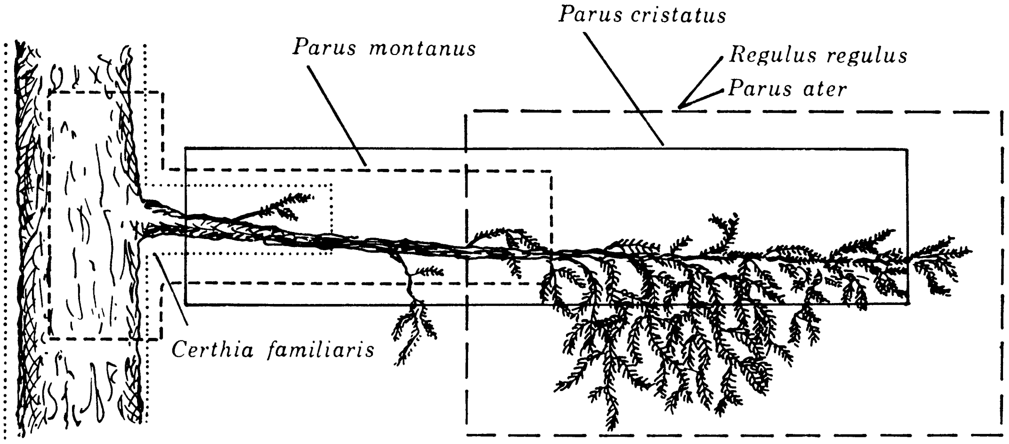


FIGURE 2. Schematic illustration of the feeding station selection in spruce by the tits, the goldcrest, and the treecreeper. [Modified from Haftorn (1956*c*)].

3.2. *Foraging behaviour*

R. regulus is very good in manoeuvring and hovers often in front of, or underneath, the branches. Hovering is used both for search for food and for picking up food items (R. Å. Norberg, personal communication). It moves about very agilely within the mesh-work of sub-branches, has a very agile food-searching behaviour, and uses the wings much more than the other species. It does not hang under the branches with the back downwards as often as the tits do. During a day in autumn (October–November) in southwest Sweden, a goldcrest hovers on average about four times per minute, and each hovering lasts for $\frac{1}{4}$–$1\frac{1}{2}$ s. (R. Å. Norberg, personal communication). About 6 % of the foraging time thus is spent hovering.

P. ater, like *R. regulus* is more acrobatic than the other species. It often hangs under the branches, even on the vertically hanging sub-branches of spruce, and also often on the cones.

P. cristatus mostly moves about with hops on branches and on the ground. It prefers the main and secondary branches, but sometimes clings directly also onto the needles, especially in pine.

P. montanus moves with hops on the branches and often clings to the trunk. When moving on the trunk it has a vertical, head-up position, often uses its wings, and often takes support from the tail (J. Ekman & R. Å. Norberg, personal communications).

C. familiaris climbs on the trunk in a vertical, head-up position. It typically starts at the base of a tree and climbs upwards, sometimes in a helical path around the trunk, flies to a lower level of another tree and climbs upwards again. As a rough estimate the treecreeper spends more than 90 % of its foraging time climbing on vertical trunks. On smooth bark it can often be seen to lose its hold. It then immediately uses its wings in a head-up position, reminiscent of hovering flight, to get hold of the bark again. In fact, the treecreeper sometimes hovers in front of branches during foraging (J. Ekman, personal communication).

TABLE 1. BODY MASSES AND ABSOLUTE MEASUREMENTS OF WINGS, LEGS AND TAIL

(n is number of animals in sample)

	Parus ater			*Parus montanus*			*Parus cristatus*			*Regulus regulus*			*Certhia familiaris*		
	n	$\bar{x}$	S.E	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
body mass, M/g	32	9.1	0.08	73	10.9	0.08	8♂	12.2	0.53	16♂	5.9	0.12	8	9.1	0.22
							8♀	10.8	0.21	11♀	5.7	0.09			
wing span, b/cm	11	18.0	0.14	15	18.5	0.15	7	18.6	0.27	8♂	14.7	0.15	7	18.9	0.18
										6♀	14.3	0.15			
wing area, S/cm²	6	63.6	2.0	6♂	74.3	1.3	5♂	73.4	1.5	8♂	45.3	1.1	5	72.3	3.2
				7♀	73.1	2.0	5♀	66.4	0.87	6♀	43.3	0.82			
area of one wing, S_w/cm²	6	26.9	1.0	6♂	31.2	0.54	5♂	31.5	0.14	8♂	18.1	0.35	5	31.2	1.4
				7♀	30.7	0.78	5♀	28.7	0.43	6♀	17.3	0.46			
arm wing length, l_{aw}/cm	5	2.3	0.06	6♂	2.5	0.04	5♂	2.5	0.13	8♂	1.8	0.05	4	2.2	0.07
				7♀	2.5	0.04	5♀	2.4	0.06	6♀	1.8	0.08			
hand wing length, l_{hw}/cm	17♂	6.2	0.36	6♂	6.0	0.05	5♂	6.1	0.06	8♂	5.3	0.05	8	6.5	0.04
	15♀	6.0	0.22	7♀	5.8	0.08	5♀	5.8	0.02	6♀	5.0	0.04			
tail length, l_{tail}/cm	8	4.7	0.05	6♂	5.9	0.10	5♂	5.2	0.02	8♂	4.2	0.03	5	6.3	0.09
				7♀	5.7	0.07	5♀	4.9	0.09	6♀	3.8	0.07			
foot length, l_{foot}/cm	7	1.8	0.04	6♂	1.7	0.02	5♂	1.9	0.03	8♂	1.6	0.01	6	1.9	0.02
				7♀	1.7	0.03	5♀	1.8	0.02	6♀	1.6	0.03			
claw digit II length/cm	7	0.52	0.013	6♂	0.57	0.012	5♂	0.49	0.006	8♂	0.45	0.010	5	0.65	0.013
				7♀	0.55	0.012	5♀	0.46	0.010	6♀	0.46	0.013			
claw digit IV length/cm	7	0.66	0.028	6♂	0.75	0.015	5♂	0.63	0.010	8♂	0.59	0.005	5	0.96	0.015
				7♀	0.72	0.017	5♀	0.61	0.010	6♀	0.60	0.007			
claw digit II index, I_c^{II}	4	4.8	0.20	19	5.1	0.14	10	5.4	0.18	8♂	5.1	0.24	5	3.5	0.14
										7♀	5.1	0.27			
claw digit IV index, I_c^{IV}	4	5.0	0.33	19	4.9	0.15	11	5.0	0.15	8♂	5.0	0.13	5	4.5	0.22
										7♀	4.8	0.19			

TABLE 2. VARIOUS MEASUREMENTS OF THE WING, TAIL AND FOOT

(The values are means of the ratios of the different variables, as calculated for the individual specimen. Those measurements marked with * are ratios based on mean values of span and wing area in table 1)

	Parus ater			*Parus montanus*			*Parus cristatus*			*Regulus regulus*			*Certhia familiaris*		
	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
wing loading, $(W/S)/(\mathrm{N\ m^{-2}})$	5	14.2	0.41	13	14.5	0.22	5♂	16.4	0.31	8♂	12.9	0.31	5	12.4	0.60
							5♀	15.9	0.21	6♀	12.9	0.26			
relative wing area, $S_w/M^{0.784}$	6	0.11	0.033	13	0.11	0.002	5♂	0.11	0.003	8♂	0.10	0.002	5	0.12	0.005
							5♀	0.10	0.002	6♀	0.10	0.002			
aspect ratio, b^2/S	4	5.0	0.16		4.7*			5.0*		8♂	4.8	0.07	4	4.8	0.09
										6♀	4.7	0.11			
relative wing span $b/M^{0.417}$	11	1.27	0.01	15	1.21	0.01	7	1.20	0.02	8♂	1.25	0.01	7	1.33	0.02
										6♀	1.22	0.01			
(length of hand wing)/(length of arm wing), l_{hw}/l_{aw}	5	2.6	0.10	6♂	2.4	0.05	5♂	2.5	0.14	8♂	2.9	0.08	4	3.0	0.10
				7♀	2.3	0.05	5♀	2.5	0.07	6♀	2.9	0.11			
relative tail length, $\bar{l}_{tail}$	7	0.23	0.002	13	0.26	0.003	5♂	0.23	0.001	8♂	0.23	0.002	5	0.30	0.005
							5♀	0.22	0.004	6♀	0.22	0.004			
relative toe span, $\bar{l}_{toe}$	7	0.14	0.002	13	0.14	0.001	5♂	0.13	0.001	8♂	0.14	0.001	5	0.17	0.001
							5♀	0.13	0.002	6♀	0.15	0.002			
$\bar{\bar{l}}_{toe}$	7	0.095	0.002	13	0.094	0.001	5♂	0.090	0.001	8♂	0.094	0.001	5	0.115	0.001
							5♀	0.090	0.001	6♀	0.095	0.002			

4. Results

The results of the measurements are summarized in tables 1–3. All species have been tested statistically against each other regarding differences in those relative measurements which are important for the functional considerations. The results are shown in matrix form in table 4.

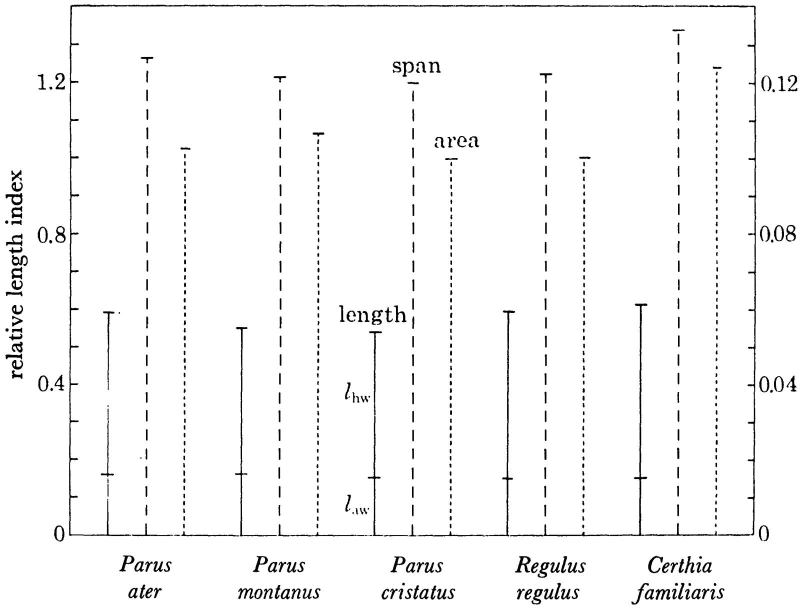


Figure 3. Relative lengths of wing, $l_w/M^{0.417}$ (full line, with arm wing length l_{aw} and hand wing length l_{hw} marked), wing span, $b/M^{0.417}$ (left dashed line), and relative wing area, $S_w/M^{0.784}$ (right dashed line). M is bird mass.

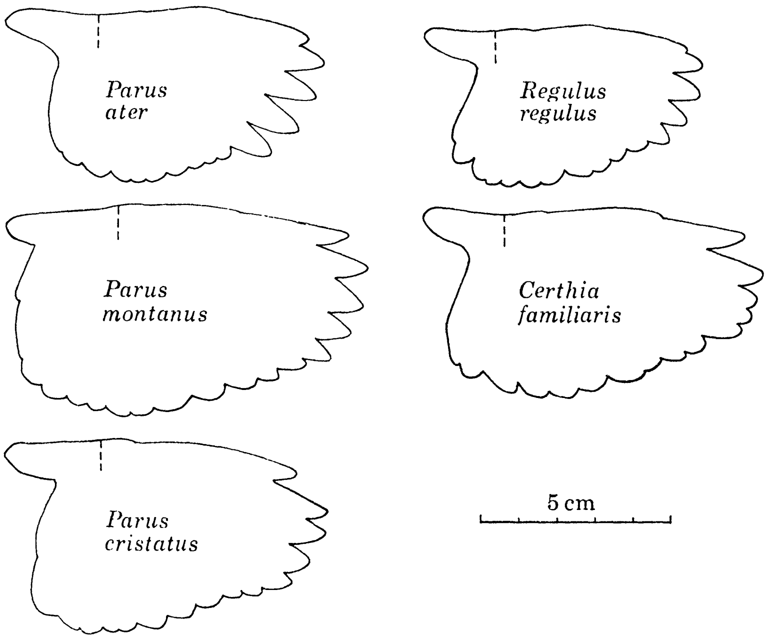


Figure 4. Contours of the wings of the three tits, the goldcrest, and the treecreeper, with the boundary between the arm wing and hand wing marked.

4.1. *Absolute measurements* (table 1)

P. cristatus is the heaviest of the species, closely followed by *P. montanus*. *P. ater* and *C. familiaris* come next and are both of about the same weight. *R. regulus* is the lightest and weighs only half as much as *P. cristatus*.

The wing lengths are almost the same in the tits and in *C. familiaris*, but less in *R. regulus*. Furthermore, *R. regulus* has the shortest tail, toes and claws. *C. familiaris* has the longest hand wing, tail, toes, and claws.

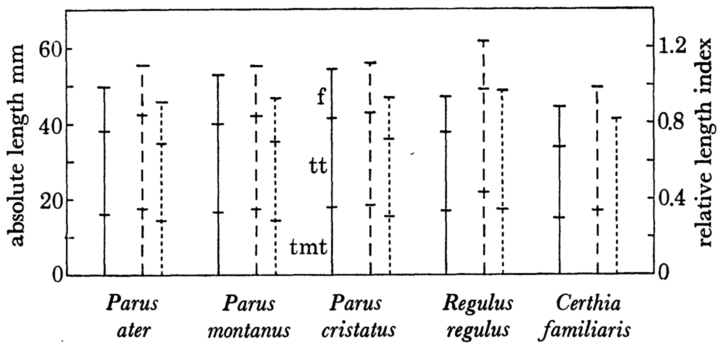


FIGURE 5. Absolute (full line) and relative (dashed lines; left with geometric similarity, right with elastic similarity) lengths of femur (f), tibiotarsus (tt), and tarsometatarsus (tmt).

4.2. *Relative measurements*

4.2.1. *Weight and wing form relations* (tables 2 and 3, figure 3)

P. cristatus has the highest wing loading (W/S) and in this respect differs significantly from the other four species. *R. regulus* has the lowest wing loading and here differs significantly from the tits but not from *C. familiaris*.

C. familiaris has the largest relative wing area ($S_w/M^{0.784}$) of the species.

4.2.2. *Wing form* (tables 2–4, figure 4)

All the species have low aspect ratio wings, which means that the wings are relatively short and broad.

C. familiaris has the longest wing span in relation to body size ($b/M^{0.417}$) and differs significantly in this respect from the other four species. *P. ater* has the second longest span but differs significantly only from *P. cristatus* (and from *C. familiaris* which has the longest). Though *R. regulus* has long wings in relation to body size ($l_w/M^{0.417}$, figure 3) its span is not very long. This is due to the bird's thin body.

C. familiaris and *R. regulus* have shorter arm wings in relation to the total wing length than any of the other three species (cf. l_{hw}/l_{aw} in table 2). In the outstretched wing, the length of the arm wing is determined by the lengths of the humerus and ulna, and also by the angle at which the ulna is held relative to the humerus. Effort was taken to stretch the wings equally much when they were measured.

The relative length of humerus ($\bar{l}_h$ and $\bar{\bar{l}}_h$) is shorter in *R. regulus* than in the other species. The ratio of humerus and ulna lengths (l_h/l_u) is much smaller in *R. regulus* than in any of the other species.

Table 3. ABSOLUTE AND RELATIVE LENGTHS OF WING AND LEG BONES

	Parus ater			*Parus montanus*			*Parus cristatus*			*Regulus regulus*			*Certhia familiaris*		
	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
humerus, l_h/mm	9	12.7	0.14	10	13.6	0.11	6	13.9	0.14	14	9.6	0.09	9	12.7	0.15
$\bar{l}_h$	9	0.061	0.001	10	0.061	0.001	6	0.062	0.001	14	0.053	0.0005	9	0.061	0.001
$\bar{\bar{l}}_h$	9	0.041	0.0005	10	0.042	0.0003	6	0.042	0.004	14	0.035	0.0003	9	0.041	0.001
ulna, l_u/mm	9	15.1	0.17	12	16.3	0.18	6	16.3	0.26	14	12.9	0.12	10	15.7	0.11
$\bar{l}_u$	9	0.072	0.001	12	0.074	0.001	6	0.072	0.001	14	0.072	0.001	10	0.076	0.001
$\bar{\bar{l}}_u$	9	0.049	0.001	12	0.050	0.001	6	0.050	0.001	14	0.047	0.0004	10	0.051	0.0004
carpometacarpus, l_{cmc}/mm	7	8.7	0.08	12	9.0	0.08	6	9.1	0.13	13	7.2	0.07	9	9.0	0.10
$\bar{l}_{cmc}$	7	0.041	0.0004	12	0.041	0.0004	6	0.041	0.001	13	0.040	0.0003	9	0.043	0.0005
$\bar{\bar{l}}_{cmc}$	7	0.028	0.0003	12	0.028	0.0003	6	0.028	0.0004	13	0.026	0.0002	9	0.029	0.0003
humerus/ulna, l_h/l_u	8	0.84	0.006	10	0.84	0.007	6	0.85	0.009	14	0.74	0.005	9	0.81	0.007
femur, l_f/mm	9	11.8	0.13	12	12.9	0.09	7	12.8	0.15	14	9.7	0.11	8	10.8	0.08
$\bar{l}_f$	9	0.056	0.001	12	0.058	0.0004	7	0.057	0.001	14	0.054	0.0004	8	0.052	0.0004
$\bar{\bar{l}}_f$	9	0.038	0.0004	12	0.040	0.0003	7	0.039	0.001	14	0.035	0.0003	8	0.035	0.0003
tibiotarsus, l_{tt}/mm	7	22.2	0.35	11	23.8	0.14	6	23.9	0.02	14	21.2	0.15	8	19.0	0.11
$\bar{l}_{tt}$	7	0.11	0.002	11	0.11	0.001	6	0.11	0.001	14	0.12	0.001	8	0.091	0.001
$\bar{\bar{l}}_{tt}$	7	0.072	0.001	11	0.074	0.0004	6	0.073	0.0001	14	0.077	0.001	8	0.062	0.0004
tarsometatarsus, l_{tmt}/mm	6	16.0	0.17	12	16.6	0.11	6	17.9	0.14	14	17.1	0.11	8	15.3	0.10
$\bar{l}_{tmt}$	6	0.076	0.001	12	0.075	0.001	6	0.079	0.001	14	0.095	0.001	8	0.073	0.001
$\bar{\bar{l}}_{tmt}$	6	0.052	0.001	12	0.051	0.0003	6	0.055	0.0004	14	0.062	0.0004	8	0.050	0.0003
femur/tibiotarsus, l_f/l_{tt}	8	0.53	0.006	11	0.55	0.003	6	0.53	0.005	14	0.45	0.003	8	0.57	0.004
tibiotarsus/tarsometatarsus, l_{tt}/l_{tmt}	5	1.4	0.02	11	1.4	0.01	6	1.3	0.01	13	1.2	0.01	8	1.2	0.003

4.2.3. *Leg length and proportions* (tables 3 and 4, figure 5)

The leg length is the sum of the lengths of all three leg bones. *R. regulus* has the longest legs in relation to body size and *C. familiaris* the shortest. The three tits have almost the same, intermediate, relative leg lengths.

The relative length of femur ($\bar{l}_f$ and $\bar{\bar{l}}_f$) is significantly shorter in *C. familiaris* and *R. regulus*

TABLE 4. STATISTICAL TEST OF THE DIFFERENCES AMONG MEASUREMENTS LISTED IN TABLES 2 AND 3

(Each species is tested against each of the other four species with the Mann–Whitney U test. The significance signs within parenthesis refer to the quantities within parentheses (in rightmost column). The same abbreviations are used as in tables 2 and 3. Significance levels: ***, $P < 0.002$; **, $P < 0.02$; *, $P < 0.05$; n.s. = not significant.)

		Parus ater	*Parus montanus*	*Paru cristatus*	*Regulus regulus*	*Certhia familiaris*	
Parus ater			** (**)	n.s. (n.s.)	** (***)	*** (***)	$\bar{l}_f$ ($\bar{\bar{l}}_f$)
			n.s. (n.s.)	n.s. (n.s.)	*** (***)	*** (***)	$\bar{l}_{tt}$ ($\bar{\bar{l}}_{tt}$)
			n.s. (n.s.)	** (**)	*** (***)	** (**)	$\bar{l}_{tmt}$ ($\bar{\bar{l}}_{tmt}$)
			*	n.s.	***	***	l_f/l_{tt}
			**	n.s.	***	**	l_{tt}/l_{tmt}
			n.s. (n.s.)	* (*)	n.s. (n.s.)	** (***)	$\bar{l}_{toe}$ ($\bar{\bar{l}}_{toe}$)
			n.s.	n.s.	n.s.	**	I_c^{II}
Parus montanus	W/S	n.s.		n.s. (n.s.)	*** (***)	*** (***)	$\bar{l}_f$ ($\bar{\bar{l}}_f$)
	$S_w/M^{0.784}$	n.s.		n.s. (n.s.)	*** (***)	*** (***)	$\bar{l}_{tt}$ ($\bar{\bar{l}}_f$)
	$b/M^{0.417}$	n.s.		*** (***)	*** (***)	* (***)	$\bar{l}_{tmt}$ ($\bar{\bar{l}}_{tmt}$)
	l_{hw}/l_{aw}	**		n.s.	***	***	l_f/l_{tt}
	$\bar{l}_{tail}$	***		***	***	***	l_{tt}/l_{tmt}
				n.s. (*)	*** (n.s.)	*** (***)	$\bar{l}_{toe}$ ($\bar{\bar{l}}_{toe}$)
				n.s.	n.s.	***	I_c^{II}
Parus cristatus	W/S	***	***		*** (***)	*** (***)	$\bar{l}$ ($\bar{\bar{l}}_f$)
	$S_w/M^{0.784}$	n.s.	**		*** (***)	*** (***)	$\bar{l}_{tt}$ ($\bar{\bar{l}}_{tt}$)
	$b/M^{0.417}$	***	n.s.		*** (***)	*** (***)	$\bar{l}_{tmt}$ ($\bar{\bar{l}}_{tmt}$)
	l_{hw}/l_{aw}	n.s.	n.s.		***	***	l_f/l_{tt}
	$\bar{l}_{tail}$	n.s.	***		***	***	l_{tt}/l_{tmt}
					*** (**)	*** (***)	$\bar{l}_{toe}$ ($\bar{\bar{l}}_{toe}$)
					n.s.	***	I_c^{II}
Regulus regulus	W/S	***	***	***		* (n.s.)	$\bar{l}_f$ ($\bar{\bar{l}}_f$)
	$S_w/M^{0.784}$	*	**	n.s.		*** (***)	$\bar{l}_{tt}$ ($\bar{\bar{l}}_{tt}$)
	$b/M^{0.417}$	n.s.	n.s.	n.s.		*** (***)	$\bar{l}_{tmt}$ ($\bar{\bar{l}}_{tmt}$)
	l_{hw}/l_{aw}	**	***	***		***	l_f/l_{tt}
	$\bar{l}_{tail}$	n.s.	***	n.s.		n.s.	l_{tt}/l_{tmt}
						*** (***)	$\bar{l}_{toe}$ ($\bar{\bar{l}}_{toe}$)
						***	I_c^{II}
Certhia familiaris	W/S	n.s.	**	***	n.s.		
	$S_w/M^{0.784}$	*	**	***	***		
	$b/M^{0.417}$	***	***	***	***		
	l_{hw}/l_{aw}	n.s.	***	**	n.s.		
	$\bar{l}_{tail}$	***	***	***	***		

than in the tits. The relative length of tibiotarsus ($\bar{l}_{tt}$ and $\bar{\bar{l}}_{tt}$) is significantly longest in *R. regulus* and shortest in *C. familiaris*. The relative length of tarsometatarsus ($\bar{l}_{tmt}$ and $\bar{\bar{l}}_{tmt}$) is significantly longer in *R. regulus* than in the other species, and significantly longer in *P. cristatus* than in the other tits and *C. familiaris*. *C. familiaris* has the shortest tarsometatarsus in relation to body size.

The ratio between the lengths of femur and tibiotarsus (l_f/l_{tt}) is significantly larger in *C. familiaris* than in all the other species, and significantly smaller in *R. regulus* than in the others. The ratio between the lengths of tibiotarsus and tarsometatarsus (l_{tt}/l_{tmt}) is significantly larger in *P. montanus* than in all the other species, and significantly smaller in *R. regulus* and *C. familiaris* than in the tits.

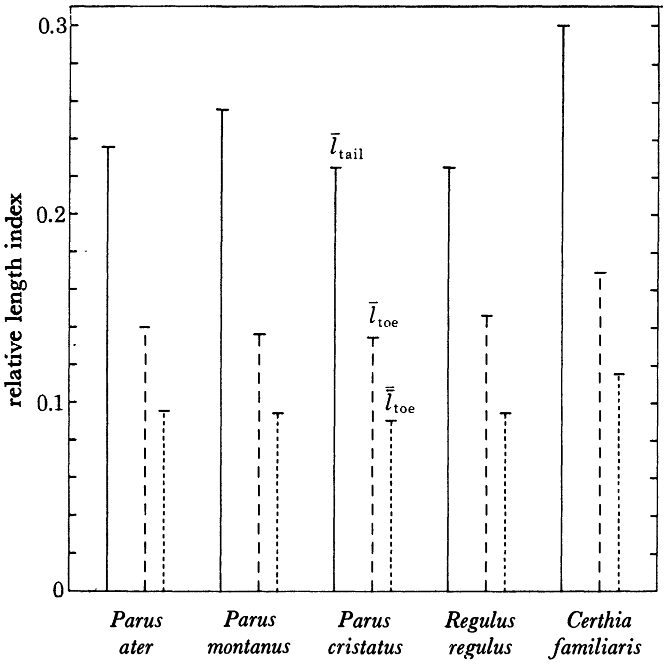


FIGURE 6. Relative lengths of tail, $\bar{l}_{tail}$ (full line) and toe span (dashed lines: left with geometric similarity, $\bar{l}_{toe}$, right with elastic similarity, $\bar{\bar{l}}_{toe}$).

4.2.4. *Toe span and claw form* (tables 1, 2 and 4, figure 6)

C. familiaris has the longest toe span in relation to body size ($\bar{l}_{toe}$ and $\bar{\bar{l}}_{toe}$) and the most curved claws, and differs significantly in these respects from the other species.

4.2.5. *Tail length* (tables 2 and 4, figure 6)

C. familiaris has a significantly longer tail in relation to the body weight ($\bar{l}_{tail}$) than any of the other species. *P. montanus* has the second longest tail and also differs significantly in this respect from the others. The other three species have almost the same relative tail length.

4.3. *Phenetic resemblances* (tables 5–7, figure 7 *a–c*)

The different characters of wings and legs, as specified below, are used to group the species in cluster phenograms to get a clearer overview of similarity between the species in different respects. The wing skeleton, wing form, and leg structure are treated separately and give three different phenograms.

4.3.1. *Wing skeleton*

The characters used are $\bar{l}_{\mathrm{h}}$, $\bar{l}_{\mathrm{u}}$, $\bar{l}_{\mathrm{cmc}}$, and $l_{\mathrm{h}}/l_{\mathrm{u}}$. The dissimilarity values, as defined in the method section, were summed and divided by the number of characters used (in this case four) to give the dissimilarity coefficients in the matrix in table 5. Thus, the coefficients obtained are the mean values of the percental differences for various wing skeleton characters. The dissimilarity coefficients were also calculated for the case of elastic similarity (McMahon 1973), i.e. the three first quantities were substituted by $\bar{\bar{l}}_{\mathrm{h}}$, $\bar{\bar{l}}_{\mathrm{u}}$, and $\bar{\bar{l}}_{\mathrm{cmc}}$, respectively. This does not change the phenogram in figure 7*a* very much. The figure shows that the tits form a cluster. *C. familiaris* resembles the tits more than *R. regulus* does, and it is also more similar to the tits than to *R. regulus*. As can be seen from table 5, *C. familiaris* is most similar to *P. montanus*. This does not come out in the diagram (figure 7*a*), since this is based on an *average* linking clustering method with the use of the values in the matrix (table 5). This method involves some loss of information in the diagram. Only the matrix gives close information on the phenetic relations between single species belonging to different clusters. The diagram, however, gives a better, but not exact, overview of the relationships.

4.3.2. *Wing form*

The following quantities are important for flight: $S_{\mathrm{w}}/M^{0.784}$, b^2/S, $l_{\mathrm{hw}}/l_{\mathrm{aw}}$, and $b/M^{0.417}$. The dissimilarity values among the species for these quantities were summed and divided by the number of characters (in this case four) to give the dissimilarity coefficients in the matrix in table 6. Other quantities on the wing form, derived from any of the principal four ones, were excluded so that a certain dissimilarity should not be represented in more than one measurement. The phenogram in figure 7*b* shows that the tits resemble each other most, and the matrix shows that *P. ater* is intermediary between *P. montanus* and *R. regulus*.

4.3.3. *Leg and foot*

The form of the leg and foot is dependent on the relative lengths of the skeletal elements and the claw form. The dissimilarity values of the following quantities were summed and divided by the number of characters (in this case seven) to give the dissimilarity coefficients in table 7: $\bar{l}_{\mathrm{f}}$, $\bar{l}_{\mathrm{tt}}$, $\bar{l}_{\mathrm{tmt}}$, $\bar{l}_{\mathrm{toe}}$, $l_{\mathrm{f}}/l_{\mathrm{tt}}$, $l_{\mathrm{tt}}/l_{\mathrm{tmt}}$, and $\frac{1}{2}(I_{\mathrm{c}}^{\mathrm{II}}+I_{\mathrm{c}}^{\mathrm{IV}})$. The dissimilarity coefficients were also calculated for the case of elastic similarity, i.e. the four first quantities were substituted by $\bar{\bar{l}}_{\mathrm{f}}$, $\bar{\bar{l}}_{\mathrm{tt}}$, $\bar{\bar{l}}_{\mathrm{tmt}}$, and $\bar{\bar{l}}_{\mathrm{toe}}$, respectively. This does not change the phenogram very much, which is illustrated in figure 7*c*. As shown in the phenogram, the tits resemble each other most. *R. regulus* and *C. familiaris* are very much unlike each other, and also very unlike the tits.

The dissimilarity coefficients, which equal the mean values of the percental differences for various characters, can be directly compared. As regards the tits only, tables 5–7 and figure 7*a–c* show that the skeleton of the legs is more diverse than that of the wings (2.6–3.8 % dissimilarity versus 0.8–1.8 %), and that the wing form (i.e. with the wing feather configuration included) is more diverse (4.3–5.6 % dissimilarity) than either the wing or leg skeletons. It is obvious then that, as regards aerial locomotion in the three tits, the adaptation to different flight patterns have led to divergent evolution of the wing feathers rather than of the wing skeleton.

R. regulus and *C. familiaris* are those species which are most unlike each other as regards wing skeleton (8–11 % dissimilarity) and leg characters (14–15 % dissimilarity). The largest

Table 5. Resemblance matrix with dissimilarity coefficients for wing skeletal elements (listed in §4.3.1)

(The coefficients are based on comparisons among the species with respect to deviations from empirically found mean trends (of specified kind) and from geometric similarity or elastic similarity (values within parentheses) when the mean trend is not known. The higher the coefficient the less the phenetic resemblance.)

	P. ater	*P. montanus*	*P. cristatus*	*R. regulus*	*C. familiarsis*
P. ater	×				
P. montanus	0.012 (0.015)	×			
P. cristatus	0.013 (0.018)	0.009 (0.008)	×		
R. regulus	0.070 (0.096)	0.073 (0.110)	0.071 (0.111)	×	
C. familiaris	0.032 (0.031)	0.029 (0.026)	0.038 (0.034)	0.084 (0.109)	×

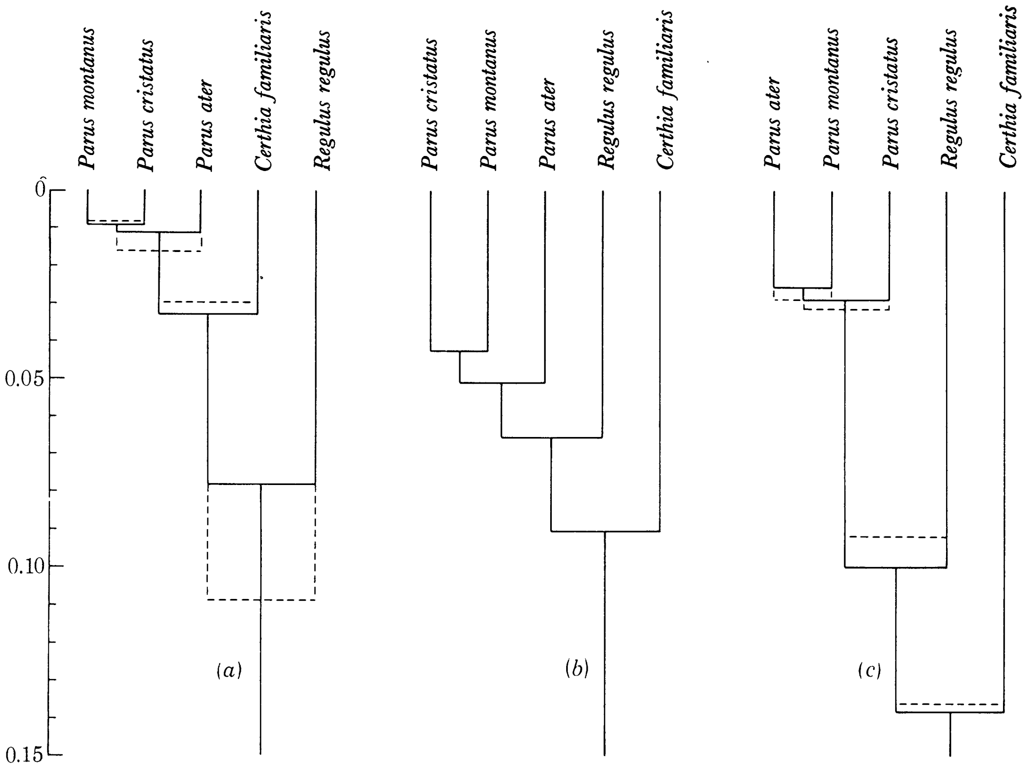


Figure 7. Phenogram of clustering of the data on (*a*) wing skeletal characters in table 5, (*b*) wing form characters in table 6, and (*c*) leg characters in table 7, based on the weighted pair-group method with arithmetic averages. In figure 7*a* and *c*, on wing skeletal and leg characters, solid lines show the result when deviations from geometric similarity are compared among the species, whereas dashed lines show the result with reference to elastic similarity. The higher up the branching point, the greater the phenetic similarity. The coefficients along the vertical axis indicate degree of dissimilarity (see tables 5–7), where each unit ($k = 0.01$) means 1 % dissimilarity.

Table 6. Resemblance matrix with dissimilarity coefficients for wing form characters (listed in § 4.3.2)

(The higher the coefficient the less the phenetic resemblance.)

	P. ater	*P. montanus*	*P. cristatus*	*R. regulus*	*C. familiaris*
P. ater	×				
P. montanus	0.056	×			
P. cristatus	0.046	0.043	×		
R. regulus	0.066	0.075	0.058	×	
C. familiaris	0.085	0.119	0.125	0.076	×

difference in wing form is found between *C. familiaris* on one hand and *P. cristatus* (*ca.* 13% dissimilarity) and *P. montanus* (*ca.* 12% dissimilarity) on the other.

The pattern for all five species taken together is most diverse in leg characters and wing form and least diverse in the wing skeleton (figure 7).

TABLE 7. RESEMBLANCE MATRIX WITH DISSIMILARITY COEFFICIENTS FOR LEG CHARACTERS (LISTED IN § 4.3.3) WHEN DEVIATIONS FROM GEOMETRIC SIMILARITY AND ELASTIC SIMILARITY (WITHIN PARENTHESES) ARE COMPARED AMONG THE SPECIES

(The higher the coefficient the less the phenetic resemblance.)

	P. ater	*P. montanus*	*P. cristatus*	*R. regulus*	*C. familiaris*
P. ater	×				
P. montanus	0.026 (0.029)	×			
P. cristatus	0.029 (0.034)	0.038 (0.037)	×		
R. regulus	0.092 (0.085)	0.108 (0.094)	0.098 (0.085)	×	
C. familiaris	0.112 (0.112)	0.120 (0.125)	0.129 (0.135)	0.149 (0.142)	×

5. FUNCTIONAL CONSIDERATIONS

Throughout this paper, the considerations about structural adaptations among the five species are relative, i.e. when one species is said to be more or less adapted in a certain respect it is regarded to be so in relation to one or more of the other species treated here. Usually it is clearly stated with which species comparisons are made. When not stated, it should be understood that comparisons are confined to within this group of five birds.

5.1. *Weight*

A bird with low weight is often more manoeuvrable and agile than larger birds. Low weight is also advantageous for slow flight and hovering (cf. below). Hovering may enable the bird to find and collect food in places which are inaccessible to other, non-hovering birds. The more agile the foraging behaviour is, and the more hovering flights that are used, the more the bird benefits from small size because of reduction of the energy cost of locomotion during foraging. On the other hand, the larger the bird the larger the fat-storing capacity in relation to the resting metabolic rate, and hence the wider the energy margin for cold periods, such as winter nights. *R. regulus*, which is the lightest of the species, utilizes the outer parts of the branches and hovers often when searching for and picking up food items. *P. ater* is the lightest of the tits, and it forages on the outer parts of the branches, too. It uses its wings to a great extent during foraging. The much heavier *P. cristatus* and *P. montanus* do not use their wings as much as *R. regulus* and *P. ater* during foraging, but move more on the branches.

5.2. *Wing loading*

Low wing loading is advantageous especially for slow flight and hovering. This appears from the following arguments.

The lift force, L, obtained when the wings beat, is proportional to the relative air speed V squared times the wing area S,

$$L \propto V^2 S. \tag{2}$$

During flight with no vertical acceleration the lift force is proportional to the weight of the bird. Hence,

$$V^2 S \propto W, \quad \text{so that} \quad V \propto (W/S)^{\frac{1}{2}}, \tag{3}$$

where V is some characteristic speed. Thus, low wing loading enables the bird to produce enough lift in slow flight and in hovering, without having to use excessively high wingbeat frequencies that would result in large moments of inertia and hence an unnecessary waste of energy for production of inertial power (cf. § 5.5).

R. regulus, which has the lowest wing loading, is the low-speed flyer and hoverer among the species investigated, and has the most power-demanding food searching behaviour. *P. cristatus*, which has the highest wing loading, hops on the branches or on the ground to a greater extent than the other species when searching for food. Hence, its foraging behaviour probably is among the energetically cheapest ones. The other species fall in between *R. regulus* and *P. cristatus* as regards wing loading and probably also as regards energy consumptions during foraging.

5.3. *Wing span and power for hovering*

Different types of flight are associated with different optimum shapes of the wings. All the species in this investigation have relatively broad and short wings although some differences occur among the species. Thus, *P. ater* and *P. cristatus* have higher aspect ratio than the other three species (table 2). Some factors affecting the wing form are discussed below.

The power required to fly is the sum of the *aerodynamic power* (power needed to elicit sufficient aerodynamic force) and the *inertial power* (power needed to oscillate the wings). The aerodynamic power is required for three distinct purposes: (i) to support the weight (*induced power*), (ii) to overcome the profile drag of the body (*parasite power*), and (iii) to overcome the profile drag of the wings (*profile power*) (Pennycuick 1968, 1969, 1972).

In hovering and slow flight the parasite power is very small because of the low relative air speed at the body. To reduce power consumption in hovering, it thus is the induced, profile, and inertial powers, rather than the parasite power, that should be minimized. To find out what structural adaptations that could bring this about, one has to see what factors influence these powers during hovering. The induced and profile powers will be considered first, the inertial power next, and, finally, the conditions for minimization of their sum.

The induced power P_i may be estimated as

$$P_\mathrm{i} = W^{\frac{3}{2}}/b(\tfrac{1}{2}\pi\rho)^{\frac{1}{2}} \tag{4}$$

(Pennycuick 1968) where ρ is air density. To reduce the induced power, the weight has to be reduced and/or the span has to be enlarged. Thus, *the longer the wings the less the induced power* (Pennycuick 1972).

Of the three aerodynamic power components, the profile power is the most difficult to calculate. Pennycuick (1968) estimated this power component in the pigeon (*Columba livia*) on the basis of strip-analysis and found that it was almost constant in the region of minimum power speed, decreasing somewhat at very low speeds, and increasing somewhat at very high speeds. The estimated profile power in *hovering flight* was *ca.* 35 % of the induced power, but was the largest aerodynamic power component (two thirds of total) at speeds from about 4 to 19 m/s.

The wing profile power is proportional to V^3S. An increase of wing span (which would decrease the induced power; see equation (4)) would increase the wing area S and thus the profile power, unless the wings are made compensatorily narrower to maintain the same wing area S. The need of large wing area, in order to keep wing beat frequency and interial power low (see § 5.5), could be met for a hovering bird by adding to the wing length. Therefore, in order to keep the power required for hovering and slow flight low, the wings should be long to reduce the induced power and rather narrow to maintain the wing area and, hence, the profile power low.

TABLE 8. THE INDUCED POWER AND INDUCED POWER PER UNIT BODY MASS (SPECIFIC INDUCED POWER) DURING HOVERING FLIGHT

	Parus ater	*Parus montanus*	*Parus cristatus*	*Regulus regulus*	*Certhia familiaris*
induced power, P_i/W	0.108	0.137	0.148	0.068	0.101
specific induced power, $P_i^*/(\mathrm{W\ kg^{-1}})$	1.21	1.28	1.31	1.19	1.13

However, the longer the wings, the larger the *inertial power* and also the *inertial loads* on the wing skeleton, and the less the manoeuvrability. The larger the inertial loads on the wing skeleton are during flapping accelerations, the stronger, and, thus, heavier, the wing skeleton needs to be, which brings with it larger inertial power (see further § 5.5). Furthermore, long wings are not practical for flapping flight in dense vegetation. Therefore, the actual wing length probably is a near-optimal compromise between the following opposing tendencies: minimization of induced power (tending towards long wings) against minimization of inertial power, inertial loads on the wing skeleton, and improvement of manoeuvrability and practicability (all tending towards short wings).

C. familiaris has the longest relative wing span of the species. During climbing it often uses its wings in a head-up position, reminiscent of hovering flight, and, therefore, is favoured by long wings. Furthermore, *C. familiaris* need not fly about among branches to the same extent as the other birds. It flies mainly between trunks and flies through the canopy of a tree essentially when leaving a tree. It usually alights on the next trunk below the branches, at least below the dense ones in coniferous trees. Selection for short wings to enhance practicability among branches thus should be lower in the treecreeper than in any of the other species. Long wings are to advantage not only in hovering but also in ordinary flight (albeit to a lesser extent because induced power is relatively lower, anyway, in forward flight than in hovering).

C. familiaris has the smallest induced power output per unit body mass (specific induced power, $P_i/M = P_i^*$) of the species (table 8). In *R. regulus* and *P. ater*, P_i^* is also relatively small. *R. regulus*, which often hovers, should also benefit by long wings. In fact, the goldcrest has relatively long wings but a short wing span due to the thin body. A reason why the goldcrest does not have still longer wings and thereby longer relative wing span than *C. familiaris* and *P. ater* may be the fact that it mostly flies about among branches and often hovers within meshworks of twigs, where long wings would be unpractical. *P. ater*, which also often hovers, has significantly longer relative wing span than *P. cristatus*. In *P. montanus* and *P. cristatus* the induced power per unit body mass during hovering is higher than in the other species (table 8), but hovering is a rare phenomenon in these two species. Contary to *C. familiaris* these tits often move about among branches and twigs and thereby need to have shorter wings.

5.4. *Wing span and migratory habit*

Migratory habits should influence wing length. During migration it is particularly important for the bird to cover long distances with a minimum of fuel. Pennycuick (1969) calculated the power required to fly at the maximum-range speed to be proportional to $b^{-\frac{3}{2}}$. Thus, migratory birds should have *long wing span* to be able to cover as long as possible a range on a given amount of fuel. *R. regulus* and *P. ater* are partly migratory, and, therefore, should benefit more by long span in this respect than the other species. In fact, *P. ater* has a long wing span. *R. regulus* has relatively long wings but a relatively short span due to the thin body.

5.5. *Relative length of arm and hand wings and inertial power for hovering*

Short arm wings in relation to the total wing length (as in hummingbirds) are associated with hovering or slow flapping flight, while long arm wings (as in albatrosses) are associated with gliding flight. One reason why short arm wings are particularly advantageous in hovering animals appears from the following:

The inertial power P_{in} is calculated as

$$P_{\text{in}} = 2n \int_{\gamma_{\min}}^{\gamma_{\max}} I \frac{\mathrm{d}^2\gamma}{\mathrm{d}t^2}\, \mathrm{d}\gamma \tag{5}$$

(Weis-Fogh 1972, 1973), where n is the stroke frequency, γ the positional angle, I the moment of inertia, and $\mathrm{d}^2\gamma/\mathrm{d}t^2$ the angular acceleration of the wing. Further,

$$I = \int_{r=0}^{r=l_{\mathrm{w}}} r^2 m(r)\, \mathrm{d}r \tag{6}$$

(Weis-Fogh 1973), where $m(r)$ is the mass of a wing element at distance r from the fulcrum (humero-scapular joint).

The stroke amplitude and wingbeat frequency usually increase with decreasing flight speed as a compensation for the reduction of flight speed. In hovering, there is no horizontal speed component, and to maintain a large resultant air speed, the stroke amplitude and/or the flapping frequency have to be increased. The faster the flapping speed the larger the inertial power output. Therefore, to reduce the inertial power, a flapping animal, especially a hovering one, should have a low mass of the wing, and/or have the mass located as proximally as possible, where the acceleration of the wing is lowest.

There is one more reason why the mass of the wing should be located as near the wing base as possible in a hovering animal. Since angular accelerations are larger in hovering than in forward flight (see above) the inertial loads on the wing skeleton are particularly high in hovering. For this reason the supporting structures of the arm wing must be strong, and hence relatively heavy, in a hovering animal if a certain load safety factor against breakage is to be maintained. Therefore, it is particularly important for a hovering animal to keep the wing's moment of inertia low by having a proximal location of the wing's mass. This may be done by reducing the lengths of humerus and ulna and/or making the angle between humerus and ulna small. Thus, *the shorter the arm wing is in relation to the total length of the wing, the less the inertial power will be and also the inertial loads on the wing skeleton*. The hand wing consists mainly of the primary feathers and thus has low mass even if long.

R. regulus and *C. familiaris* both have shorter arm wings in relation to the total length of the wings than the other species. In these two species the increase of the hand wing length compensates for the shortened arm wing, but does not add much to the total mass of the wing, since the hand wing is made up mainly of the light primaries.

One uncertainty with the above arguments for minimization of inertial power is to what extent inertial power is converted into useful aerodynamic power. If all inertial power were converted into aerodynamic power there would be little reason to minimize it. (The wing's moment of inertia would still have to be low, though, to keep inertial loads on the wing skeleton low.) This will be briefly discussed now.

Work has to be done to accelerate the wing at the beginning of the downstroke, but at the end of the downstroke in fast forward flight the kinetic energy of the wing can be transferred to the air, giving lift. In very slow flight and hovering this transfer of energy is not as easily achieved, since the airspeed at the wing is probably too low at the turning points. Therefore, the loss of inertial power should be especially large in hovering flight, unless kinetic energy can be removed and stored by some other means, like the resilin and thorax cuticle system in certain insects (Pringle 1965).

Pennycuick & Lock (1976) described a mechanism whereby primary feathers might increase the efficiency of transfer of the wing's kinetic energy to the air towards the end of the downstroke when the primary feathers unbend (after being bent by aerodynamic loads in the beginning of the stroke). The authors propose that the mechanism exists but cannot transfer the whole of the wing's kinetic energy to the air in hovering; only at some low forward speed might the mechanism become fully effective.

Norberg (1976) calculated the power requirements of a bat of mass 9 g in slow forward flight, and found that the inertial power was only 2–3 % of the total power. Weis-Fogh (1972) calculated the energetics of hovering flight in hummingbirds and found that the inertial power was 43 % of the total power, provided that there was no energy-saving elastic system. His estimate of total power output lies near to values from respiratory measurements; this lends support to the view that all inertial power in hovering cannot be converted into useful aerodynamic power but is (at least to some extent) wasted power that should be minimized.

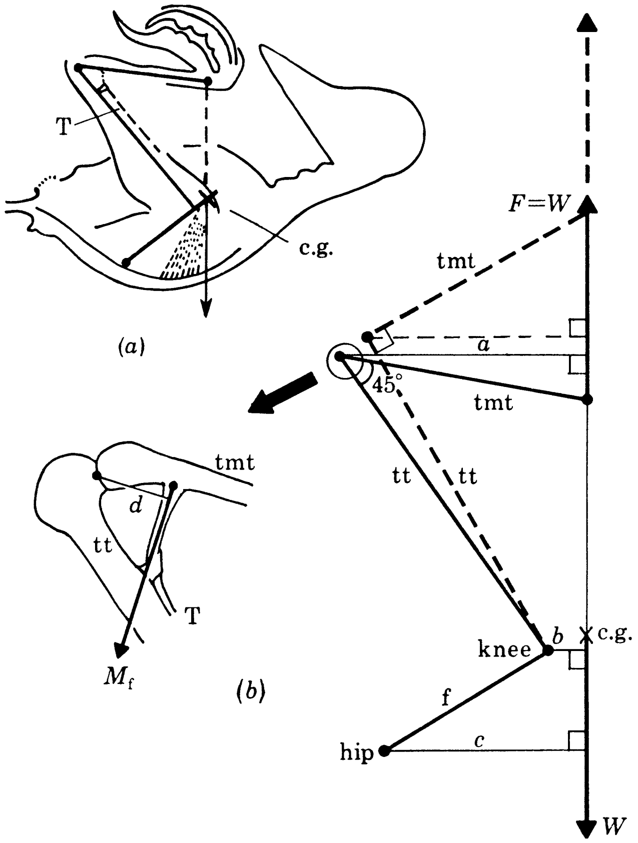
It is apparent from the above that the transfer of inertial power into useful aerodynamic power is most difficult to bring about in hovering flight. The argument above about the benefits from minimization of inertial power in hovering flight, by means of reduction of the wing's moment of inertia (by reduction of the length of the arm wing), rest upon the assumption that at least some of the inertial power cannot be converted into useful aerodynamic power in hovering.

5.6. *Summary on wing adaptations*

To summarize, *P. ater* has relatively low weight and relatively long wings and, therefore, low wing loading, but not very short arm wings. The low wing loading makes it adapted to slow flight and high manoeuvrability but the relatively long arm wing does not make it particularly well adapted to hovering. *P. montanus* has relatively high weight and high wing loading, and the longest arm wings in relation to the total wing length. It, therefore, is not adapted to hovering or to manoeuvrable flight. *P. cristatus* also has high wing loading (higher than *P. montanus*) and short and broad wings. It often hops about on the branches or on the ground when searching for food instead of flying about among the branches as the other tits and, in particular, *R. regulus* more often do. It is not adapted to slow and manoeuvrable flight. Its large weight instead makes it better adapted to survive cold winter nights, since the fat-storing capacity should increase about linearly with the mass, whereas the standard metabolism increases with the mass raised to the power of about 0.72 (Lasiewski & Dawson 1967). *R. regulus* and *C. familiaris* both have low wing loading and relatively short arm wings. Furthermore, *C. familiaris* has relatively long span. Both are adapted to slow flight and to hovering.

5.7. *Leg length and proportions*

The absolute length of the legs is shorter in the goldcrest than in the three tits, but the relative leg length ($([l_f+l_{tt}+l_{tmt}]/W^{\frac{1}{3}})$) is longest in the goldcrest (figure 6). Hence, if the goldcrest had been of similar geometry as the tits, i.e. like a tit scaled down to goldcrest size, its legs would have been still shorter than they are. It is possible that the goldcrest has a near-minimum leg length with respect to the dimensions and structures of branches, twigs and needles in coniferous trees. This might partly explain why its legs are longer in relation to the body size than in the other species.



moment	muscle force for
aW	flexion at the tt/tmt joint
bW	extension at the knee
cW	forward swing at the hip

moments, muscle force, and specific muscle force (*) at the tt/tmt joint:

$aW = d\,M_t$

$M_t = (a\,W)/d$; $M_t^* = M_t/M$

FIGURE 8. (*a*) *Parus montanus* in a hanging position under a branch. [Slightly modified from Palmgren (1932, figure 31).] (*b*) Diagram showing how moments about the leg joints are calculated for a bird hanging as in (*a*). The distances *a*, *b*, and *c* are the resistance lever arms about the respective joints, and *d* is the muscle lever arm of the flexor of the tarsometatarsus, M. tibialis anticus (tendon labelled T).

Several authors (e.g. Palmgren 1932) have remarked that species which often hang under slender perches tend to have relatively short tarsometatarsi. Of the five species in this investigation, *P. ater* and *P. montanus* hang more often than *P. cristatus* and *R. regulus*. In fact, the two former species have relatively shorter tarsometatarsi than *P. cristatus* and *R. regulus* (tables 3 and 4).

Palmgren (1932) compared the legs of *P. montanus* and *R. regulus* with respect to adaptations for hanging. His analysis will be reviewed here and applied to data for all five species. The method of analysis will be modified to suit also climbing behaviour.

Figure 8*b* shows how the moments about the three leg joints are calculated for a bird hanging by its feet. The figure is based on figure 8*a*, adopted from Palmgren (1932, fig. 31), and on Palmgren's discussion of the different moments which tend to rotate the leg elements around their proximal joints. The shorter the resistance lever arms are, the less moments the muscles need to set up to maintain the leg elements in fixed positions.

The resistance lever arm, *c*, for the femur, is dependent on the length of the femur and on the position of the hip joint relative to the centre of gravity. The relative length of the femur is almost the same in the five species (somewhat shorter in *C. familiaris* than in the other species) and thus offers no clues to different adaptations. Palmgren found that the hip joint has a more caudal position in *R. regulus* than in *P. montanus*, giving a larger torque about the hip joint in the former species.

The lever arm, *b*, for the tibiotarsus, is short and, therefore, of little interest. Left is the force system involving tarsometatarsus, and this system is of great importance.

The force lever arm, *a*, for the tarsometatarsus, is proportional to the length of this element. Flexion of the joint between tibiotarsus and tarsometatarsus is brought about by Musculus tibialis anticus. This muscle acts on tarsometatarsus with a relatively long lever arm, *d*, as can be seen from the geometry in figure 8*b*. The moment of the muscle force, M_t, about the tt/tmt joint must equal the moment of the bird's weight W about this joint:

$$d\,M_t = a\,W. \tag{7}$$

Hence, the muscle force, M_t, needed to maintain the tarsometatarsus in a flexed postion when the bird is hanging is inversely proportional to *d*. Therefore, a bird which often hangs under branches should have a short tarsometatarsus and a long lever arm for the force of M. tibialis anticus (Palmgren 1932).

I calculated the muscle force needed in the five species when they hang with 45 and 90° flexion of the joint between tibiotarsus and tarsometatarsus. For these angles the tarsometatarsus was set at -10 and $+30°$, respectively, to the horizontal (figure 8*b*), and the lever arm, *a*, was calculated with the use of the mean value of the length of the tarsometatarsus for the various species. The perpendicular distance (*d* in figure 8*b*) from fulcrum to the tendon of M. tibialis anticus was measured at 45 and 90° flexion of the tt/tmt joint. Table 9 gives values of the specific muscle force, M_t^*, of M. tibialis anticus, i.e. the muscle force per unit body mass, for the five species. At 45° flexion *R. regulus* has to produce 36–54 % more muscle force per unit body mass than have the other species, and at 90° flexion 42–61 % more. *P. cristatus* has to produce more muscle force per unit body mass than have the remaining three species. Hence, a hanging behaviour is particularly uneconomical in *R. regulus* and also in *P. cristatus*.

Palmgren's calculations showed that, at 45° flexion, the flexor muscle of tibiotarsus has to perform about twice as large a force per gram muscle mass (not body mass as in my calculations) in the goldcrest than in the willow tit, which is in line with my result.

P. cristatus, *C. familiaris*, and especially *R. regulus* have shorter force lever arms, *d*, in relation to body size than have *P. montanus* and *P. ater* (figure 8*b*, table 9). Obviously there are opposing selection pressures affecting the length of the lever arm *d*, as indeed most characters. In this case the optimal length probably results mainly from a compromise between demands for small muscle force and high speed. The force which the muscle needs to develop and the speed of movement of the tarsometatarsus both vary inversely with the length of the force lever arm *d* (the rate of contraction of the muscle being constant). Since the muscle force generally should

Table 9. Absolute and relative lengths of the resistance lever arms and force (muscle) lever arms at the joint between tibiotarsus and tarsometatarsus (figure 8*b*) for 45 and 90° flexion of the joint

	Parus ater			*Parus montanus*			*Parus cristatus*			*Regulus regulus*			*Certhia familiaris*		
	n	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.
resistance lever arm, a_{45°/mm		15.8			16.3			17.6			16.8			15.1	
resistance lever arm, a_{90°/mm		13.9			14.4			15.5			14.8			13.3	
force lever arm, d_{45°/mm	2	1.83	0.03	6	2.03	0.02	4	1.91	0.07	6	1.35	0.03	2	1.76	0.03
force lever arm, d_{90°/mm	2	1.39	0.02	6	1.50	0.03	4	1.44	0.06	6	0.96	0.04	2	1.38	0.05
relative force lever arm, $\bar{d}_{45^\circ}$	2	0.88	0.02	6	0.91	0.01	4	0.85	0.03	6	0.75	0.02	2	0.84	0.01
relative force lever arm, $\bar{d}_{90^\circ}$	2	0.67	0.01	6	0.67	0.01	4	0.64	0.03	6	0.53	0.02	2	0.66	0.02
specific muscle force, $M^*_{\mathrm{f}\,45^\circ}$/(N kg^{-1})		85			79			90			122			84	
specific muscle force, $M^*_{\mathrm{f}\,90^\circ}$/(N kg^{-1})		98			94			106			151			95	

be minimized and the leg speed maximized, the optimal compromise depends on the locomotor pattern of the animal. The more a species hangs and the less it depends on speed of movement, the longer the muscle lever arm should be (i.e. the greater the equilibrium length at which the opposing selection pressures cancel). During foraging *R. regulus*, *P. cristatus*, and *C. familiaris* all use their legs more for hopping (which requires speed of leg movements) and less for hanging than do *P. ater* and *P. montanus*, which is in accordance with the short force lever arms in the former group. Obviously, rapidity in this respect is particularly important in *C. familiaris* during the recovery stroke in climbing. After the power stroke it will need to move the feet forwards (which involves flexion) very fast to get a new hold of the bark at the end of the floating phase (before falling back). In view of this the seemingly conflicting adaptations in *C. familiaris* make sense; short tarsometatarsus for small muscle force in hanging and clinging to trunks but also short muscle lever arm for rapidity which necessitates greater muscle force.

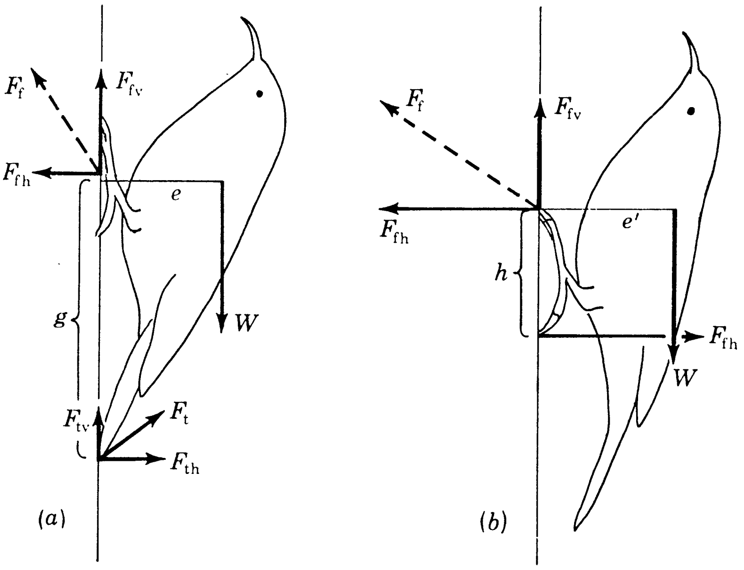


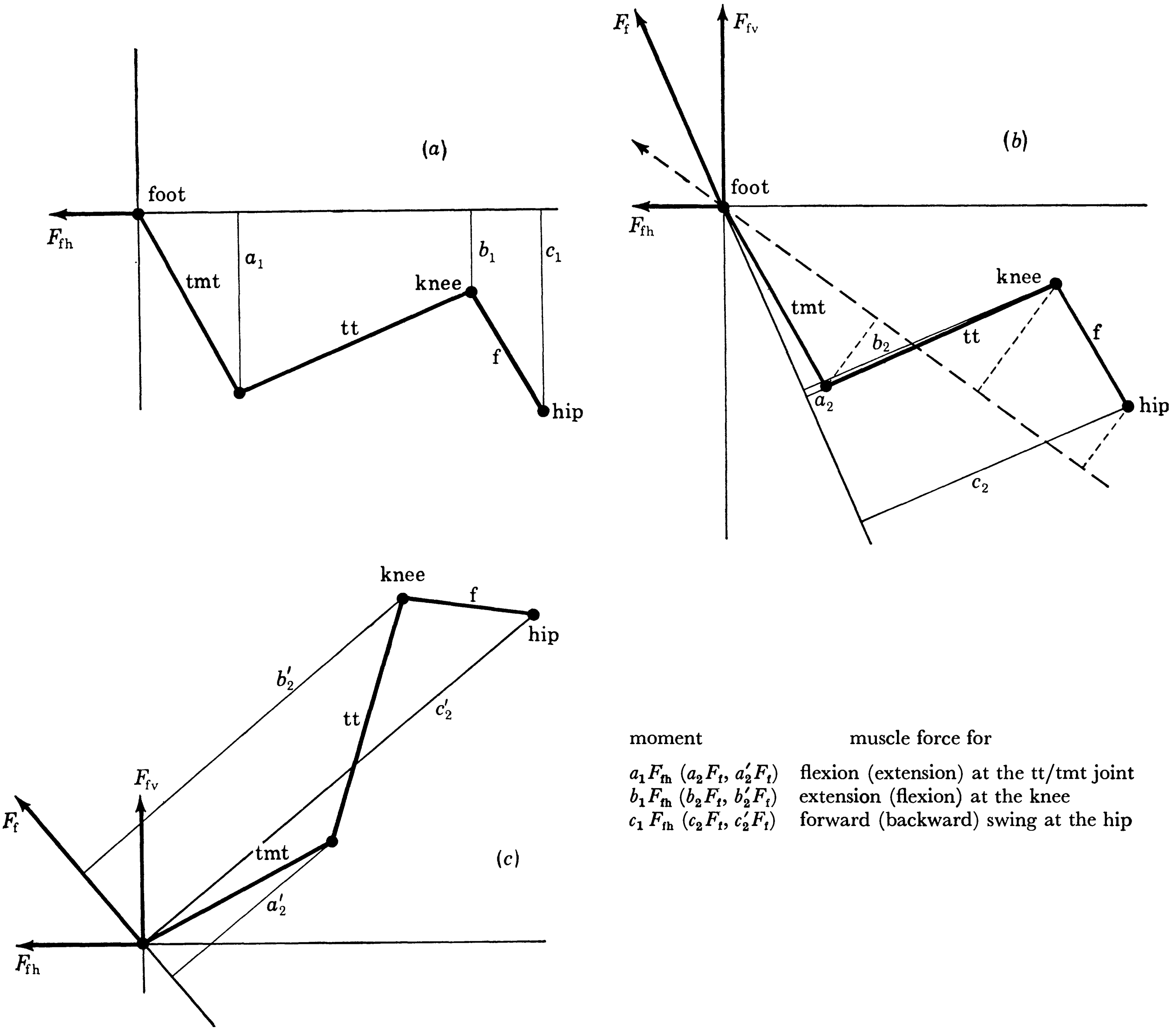
FIGURE 9. The force lever systems at the claws and tail of a bird clinging motionless to a vertical trunk, (*a*) with and (*b*) without tail support. [Slightly modified from Winkler & Bock (1976).]

Short legs are also advantageous for clinging to vertical or oblique surfaces. This comes out from the following consideration.

The mechanical treatment of the forces acting on tarsometatarsus during hanging can easily be transformed to the case of clinging with tail support on trunks and under branches. Figure 10 shows the force lever systems at the different leg bones during clinging. The horizontal force, F_{fh}, on the claws away from the bark, can be deduced from figure 9*a*, which is slightly modified from Winkler & Bock (1976), who analysed the forces acting on the feet and tail in climbing birds. The moment of force F_{fh} about the tail tip (or back claws in those phases of climbing when the tail is not held against the trunk, figure 9*b*) must equal the moment of the weight W about the same point, and hence

$$F_{fh} = We/g, \tag{8}$$

where e is the distance between trunk and centre of gravity of the bird, and g is the distance between claws and tail tip (figure 9*a*). Thus, the longer the feet and tail are, the less the



moment	muscle force for
$a_1 F_{fh}$ ($a_2 F_f$, $a'_2 F_f$)	flexion (extension) at the tt/tmt joint
$b_1 F_{fh}$ ($b_2 F_f$, $b'_2 F_f$)	extension (flexion) at the knee
$c_1 F_{fh}$ ($c_2 F_f$, $c'_2 F_f$)	forward (backward) swing at the hip

FIGURE 10. Force lever systems with resistance lever arms *a*, *b*, and *c* at the three leg joints of a treecreeper on a vertical trunk. The mechanics depends on the activity of the bird and on the friction between tail and trunk for the case when the tail is used for support. (*a*) Bird at rest in a clinging position, with tail support, as in figure 9*a*. The tail is supposed to support the *whole* weight of the bird (large friction between tail and trunk). Then only the horizontal force F_{fh} acts on the claws which hold on to the bark. (*b*) Bird at rest in a clinging position, with tail support, as in figures 9*a* and 10*a*. The trunk is supposed to be free of friction so that the claws have to support the whole weight of the bird. Then the claws are subjected to force F_f. This diagram also applies roughly to a moving bird in the beginning of the power stroke (but still with tail support), although the size and direction of the resultant force F_f are varying because of acceleration of the body towards the trunk and upwards. In reality, the tail of a *bird at rest* in a clinging position is likely to support a part of the body weight but possibly not all of it. The arrow in broken line and the associated lever system indicate some compromise with the claws taking up part of the body weight. (*c*) Moving bird at the end of the power stroke, without tail support, as in figure 9*b*. The tail does not support any part of the weight. Because of accelerations and retardations the vertical force F_{fv} at the claws may vary from larger than the weight to smaller than the weight during the power stroke. The horizontal force at the claws is relatively large since the tail is not used for support. The size and direction of the resultant force are varying because of body accelerations.

horizontal force, F_{th}, and the resultant force, F_t, become, against which the treecreeper has to do work during the power stroke. The mechanical analysis is somewhat more complicated when the bird is clinging to an oblique surface (Winkler & Bock 1976) but the conclusions are similar.

The functional significance of the lengths of the leg elements of a climbing bird will be considered now; first for the stationary case and then for the dynamic case.

5.7.1. *Stationary case*

For a stationary bird clinging with tail support to a trunk the moment arms and thus the moments about the different joints depend on the amount of friction between tail and trunk. Two extreme cases are treated here, (i) 'high friction' and (ii) 'frictionless' (figure 10).

(i) The tail is supposed to support the *whole* weight of the bird when it is at rest in a clinging position on a trunk even if the force of the tail normal to the trunk is small as it is with long tails. Then only a horizontal force, F_{th}, acts on the claws, which hold on to the bark. In figure 10*a* the legs are in their most forward position as in the beginning of the power stroke (see figure 11). The force F_{th} acts about the three leg joints with the moment arms a_1, b_1, and c_1.

(ii) The trunk is supposed to be free of friction, i.e. the claws are supposed to support the whole weight of the bird when it is at rest in a clinging position on a trunk. Then the claws are subjected to force F_t, which is the vector sum of the horizontal force, F_{th} (same as above), and a vertical force, which equals the weight, W. The force F_t acts about the three leg joints with the moment arms a_2, b_2, and c_2. The actual resultant force for F_{tv} and F_{th} should lie somewhere between F_{th} and F_t in figure 10*b* (since the tail probably supports part of the body weight but possibly not all of it).

From the geometry of figures 10*a* and *b* it can be seen that the shorter the leg elements are, the shorter the resistance lever arms become, and the less the moments about the tt/tmt, knee, and hip joints. Thereby, the muscle forces needed for flexion or extension of the leg elements may be correspondingly reduced for a bird clinging stationary to the trunk. This holds for both case (i) and (ii) (tail supports all and no weight, respectively).

5.7.2. *Dynamic case*

In the beginning of the power stroke the claws support the whole weight of the bird, as in case (ii) above (since the tail cannot carry any part of the body weight during the power stroke). The bird accelerates towards the trunk and upwards. The horizontal and vertical forces and their resultant are then increased over their values for a stationary bird. Likewise, the direction of the resultant force, F_t, and hence the directions of the moment arms a_2, b_2, and c_2 may deviate from those for a stationary bird. Nevertheless, short leg elements generally reduce the moments about the leg joints during most of the power stroke. As can be deduced from figure 10, it is especially important for the tibiotarsus to be short, the element most affecting the lever arm about the knee joint (b_2, b_2'). A short tarsometatarsus is also to the advantage during the later part of the power stroke, when it strongly affects the lever arm about the tt/tmt joint (a_2' in figure 10*c*).

Another variable dependent on the lengths of the various leg element is the step length which will be considered next. The kinematics of climbing in *C. familiaris* is shown in figure 11*a* which is based on work of R. Å. Norberg (in preparation) and on reconstructions with a dead specimen. The positions of femur, tibiotarsus, and tarsometatarsus are marked out. When the angles,

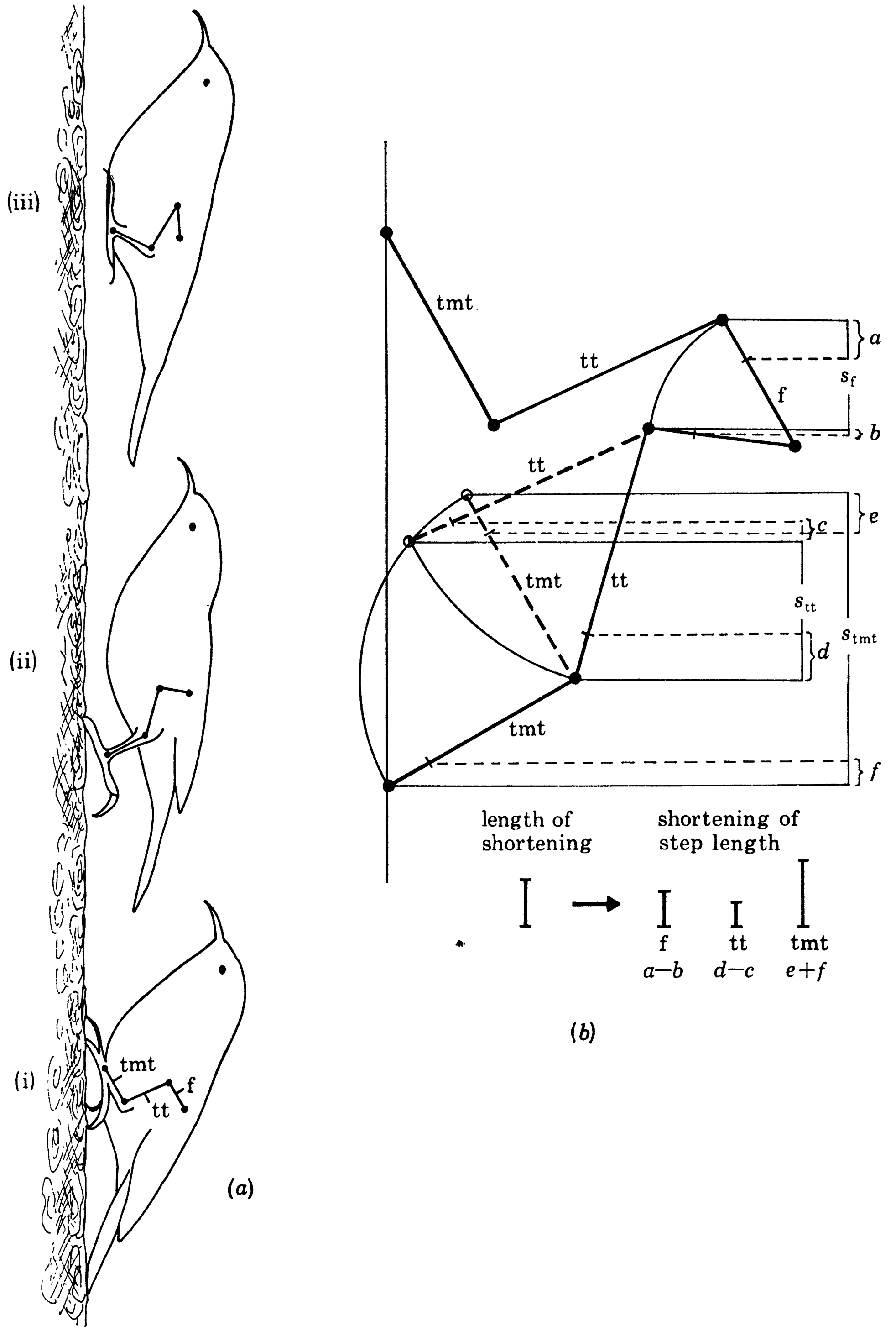


Figure 11. (*a*) Climbing locomotion in the treecreeper. (i) Bird at rest. (ii) Bird near completion of the power stroke. (iii) Bird in the floating phase. [Modified from R. Å. Norberg (in preparation).] The positions of femur (f), tibiotarsus (tt), and tarsometatarsus (tmt) are indicated. Only the tarsometatarsus is seen in the film from which this diagram was drawn. The positions and attitudes of the femur and tibiotarsus, as drawn in the figure were obtained as follows. After examination of intact birds the hip joint was localized with reference to the tail tip and the contour of the back. With use of dimensional data of femur, tibiotarsus, and tarsometatarsus the attitudes of these bones were then constructed for the various movement phases. (*b*) Diagram showing the forward and backward positions of the legs during climbing (from (*a*), (i) and (ii), respectively), and how the different leg elements influence the step length (*s*). The bars at the bottom indicate how much an equally large shortening of each of the three leg elements, one at a time, reduces the step length. The tibiotarsus can be shortened most with the less loss of step length.

through which the various leg elements rotate, are as shown in figure 11*b*, it is primarily the length of the tarsometatarsus which determines the length of the step. Therefore, the longer this bone is, the longer the step becomes, provided that the angles of rotation remain the same. However, it is to the advantage of a trunk-climbing bird to have relatively short legs in order to reduce the moments about the leg joints (see above) and since the body should be as near the trunk as possible. This is in order to reduce the horizontal force, F_h, between the trunk and claws.

Figure 11*b* shows how an equally large shortening of the three leg elements influences the step length. A shortening of tibiotarsus influences the step length less than does a shortening of femur and tarsometatarsus. Therefore, with the rotation pattern described above, *the legs can be shortened most with the least loss of step length by reducing the middle element, the tibiotarsus.*

The ratios femur/tibiotarsus (l_f/l_{tt}) and tarsometatarsus/tibiotarsus (l_{tmt}/l_{tt}, cf. l_{tt}/l_{tmt} in table 3) actually are significantly larger in *C. familiaris* than in the tits. The ratio femur/tibiotarsus is also larger in *C. familiaris* than in *R. regulus*. Since *C. familiaris* probably has evolved from a non-climbing ancestor that most likely had longer legs (because it was not specialized for climbing), the present leg pattern probably has been achieved via a stronger shortening of the tibiotarsus than of the femur and tarsometatarsus, the femur being reduced least (cf. the ratio l_f/l_{tt} among the species in table 3). Promptov (1956; cited by Partridge 1976) stated that in arboreal passerines, the shortening of the legs affects the tarsometatarsus most, the tibiotarsus less, and the femur least.

Further functional considerations regarding leg lengths and proportions are difficult to make without knowledge of the exact movements of the legs in the different types of locomotion.

5.8. *Summary on leg adaptations*

The lengths of the different leg elements are related to the bird's feeding behaviour. A bird which often hangs under branches and/or climbs should have a short tarsometatarsus and a long lever arm for the flexor muscle of tarsometatarsus (Palmgren 1932). This is to minimize the muscle force (and hence energy) needed for flexion of tarsometatarsus during hanging. On the other hand, the longer the muscle lever arm is, the less the speed of flexion becomes. Hence, birds with need of rapid leg movements should have a short lever arm for the flexor muscle of the tarsometatarsus.

P. ater and *P. montanus* hang more than the others, and *C. familiaris* climbs more than any of the other species while foraging. All three also have relatively short tarsometatarsus.

During foraging *R. regulus*, *P. cristatus*, and also *C. familiaris* use their legs more for hopping, which requires speed of leg movements, and less for hanging than do *P. ater* and *P. montanus*. The first three also have shorter muscle lever arms of the flexor of the tarsometatarsus than have *P. ater* and *P. montanus*. Rapidity is particularly important in *C. familiaris* during the recovery stroke in climbing. After the power stroke it will need to move the feet forwards (which involves flexion) very fast. In view of this the seemingly conflicting adaptations in *C. familiaris* make sense; short tarsometatarsus for small force in hanging but also short muscle lever arm for rapidity which necessitates greater muscle force.

When the bird is hanging under a perch with 45° flexion of the tarsometatarsus relative to the tibiotarsus, then the muscle force (of M. tibialis anticus) per unit body mass is larger in *R. regulus* (44–54 %) and in *P. cristatus* (6–14 %) than in the other three species.

C. familiaris has the relatively shortest legs of the species. Short legs are to the advantage for reduction of the distance between the body and trunk and thus reduction of the horizontal force away from the bark on the claws during climbing and clinging on a vertical trunk. Short legs also reduce the muscle forces needed for flexion and extension of the leg elements during clinging on a vertical trunk. It is especially important for the tibiotarsus to be short to minimize the muscle force, and also to shorten the legs with least loss of step length. In fact, the reduction of the leg length in *C. familiaris* has affected the tibiotarsus most and the femur least.

5.9. *Toes and tail*

Long toes and curved claws are desirable as support in climbing, as in *C. familiaris*. Curved claws increase the ability to get hold of the bark. In vertical climbing the toes are held in a near vertical direction on the trunk and have to support the whole weight of the bird, at least during the power stroke of the legs. In most phases (but not during the floating phase) the bird uses also the tail as support. The claws of the upwardly directed toes tend to be pulled away from the bark, and the backwardly directed claw, as well as the tail, are pushed against the bark. Therefore, the longer the toe span and tail, the smaller the horizontal force away from the bark on the forwardly directed claws (cf. the mechanical analysis in figure 9*a* and *b*, from Winkler & Bock 1976). On the other hand, the longer the tail is the more muscle force is needed for keeping the tail tip against the trunk. Furthermore, whether a long tail is to the advantage or not to a bird at rest on a vertical trunk depends on the friction between tail and trunk. If the trunk is smooth, the horizontal force at the tail, F_{th}, may need to be large to prevent the tail from slipping and hence permit the tail to take up much of the body weight. Since the horizontal force at the tail equals the horizontal force at the feet, $F_{\text{th}} = F_{\text{fh}}$, both are large if the tail is short (figure 9). If, on the other hand, the trunk is rough, the friction coefficient is large and F_{th} can be allowed to be small. Then, a long tail is to the advantage. Winkler & Bock (1976) treated these matters briefly for the static case.

The dynamic case will now be briefly considered here. At the beginning of the power stroke, when the tail is still held against the trunk, the friction is immaterial since the tail can not support any part of the body weight anyway. Then a long tail is favourable because the horizontal force F_{fh} should be minimized. The horizontal force F_{fh} and the resultant force F_{f} become smaller the longer the tail (or toe span, if the tail is not touching the trunk), and/or the shorter the distance between the body and trunk (short legs) (figure 10*a* and *b*). Summarizing, a long tail is to the advantage during the power stroke of climbing, but when the bird is resting a long tail is favourable only if the trunk is relatively rough. The more a bird climbs and the less it clings statically to a trunk, the more it benefits from a long tail. *C. familiaris* moves about most of its foraging time which may explain why it has such a long tail.

P. montanus also has a long tail and relatively long and curved claws, but a short toe span in relation to its body size. This species climbs and clings more than the others, except *C. familiaris*.

R. regulus has long toes and claws relative to its body size, but short absolute toe span.

P. cristatus has the shortest toe span in relation to body size. Since it jumps about on branches or on the ground to a greater extent than the other species, it does not have the same use of long toes for grasping branches, needles, etc., as the others. Further, short toes contribute to making the area/mass ratio small, which is to advantage in cold climates (Allen's rule).

6. CONCLUSION

In winter, the birds treated in this investigation are forced to forage for 70–100% of the day, the time varying inversely with the weight of the bird (Gibb 1954). Therefore, there should be a high selection pressure for effectivity in foraging. Even minor functional adaptations of the wings and legs are likely to be important at the very high feeding rates that these birds must attain.

The considerations about structural adaptations among the five species are relative, i.e. when one species is said to be more or less adapted in a certain way it is regarded to be so in relation to one or more of the other species treated here.

There are more differences in leg morphology than in wing morphology among the species (cf. tables 5–7 and figure 7). Furthermore, as one could expect, there are more differences between *R. regulus* and *C. familiaris* on one hand and the tits on the other, than there are among the tits, which are congeneric. There are also many significant differences between *R. regulus* and *C. familiaris*.

The different wing and leg forms of the species can in many cases easily be correlated with different types of locomotion, though the differences in many cases are not large.

The coal tit, *P. ater*, searches for and collects food mainly on the needled outer parts of the branches. Then it is favoured by a manoeuvrable flight and ability to fly slowly. It is adapted to this by having relatively low weight and long wing span.

The willow tit, *P. montanus*, mainly occupies the un-needled parts of the main-branches, and even the trunk, on which it moves mostly in a vertical head-up position, often using the tail for support. It does not perform especially manoeuvrable flight. It has relatively high wing loading, and is more adapted to a clinging and climbing behaviour with its relatively long tail and claws than are the other tits and the goldcrest.

P. ater, *P. montanus*, and *C. familiaris* all have relatively short tarsometatarsi, which characterizes birds that often hang under slender perches and/or birds that often climb.

The crested tit, *P. cristatus*, utilizes mainly the main-branches and usually hops about on them. It is also often seen on the ground. It is neither well adapted for slow or manoeuvrable flight because of its high wing loading and short, broad wings, nor for a climbing behaviour because of its short tail and toes. Since using terrestrial locomotion more than the other species when searching for and collecting food, its body size can be allowed to be relatively large. The larger the weight is, the larger the fat-storing capacity becomes relative to the standard metabolism, and hence the better the ability to survive cold winter nights. A large body size is also to advantage when the food items need to be picked out or broke loose from crevices in wood or bark. All tits, but especially *P. montanus* and *P. cristatus*, use their bill to a large extent to expose and get at food items. Therefore, they benefit particularly from a relatively large body size.

The goldcrest, *R. regulus*, occupies almost the same feeding stations as the coal tit, but is still more adapted to utilize the outer parts of the branches. It is well adapted to hover, which enables the bird to find and collect food in places which the other species can not utilize as efficiently and economically. It has a short arm wing in relation to the total length of the wing. The shorter the arm wing is, the more proximally the location of the main mass of the wing will be. This decreases the moment of inertia of the wing and thus also the inertial power that the wing muscles must produce for acceleration of the wings during flapping flight and also the inertial loads on the wing skeleton (cf. equations 5 and 6). The inertial power and inertial loads on the wing skeleton are larger in hovering flight than in horizontal forward flight and thus the need of low wing inertia is greater in the goldcrest than in the other species.

The goldcrest has very low wing loading, which can be seen as an adaptation for slow and manoeuvrable flight. Moreover, *R. regulus* as well as *P. ater* are partly migratory and, therefore, should benefit by long span. In fact, *P. ater* has relatively long span, while *R. regulus* has not. The relatively short span in the goldcrest is probably some compromise between the need of long wings for minimization of induced power, in slow and hovering flight as well as during migration, and the need of short wings for manoeuvrability and practicability in the dense vegetation where it usually forages. *R. regulus* very often flies among the twigs and sub-branches under the main-branches in spruce.

The treecreeper, *C. familiaris*, climbs mainly on the trunk in a vertical head-up position. Long curved claws, long toes, short legs and a long tail make it highly adapted for this type of locomotion. The longer the toes and tail the less the horizontal pull on the claws of the forwardly (upwardly) directed toes, which hold on to the bark, and, hence, the less the energy expenditure during climbing. The legs can be shortened most with the least loss of step length by reducing the middle element, the tibiotarsus. In fact, shortening of the legs in *C. familiaris* during the course of adaptations for climbing has effected the tibiotarsus most and the femur least.

The wings of the treecreeper are more like those of the coal tit and goldcrest than those of the other tits. Low wing loading, relatively long wings and short arm wings make the treecreeper adapted to slow, manoeuvrable flight and to hovering. Hovering is not a type of flight which one usually connects with the treecreeper. However, it can hover and sometimes does so. Furthermore, it can often be seen to lose its hold on smooth bark. It then immediately uses its wings in a head-up position, that can best be described as hovering flight. Furthermore, since it usually flies between tree trunks long wings are not the same hindrance to it as to the other birds that have to fly among branches and twigs.

The three tits resemble each other to a great extent regarding the wing and leg skeletons. The wing form, however, is not dependent on the wing skeleton, but primarily on the lengths of the feathers; the wing form is, in fact, rather diverse among the tits. Thus, as regards aerial locomotion in these three tits, the adaptations to different niches, and hence to different flight patterns, have led to divergent evolution of the wing feathers rather than of the wing skeleton.

In the tits, the skeleton of the legs is more diverse than that of the wings, and thus seems to have been subjected to more divergent selection pressures than the wing skeleton. This may be so because the leg form is determined exclusively by its skeleton (except the claws), the wing form mainly by the feathers. However, when the leg skeleton is compared with the wing form (i.e. with the wing feather configuration included), then the wings stand out as much more diverse than the leg skeleton.

As is shown in the phenograms in figure 7 the pattern for all five species is most diverse in leg characters and wing form and least diverse in the wing skeleton.

The niche differentiation among the five species is associated with clear structural differentiation of the locomotor apparatuses but to rather different degrees for various structures.

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