# 13 Correlation of foot sole morphology with locomotion behaviour and substrate use in four passerine genera

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## 13.1 Abstract

In this study, I relate plantar skin morphology (size and shape of pads, papillae and furrows) to locomotor behaviour and use of microhabitat in 37 passerine bird species in 4 distantly related genera (*Carduelis*, *Dendroica*, *Regulus* and *Parus*). If parallel evolution is present plantar skin morphology in the four passerine genera, I expect to find significant predictors among plantar skin traits for habitat use and locomotor behaviour. Plantar skin morphology was obtained by macro-photographs of the feet of wild caught birds. The number of plantar traits was reduced by elliptic Fourier analysis and principal component analysis to 13 morphological traits which were related to ecological factors by logistic regression models.

As expected, I found strong relationships between plantar skin morphology and microhabitat and non-volant locomotor behaviour, whereas the correlation between plantar morphology and aerial behaviour is poor.

I found patterns of parallel evolution in plantar integumentary traits within four distantly related genera. Furthermore, I found significant relationships between substrate use, locomotion behaviour and plantar morphology implying an adaptive function of the plantar integument to locomotion and substrate.

**Keywords:** Plantar integumentary morphology, elliptic Fourier analysis, ecomorphology, birds.

## 13.2 Introduction

Efficient foraging is crucial for successful performance of animals. Thus body systems related to foraging are expected to be subject to strong selection. Many studies have shown significant correlation between feeding ecology and

morphological characters (Karr and James 1975; Leisler 1980; Carrascal et al. 1990; Losos 1990; Barbosa and Moreno 1995). In particular, the locomotor system plays an important role in foraging behaviour (Moreno 1991; Moreno and Carrascal 1993; Miles et al. 2000). Most ecomorphological studies of birds have focused on flight and the feeding apparatus (Norberg 1986; Price 1991; Winkler and Leisler 1992; Barbosa and Moreno 1995; Keast 1996). Some studies relate tarsus, toe and claw lengths to locomotion or habitat use (e.g. Blechschmidt 1929; Palmgren 1936; Rüggeberg 1960; Norberg 1979; Raikow 1985; Barbosa and Moreno 1999). Most of these focused on skeletal and muscle morphology, although the toe pads are very pronounced in passerines, and it seems reasonable to assume a function during locomotion (Lennersted 1975a). Whether this assumption is true, or whether the pads have other functions such as insulation (Lennersted 1985), or both, has never been tested. Some authors propose that differences in pad morphology are related to ecological differences between closely related species (Goldcrest *Regulus regulus* vs. Firecrest *R. ignicapillus*, Leisler and Thaler 1982; Golden-crowned kinglet *R. satrapa* vs. Ruby-crowned kinglet *R. calendula*, Keast and Saunders 1991). Up to now, a comprehensive study relating locomotor behaviour and plantar integumentary morphology has never been done.

In this study, I relate external plantar integumentary morphology (size and shape of pads, papillae and furrows) to substrate use and locomotor behaviour in 37 passerine bird species belonging to 4 distantly related genera belonging to three different families: *Parus* (Paridae), *Regulus* (Regulidae), *Carduelis* and *Dendroica* (Fringillidae) (Sibley and Ahlquist 1990). Within the Fringillidae, *Carduelis* belongs to the subfamily Fringillinae, whereas *Dendroica* is phylogenetically related to the Emberizinae (Yuri and Mindell 2002). Within a genus, the selected species cover, where possible, a broad ecological spectrum. This selection of species allows for testing for parallel evolution. Futuyma (1998, p 110) defines parallel evolution as similar developmental modifications that evolve independently. If parallel evolution is present in plantar integumentary morphology in the four passerine genera studied here, I expect to find significant predictors among the traits of the plantar surface for habitat use and locomotor behaviour using regression models. Predicting ecology from morphology is the general approach of an ecomorphological study (Winkler and Leisler 1985; Leisler and Winkler 1991; Bock 1994; Wainwright and Reilly 1994).

## 13.3. Species and data

### 13.3.1 Species and sample size

Species were selected so that the sample showed a broad variation in habitat use. Particularly, I first selected species inhabiting an extreme arboreal habitat. The

outermost twigs of conifers provide an extreme microhabitat due to the thin structures (needles) birds have to cling to during locomotion. Therefore, I selected four genera that contain at least one species that forages in the outermost twigs of conifers. Then, I selected congeneric species so that within each genus a broad ecological spectrum was present. However, the species selection was mainly dictated by the range of species caught at the following bird ringing stations during the indicated time: August/September 2000 at Rybachy (RU), October 2000 at Col de Bretolet (CH), August to October 2001 at Powdermill (Pennsylvania, USA) and March 2002 at Bolle di Magadino (CH). For two species, *Parus inornatus* and *P. rufonuchalis*, I used museum specimens preserved in ethanol housed at the British Museum, Natural History Museum Tring, GB.

The sample size ranged from 1 to 13 (median=3) individuals per species.

### 13.3.2 Morphological data

I took pictures of the plantar foot surface of wild caught live birds using a Nikon camera with a macro lens (Medical-Nikkor 120mm, 1:4) equipped with a ring flash. For standardisation of foot position, I softly pressed the birds' right foot against a sheet of glass (Fig. 1). The pictures, one from the plantar side and one from the lateral, were taken through the glass (Fig. 2). I used the program tpsDig Version 1.30 (Rohlf, 2001) to measure length, width and height of each digital pad and the width of the furrows between the pads. Additionally, I digitised the outline of the proximal pad (the largest pad) on digit I in plantar view, measured its area electronically and counted the number of papillae. The length of the claw on digit I and its curvature were measured and calculated as described by Feduccia (1993).

From each of these measurements, species means were calculated. The species mean shape of the outline of the proximal pad of digit I was obtained by abstracting the outlines by elliptic Fourier decomposition (Ferson et al. 1985). Using this method, the outline is decomposed in a sum of sine- and cosine-functions. The more terms ("harmonics" with four coefficients each) that are added to the function, the closer the outline is described by the function. I used 8 harmonics. The shapes were rotated and stretched to match standard size and direction. From the individual coefficients, species means were calculated and from them, the species mean pad shape was reconstructed (Fig. 3). The elliptic Fourier analyses were carried out on the computer program Morpheus et al. (Slice, 1998).

**Fig. 1.** Photographic set up for taking pictures of the foot. The bird's right foot was softly pressed against the glass while taking the pictures
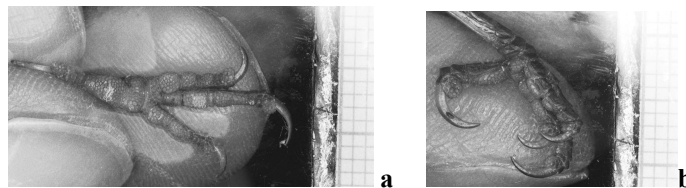


**Fig. 2. a**) Ventral and **b**) lateral view of the right foot of a *Dendroica magnolia*
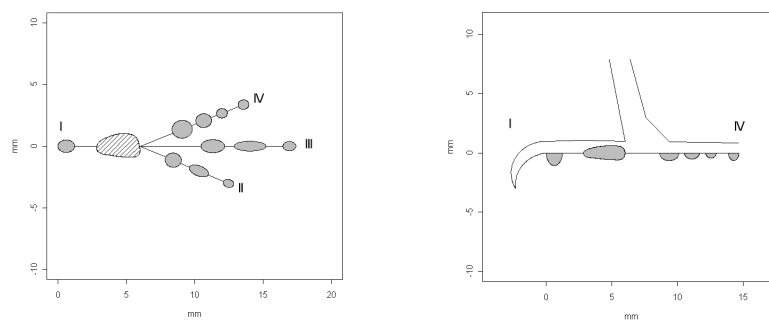


**Fig. 3.** Reconstruction of the mean right plantar surface of *Dendroica magnolia* in ventral view (left) and lateral view (right). The reconstruction of the pads is based on length, width and height and approximated by ellipses, except for the proximal pad on digit I. This pad was reconstructed via the mean elliptic Fourier coefficients as described in the text. The density of the hatching is proportional to the number of papillae on this pad. The angles between the toes are arbitrarily set to 25° between toe II and III, and 24° between toe III and IV, respectively. In lateral view, the claw of digit I is reconstructed by its length, its height at the base and its inner and outer curvature. The curvatures are approximated by circle segments. The units of the axis are in mm

### 13.2.3 Behavioural data

Substrates were divided into 7 categories and bird behaviours into 9 categories (Table 1), based on the definitions given in Remsen and Robinson (1990). For

each species, I asked experts (see acknowledgements and Appendix) to specify how often the species uses each substrate and how often the species performs each behaviour. The species experts could choose between three frequencies: never, seldom, often. For 29 species, I received an answer from one to three experts. For 8 species, I extracted the information about substrate use and foraging behaviour from the following literature: Knox and Lowther (2000): *Carduelis cabaret*, Dawson (1997): *C. pinus*, Hunt and Flas-pohler (1998): *Dendroica coronata*, Curson (1994): *D. discolor*, Harrap and Quinn (1996): *Parus carolinensis, P. inornatus. P. rufonuchalis*, and Ingold and Wallace (1994): *Regulus calendula*.

**Table 1.** Definitions of categories of substrate and behaviour

| Category | Description |
|---|---|
| **Substrate** | |
| Needles | coniferous foliage |
| Leaves | deciduous foliage |
| Twigs | canopy of trees or bushes, not in foliage |
| Trunk | trunk of a tree or a bush |
| Elsewhere | on grass or ground |
| Vertical | bird contacts with its feet a vertical substrate |
| Air | bird's feet don't touch any substrate |
| **Behaviour** | |
| Sideways | bird hangs sideways, flank up (Fig. 15.4 a) |
| Belly up | bird hangs with its belly up (Fig. 15.4 b) |
| Upside down | Birds head hangs below the body (Fig. 15.4 c) |
| Flutterhop | hopping supported by fluttering |
| Hover | flying in place or stalling, combination of the categories "sally-stall" and "sally-hover" defined by Remsen & Robinson (1990) |
| Flycatch | short bout of flight in order to catch a prey, this category was named by Remsen & Robinson (1990) "sally-strike" |
| Aerial hawk | longer foraging flight |
| Beside | the bird's body is situated beside the substrate (e.g in Fig. 15.4 a, c) |
| Below | bird hangs below the substrate, either flank, belly or tail is pointing upwards (e.g. in Fig. 15.4 b) |

The species scores for each microhabitat and behaviour/position category are given in the appendix.
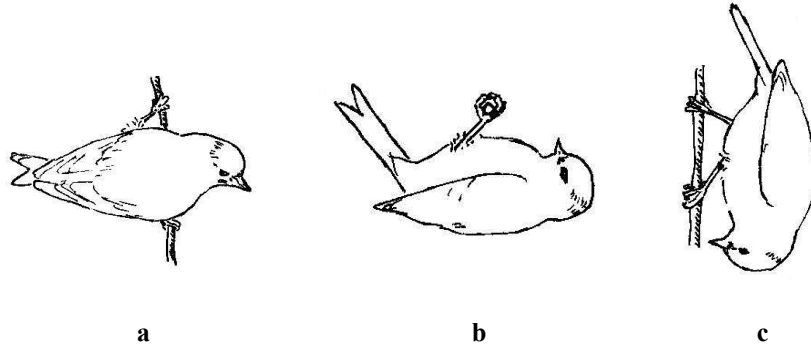
**Fig. 4.** Illustration of the behavioural categories **a**) sideways, **b**) belly up, and **c**) upside down

### 13.2.4 Statistics

All statistical analyses were performed using R 1.5.1 software (R Development Core Team, 2002).

#### *Data transformation and correction for size*

The curvature of the claw of digit I was arc-sin and square-root transformed and not corrected for size. All other morphological variables of the plantar morphology were log-transformed and then corrected for size by dividing them by the log-transformed foot span (between digit I and II, Fig. 5). The area of the proximal pad on digit I was divided by the square of the digital span. The number of papillae of the pad was divided by the papillar area of this pad. The digital span itself was divided by the cube root of the birds' weight (Leisler and Winkler 1991). Bird's weights were taken from Dunning (1992).

#### *Reduction of variables*

Since the chance of finding significant but biologically irrelevant relationships between dependent and independent variables increases with the number of variables, it is recommended that the number of variables be kept low compared to the number of observations (e.g. Sachs 1978). Furthermore, autocorrelated dependent variables might impair the results of regressions. Therefore, I reduced the original number of morphological variables (57) to 13, which were as little as possible correlated to each other, showed a high variability within the data, and which covered most of the functional aspects of the bird's foot. In order to achieve such a reduction, I performed 6 principal component analyses (PCA) on subsets of functionally related variables. These subsets were: 1) pad lengths, 2) pad widths (12 variables each), 3) pad heights (6 variables), 4) furrow widths (8 variables),

and 5) diverse traits, which did not belong to one of the groups above (number of papillae, pad area, claw length, curvature of claw, foot span, distance from the foot centre to the first pad on each toe (distance 5)) and 6) shape coefficients of the pad outline. Of the PCAs 1) to 4), principal components that explained more than 30% of the variance were selected (Table 2). Of PCA 5), principal components that explained more than 4% of the variance were selected, since the miscellaneous variables cover a number of different morphological functions. These threshold values were arbitrary set. Within each principal component, the variable with the highest loading was retained for further analysis, whereas the others were discarded (Table 2). The 10 selected variables cover a broad range of functional aspects of plantar morphology (Fig.5). The first components of the PCAs 1) to 4) measure size of the corresponding variable set, since all loadings have the same signs. Therefore, the variables selected from these components are interpreted as follows: The length of pad 2 measures general pad lengths, width of pad 11 measures general pad widths, and height of pad 1 represents general pad heights. An alternative method for variable reduction would be factor analysis instead of PCA.

**Table 2.** The first few components of the five principal component analyses on each group of variables and the selected variables according to their loading values

| variable group and number of variables | principal components | proportion of variance | variable with the highest loading | loading |
|---|---|---|---|---|
| 1) pad lengths (12) | 1 | 38.8% | length of pad 2 | -0.408 |
| | 2 | 30.8% | length of pad 1 | 0.446 |
| 2) pad widths (12) | 1 | 68.4% | width of pad 11 | -0.314 |
| 3) furrow widths (8) | 1 | 48.2% | width of furrow 9 | -0.438 |
| 4) pad heights (6) | 1 | 73.1% | height of pad 1 | -0.437 |
| 5) miscellaneous (10) | 1 | 56.4% | hind claw | -0.378 |
| | 2 | 15.2% | area of pad 2 | 0.597 |
| | 3 | 13.2% | curvature of claw of digit I | -0.452 |
| | 4 | 5.4% | distance 5 | -0.513 |
| | 5 | 4% | number of papillae | -0.556 |

The last subset of morphological variables 6) consists of the Fourier shape coefficients of the pad outline. Only the coefficients from the first three harmonics were used. Since the first three coefficients of the first harmonic for all species are 1, 0, and 0 due to standardisation in relation to size, rotation and starting point, they were omitted, and only 12-3=9 coefficients were entered into the principal components analysis. The first two principal components accounted for 77.05% and 13.07% of the variance, respectively.

These components were used as pad shape variables. The meaning of PC1 is seen in the ratio length/width and in the position of the maximal width (Fig. 6). A high value of PC1 means a large ratio and a proximal maximal width. PC2 describes the asymmetry of the pad. The higher the score on PC2, the more convex is the lateral edge of the pad, whereas the medial edge tends to be flatter.
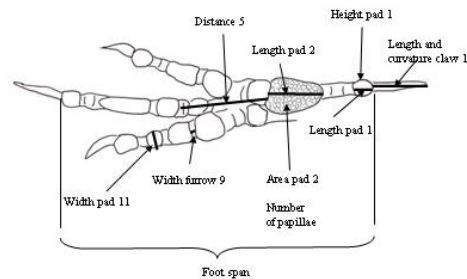
**Fig. 5.** The variables of plantar morphology that remained after the redundant variables were discarded
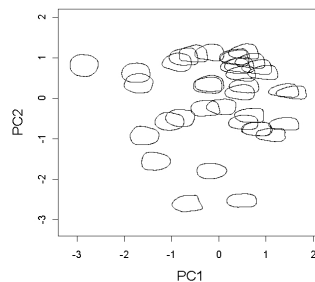


**Fig. 6.** The first two principal components of the pad shape coefficients; Left=distal, right=proximal, upper=lateral/outer/right, lower=medial/inner/left; along the x-axis (PC1) the pads became narrower and their maximal width changes from distal to proximal; along the y-axis (PC2) they become more asymmetric

Therefore, 13 variables of plantar morphology were selected: lengths of pad 1 and 2, height of pad 1, width of pad 11, width of furrow 9, distance 5, length of the hind claw, the area of pad 2, the curvature of the claw of digit I, the number of papillae on pad 2 (Fig. 5), and two shape coefficients of the outline of pad 2 (Fig. 6). Finally, foot span was used as size variable.

### *Relationships between ecology and morphology*

Significant relationships between microhabitat use or locomotor behaviour and the 13 morphological variables were obtained by applying the following procedure to each of the 16 variables of substrate and behaviour:

(1) A linear regression model was obtained by backward selection from the full linear model with the 13 morphological variables and the factor "genus" (4 levels) as independent variables, and the ecological variable as dependent variable. The influence of single species on the result was obtained by the Cook's distance (Hair

et al. 1995). In one case (twigs) one species had to be omitted due to a Cook's distance higher than 0.5.

(2) The variables remaining in the linear model after the backward selection were used for a proportional odds regression model (Hosmer and Lemeshow 2000; Stahel and Pritscher 2002). Since the ecological variables in this study take ordered discrete values (never, seldom, often), a proportional odds regression, which is a type of ordinal logistic regression, is the appropriate method to determine the significances of single morphological variables in predicting substrate use or behaviour.

Before the odds regression was performed, the means of the ecological scores were rounded to one of the three levels "never", "seldom" and "often". The final model was selected by a stepwise backward method minimising the AIC-criteria.

(3) The final proportional odds regression models were tested by comparing their deviances with the deviances of the null models using a Chi-square test (Stahel and Pritscher 2002).

(4) The goodness of fit of the proportional odds model was tested by a modified Hosmer-Lemeshow test (Hosmer and Lemeshow 2000). This test was originally devised for testing a binary logistic regression: The observations are ordered according to their fitted values.

Then, the observations were summarised in 10 groups. Finally, a Chi-square test on the 10x2 table of observed and fitted values was performed, using 20-10-(2-1)-1=8 degrees of freedom. Applying this test to an ordinal logistic regression with three levels in the dependent variable, the 10x2 table has to be modified to a 10x3 table, and the degrees of freedom for the Chi-square test to 30-10-(3-1)-1=17. A significant Chi-square-test means that the model does not fully explain the variability in the dependent variable.

Two ecological variables, namely "twigs" and "trunk", contain only two levels. Here, instead of the proportional odds regression a binary logistic regression was performed. The models were tested for significance by comparing their residual deviances with the residual deviance of the null model, containing only the intercept (Stahel and Pritscher 2002).

The Hosmer-Lemeshow test was used as a goodness of fit test, as described by Hosmer and Lemeshow (2000).

## 13.3 Results

The substrate variables, "needles", "trunk" and "vertical" can be accurately predicted by morphological variables of plantar morphology (Table 3). From the variables of locomotor behaviour, only the behaviours related to bipedal locomotion, except "upside down" and "below", can be fully predicted by plantar morphological variables (Table 4). The locomotor variables describing aerial behaviour have a poor fit with plantar morphology (significant goodness of fit test, Table 4). Since I corrected for genus in the regressions, the relationships discovered are parallel within each genus.

**Table 3.** The proportional odds (or binary logistic) regression models for substrate use. If not otherwise indicated, the results stem from a proportional odds model fit. *: a significant goodness of fit test means that the model does not explain the entire variation of the ecological variable. In bold are significant variables in models with a good fit

| substrate | variables in the model | estimated b | se of b | p |
|---|---|---|---|---|
| **needles** | **genus** | **.** | **.** | **0.002** |
| | **pad length** | **-1.33** | **0.59** | **0.014** |
| | **number of papillae** | **-2.15** | **0.83** | **0.004** |
| | total model | | | <0.001 |
| | goodness of fit | | | 0.316 |
| leaves | genus | . | . | <0.001 |
| | curvature of claw | 2.94 | 0.99 | <0.001 |
| | foot span | -2.15 | 0.74 | <0.001 |
| | total model | | | <0.001 |
| | goodness of fit | | | 0.002* |
| twigs[a] | intercept | 1.37 | 0.47 | 0.004 |
| (binary | number of papillae | -1.07 | 0.46 | 0.020 |
| logistic | test of the total model | | | 0.010 |
| regression) | goodness of fit | | | 0.020* |
| **trunk** | intercept | -15.28 | 34.08 | 0.654 |
| (binary | genus | . | . | 0.670 |
| logistic | **length of pad 1** | **-2.65** | **1.19** | **0.026** |
| regression) | **curvature of claw** | **-3.37** | **1.54** | **0.029** |
| | test of the total model | | | 0.002 |
| | goodness of fit | | | 0.067 |
| elsewhere | pad length | 1.97 | 0.69 | 0.001 |
| | length of pad 1 | -1.17 | 0.76 | 0.106 |
| | length of hind claw | -1.18 | 0.66 | 0.061 |
| | area of pad 2 | -1.35 | 0.63 | 0.022 |
| | curvature of claw | -1.78 | 0.63 | 0.004 |
| | total model | | | 0.003 |
| | goodness of fit | | | <0.001* |
| **vertical** | **pad shape component 1** | **-61.67** | **20.23** | **<0.001** |
| | **pad shape component 2** | **-53.82** | **21.20** | **0.003** |
| | pad length | 1.39 | 1.00 | 0.145 |
| | **height of pad 1** | **-1.66** | **0.84** | **0.026** |
| | foot span | 1.02 | 0.75 | 0.144 |
| | total model | | | <0.001 |
| | goodness of fit | | | 0.410 |
| air | pad shape component 2 | -9.12 | 5.91 | 0.113 |
| | pad width | 2.11 | 0.72 | <0.001 |
| | length of claw | -1.02 | 0.67 | 0.115 |
| | foot span | 2.00 | 0.72 | <0.001 |
| | distance 5 | 1.10 | 0.62 | 0.066 |
| | number of papillae | 1.97 | 0.90 | 0.019 |
| | total model | | | 0.003 |
| | goodness of fit | | | 0.023* |

[a]I omitted *Carduelis cannabina* from this analysis due to its too strong influence on the result.

**Table 4.** The proportional odds regression models for the locomotor behaviour. Legend as in Table 3

| locomotion behaviour | variables in the model | estimated b | se of b | p |
|---|---|---|---|---|
| **sideways** | **pad length** | **-1.89** | **0.59** | **<0.0001** |
| | **length of pad 1** | **2.06** | **0.74** | **0.001** |
| | foot span | 0.76 | 0.48 | 0.09 |
| | **number of papillae** | **1.83** | **0.78** | **0.008** |
| | total model | | | 0.001 |
| | goodness of fit | | | 0.286 |
| **bellyup** | **pad length** | **-2.55** | **0.71** | **<0.0001** |
| | furrow width | -0.75 | 0.43 | 0.067 |
| | total model | | | <0.0001 |
| | goodness of fit | | | 0.090 |
| upside down | pad shape component 2 | 33.76 | 15.44 | 0.010 |
| | pad length | -2.05 | 0.62 | <0.0001 |
| | pad height | 0.80 | 0.42 | 0.049 |
| | total model | | | <0.0001 |
| | goodness of fit | | | <0.0001* |
| flutter-hop | genus | . | . | 0.038 |
| | length of pad 1 | 1.95 | 0.87 | 0.012 |
| | furrow width | 0.92 | 0.58 | 0.098 |
| | area of pad 2 | -1.03 | 0.54 | 0.048 |
| | number of papillae | 3.07 | 1.18 | 0.002 |
| | total model | | | 0.046 |
| | goodness of fit | | | 0.023* |
| hover | furrow width | -0.96 | 0.44 | 0.019 |
| | pad shape component 1 | 11.21 | 6.86 | 0.067 |
| | pad shape component 2 | 20.22 | 14.26 | 0.107 |
| | length of hind claw | -2.29 | 0.71 | <0.001 |
| | number of papillae | -1.87 | 0.84 | 0.006 |
| | total model | | | <0.001 |
| | goodness of fit | | | <0.001* |
| flycatch | genus | . | . | 0.010 |
| | pad length | 1.34 | 0.91 | 0.126 |
| | pad width | 1.57 | 0.74 | 0.020 |
| | area of pad 2 | -1.74 | 0.81 | 0.019 |
| | distance 5 | -2.51 | 0.91 | <0.001 |
| | total model | | | <0.001 |
| | goodness of fit | | | <0.001* |
| aerial hawk | pad shape component 1 | -11.46 | 6.41 | 0.061 |
| | pad height | 1.27 | 0.70 | 0.057 |
| | length of hind claw | -1.76 | 0.69 | 0.005 |
| | total model | | | 0.008 |
| | goodness of fit | | | <0.001* |
| **beside** | **pad shape component 1** | **-27.61** | **9.09** | **0<0.001** |
| | **pad shape component 2** | **-29.64** | **15.10** | **0.037** |
| | length of pad 1 | 0.93 | 0.64 | 0.139 |
| | **number of papillae** | **2.49** | **1.06** | **0.008** |

**Table 4** (cont)

|       |                      |        |      |        |
|-------|----------------------|--------|------|--------|
|       | total model          |        |      | 0.003  |
|       | goodness of fit      |        |      | 0.228  |
| below | pad shape component 1 | -20.50 | 6.15 | <0.001 |
|       | furrow width         | -0.81  | 0.42 | 0.040  |
|       | area of pad 2        | -0.59  | 0.41 | 0.143  |
|       | total model          |        |      | <0.001 |
|       | goodness of fit      |        |      | 0.016* |

In particular, I found the following relationships between substrate use and foot morphology within 37 species of 4 genera (Table 3):

1) The higher the proportion of coniferous foliage utilisation in the substrate of a bird, the shorter are their pads and the fewer is the number of papillae on the proximal pad on the first toe (Fig. 7).

2) Birds often foraging on trunks, have a short length of the distal pad of the first toe, and a weakly curved hind claw.

3) Round and symmetric proximal pads with a distal maximal width and a flat distal first toe pad are correlated with a high proportion of vertical structures in the substrate of a bird (Fig. 8).

Most of the non-volant behaviour types can well be predicted by plantar morphology, whereas none of the aerial behaviours can fully be predicted by plantar morphology (Table 4). The significant relationships between plantar morphology and behaviour types are the following:

1) The more a bird hangs sideways, the shorter are its pads except the distal pad on the first toe, which becomes longer (Fig. 9a). Furthermore, the proximal pad of digit I exhibits a high number of papillae.

2) Birds that often hang under the substrate with their belly upwards, have short pads (Fig. 9b).

3) A body position beside the substrate is correlated with symmetric, round proximal pads of digit I exhibiting a large number of papillae.
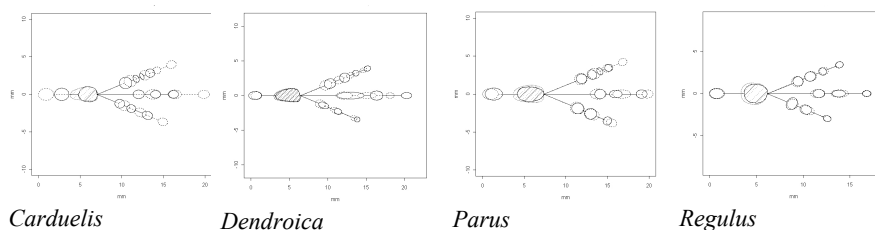


*Carduelis*          *Dendroica*          *Parus*          *Regulus*

**Fig. 7.** Mean right plantar morphologies (ventral view) by genus (dotted lines) and the plantar morphology of a typical needle specialist of each genus (solid lines). Within each genus, the needle specialist has a shorter proximal toe pad on the first toe compared to the genus' mean, and fewer papillae (represented by the density of the hatching). For digit numbers see Fig.2
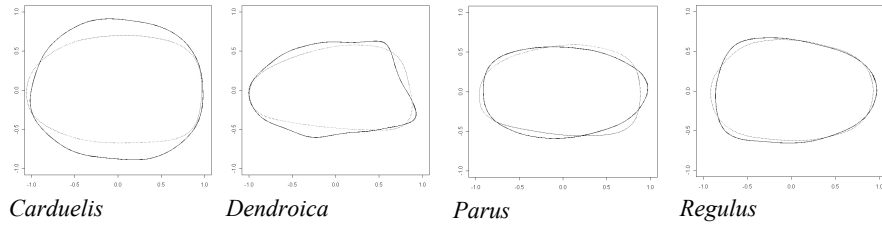
*Carduelis*          *Dendroica*          *Parus*          *Regulus*

**Fig. 8.** Mean outline of the proximal pad of digit I by genus (dotted lines) and that of a specialist on vertical structures (solid lines) overlaid. The size of the pads has been standardised. Distal=left, lateral=upper (same orientation as in Fig.2). Within each genus the distal (left) part of the toe pad of the specialist on vertical structures is broader than that of the mean pad of the genus
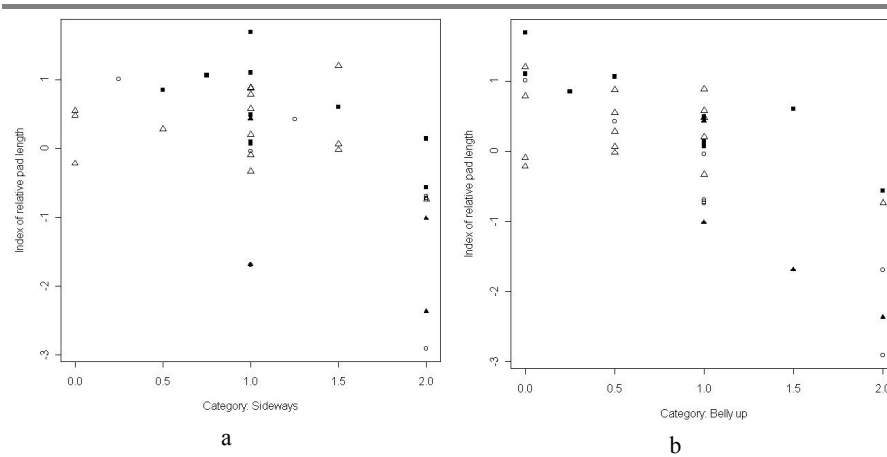


**Fig. 9.** Relationship of the length of the proximal toe pad of digit I to a) the frequencies of sideways orientation, b) proportion of belly up positions. O: *Carduelis*, △: *Dendroica*, ▲: *Regulus*, ■: *Parus*

## 13.4 Discussion

### 13.4.1 Reconstruction of mean foot sole shapes

It was difficult to fully standardise foot pictures of living birds. The position of the toes varies especially in the distal regions in ventral view (Fig. 2a), due to lateral deflection of the distal phalanges. In such cases, I did not measure the width of the pads. Consequently, the species means of most of the distal pad widths are based

on a lower number of individuals than are the proximal ones. The proximal pads are not affected by toe deflection, and the within species variability (due to methodology or biology) in the shape of the outline of the proximal pad on the hind toe is small, as e.g. in *Dendroica virens* (Fig. 10). However, individual pad shapes might differ considerably from the mean shape. For the following species, only one individual was available for study: *Carduelis barbata*, *Dendroica cerulea*, *D. discolor*, *D. pinus*, *Parus inornatus*, *P. montanus* and *P. rufonuchalis*.

   A higher standardisation of the pictures could have been obtained by using study skins instead of living birds. However, for study skins, the pads are dried and often hollow, and do not show their natural shapes; therefore canceling any possible advantage of using them.
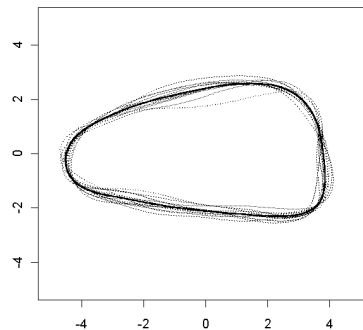


**Fig. 10.** Within-species variability of the shape of the proximal pad of digit I in *Dendroica virens*. Distal=left, lateral=upper (same orientation as Fig. 2), n=11.

### 13.4.2 Parallelism

I expected to find correlations of plantar morphology with substrate use and locomotor behaviour only if parallel evolution is present, i.e. each genus shows the same trend of morphological adaptation to substrate or behaviour. For a narrower definition of parallelism see Russell (1979). The fact that I found significant predictors among the foot sole traits for substrate use and behaviour indicates that parallel evolution exists in the majority of the four genera. Few relationships that I found do not show the same trend in each genus. For example, the negative relationship between the length of the proximal pad on digit I and two behavioural categories (sideways and belly up) is not or only weakly pronounced in *Dendroica*, whereas the other three genera show a clear negative relationship (Fig. 10). This observation indicates that for some ecological or behavioural problems, alternative morphological or behavioural solutions might exist, as for example in trunk climbing birds (Richardson 1942).

### 13.4.3 Functional aspects of plantar morphological traits

#### *Curvature of the hind claw*

I found that the curvature of the hind claw is negatively correlated with climbing on trunks. This result contrasts to earlier findings. According to Rüggeberg (1960), clinging and climbing specialists, such as *Certhia*, *Sitta*, *Parus atricapillus*, *Regulus*, *Acrocephalus*, *Carduelis spinus* and *Loxia*, have stronger curved, higher claws compared to the ground living birds *Alauda*, *Locustella* and *Carduelis cannabina*. Also Fedducia (1993) found that tree dwellers and trunk climbers have stronger curved claws than ground living birds. Both authors compared arboreal birds including trunk climbers with ground living ones. Contrastingly, I compared trunk climbers with mostly arboreal birds. Therefore, my results indicate that birds clinging to small twigs might have stronger curved claws than trunk climbers. For trunk climbers, strong (high) claws might be advantageous in order to grip into the rough bark of trunks. Accordingly, Zani (2000) found that the higher the claws of lizards are, the better these animals cling to rough substrate. To fully elucidate the function of well curved claws, experimental studies are needed.

#### *Toe pads: size and shape*

Several authors have assumed that toe pads of passerine birds are adapted to their locomotor behaviour and substrate (Rüggeberg 1960; Lennersted 1974; Leisler and Thaler 1982; Winkler and Leisler 1985; Keast and Saunders 1991; Korner-Nievergelt and Leisler in press). However, extensive tests or even descriptions of the relationship between pad morphology and locomotor behaviour and substrate use are lacking. This study describes for the first time statistically significant relationships between pad morphology and locomotor behaviour and substrate use. However, because statistical correlation do not elucidate function, the functional hypothesis I propose here need to be tested experimentally.

Pad length is negatively correlated with needles, and positively associated with foraging on the ground or grass. Furthermore, all body stances deviating from an upright position (sideways, belly up, upside down) are correlated with short pad length. Short pads might enhance the flexibility of the toes. Such flexible toes might be advantageous for clinging with force to a twig or needle. On the other hand, long toe pads might stiffen the toes and provide stability while walking on the ground. Blechschmidt (1929) and Rüggeberg (1960) found that basal (proximal) phalanges are shorter relative to the distal phalanges in arboreal birds than they are in ground foragers. Normally, each pad lies ventral to a phalanx (Lennersted, 1975b). Therefore, the lengths of phalanges and pads might correspond to each other.

The length of the distal pad of digit I is short in trunk climbers. Rüggeberg (1960) already noted that trunk climbers typically have small distal pads, however it is not clear what this "small" refers to: height, length or width. For trunk

climbers it is important to have a large foot span (Rüggeberg 1960; Winkler and Bock 1976; Norberg 1979), whereas tall pads might hinder the claws' ability to hook into the bark.

The height of the distal pad of digit I is small in birds often using vertical structures, but large in birds often found hanging upside down. In order to firmly grip the substrate while hanging upside down, it might be important to have tall distal pads. Such tall pads help closing the grip around a twig, whereas the claws might be less important than in trunk climbers. Similarly, for clinging to vertical structures, it might be important to have a large contact area between the plantar surface and the substrate, which is better provided by flat and long pads. The positive correlation of the length of this pad with hanging sideways supports this hypothesis.

Beside the lengths and heights of pads, their shapes are also important, namely for clinging to vertical structures and holding the body beside the substrate. For clinging to vertical structures (which is highly correlated with holding the body beside the substrate) it is plausible that a symmetric, broad pad with a distal maximal width provides a large contact area between the substrate and the plantar surface and therefore enhances the friction. Such a relationship has, as far as I know, never been described, before.

### *Papillae*

In a descriptive study of pads and papillae of passerines Lennersted (1975b) supposed that the structure of papillae and pads are adapted to the substrate. However, he did not correlate the number of papillae per pad with substrate use. Such studies exist only for geckos (Autumn et al. 2000), lizards (Zani 2000), possums (Rosenberg and Rose 1999) and mice (Krättli 2001). Autumn et al. (2000) described small adhesive structures in the toe pads of geckos which enable them to adhere to smooth surfaces. Similar adhesive lamellae have been found in geckos and lizards (Zani, pers. comm.). However, these hair-like structures are much smaller (diameter ~5 μm) than the papillae of a bird's toe pad (diameter 200-850 μm). Furthermore, the papillae of a bird do not resemble hair-like structures but look more like round cushions. I did not find any hair-like structure on REM-pictures of birds pads (Fig. 11). I looked at four species *Parus ater*, *P. caeruleus*, *Regulus regulus*, and *Phylloscopus trochilus* under four different magnifications (25x, 100x, 500x, and 2000x). It is unlikely that bird's papillae produce an adhesive force due to their microscopic structure. They are simply too large. Bird's pad papillae are with regard to histology and size more similar to the ridges of mammal's toe pads. In mice, the density of these ridges is highly correlated with clinging ability (Krättli 2001). The smaller and more numerous the ridges are, the better is the clinging ability to a thin substrate such as small twigs. We might, therefore, expect, also in birds, a negative correlation between size of papillae and the diameter of the substrate. Respectively, since size of papillae is inversely proportional to the number of papillae per unit area, I would expect a positive correlation between number of papillae and the diameter of the substrate. However, I found a negative correlation between the number of papillae and

foraging in needles, whereas hanging sideways and holding the body beside the substrate were positively correlated with the number of papillae per unit area. Similar observations were made by Lennersted (1975b). He found a reduced number of papillae in birds living on the ground, on tree trunks and on very thin twigs. However, he did not provide a functional interpretation. Furthermore, Lennersted (1975b; 1985) described that Palearctic sedentary passerines have generally few and large papillae, whereas passerines of similar size wintering in tropical Africa have many and small papillae. He supposed an insulating function of the few but large papillae. However, an insulating function of the foot sole might not be important in birds since they can regulate the temperature of their feet by a rete mirabile. I have not found any plausible interpretation for the function of the papillae of a bird's toe pad.
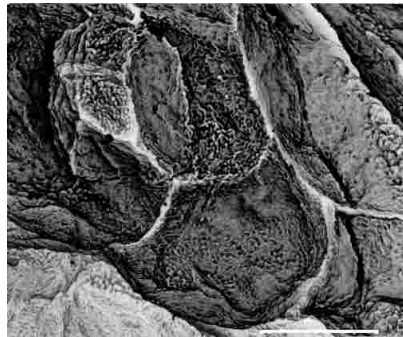


**Fig. 11.** REM-picture of the pad surface of a typical needle-dweller *Regulus regulus*. No special structures can be seen. White bar: 9 μm

## 13.5 Acknowledgements

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# Appendix

## Mean ecological scores

The means of the ecological scores are calculated from the answers of the species experts. 0=never, 1=seldom, 2=often. A "li" stands for those species, for which the information stems from the literature (see text). The names of the species experts are given in the acknowledgements. na: missing values.

| | needles | leaves | twigs | trunk | elsewhere | vertical | air | side ways | belly up | upside down | flutter hop | hover | flycatch | aerial hawk | beside | Below | expert(s) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Carduelis barbata* | 0.5 | 2 | 1.5 | 0 | 1.5 | 0.5 | 0 | 1.3 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0.5 | 0 | CV, WE |
| *C. cabaret* | 2 | 2 | 2 | 0 | 1 | 2 | 1 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 2 | 2 | li |
| *C. cannab.* | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | JD |
| *C. card.* | 1 | 2 | 2 | 0 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 2 | 2 | FK |
| *C. chloris* | 0 | 0 | 2 | 0 | 1.5 | 1.5 | 1 | 0.3 | 0 | 0 | 2 | 0 | 0 | 0 | 0.5 | 0 | KL, FK |
| *C. pinus* | 2 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | li |
| *C. spinus* | 2 | 2 | 2 | 0 | 0 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 0 | 2 | 2 | JCS |
| *C. tristis* | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | FK |
| *Dendroica caerulesc.* | 1 | 2 | 1.5 | 0.5 | 1 | 1 | 1 | 1 | 0.5 | 0 | 1 | 1.5 | 1.5 | 0.5 | 1.5 | 1 | MAV RTH |
| *D. castanea* | 1.5 | 1.5 | 1.5 | 0.5 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1.5 | 1 | 1 | 0 | BM, li |
| *D. cerulea* | 0.5 | 2 | 1 | 0 | 0 | 2 | 1.5 | 1.5 | 0.5 | 0.5 | 2 | 0 | 2 | 0.5 | 2 | 0.5 | TF, JJ |
| *D. coronata* | 2 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | li |
| *D. discolor* | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | li |
| *D. fusca* | 2 | 1 | 2 | 0 | 0.5 | 1.5 | 0.5 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1.5 | 0 | TF, FK, li |
| *D. magnol.* | 2 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | FK, li |
| *D. palmar.* | 1.5 | 1 | 2 | 0 | 2 | 0 | 2 | 1.5 | 0.5 | 0.5 | 1.5 | 0.5 | 1 | 0.5 | 1 | 0 | WHW, li |
| *D. pensylv.* | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | BB |
| *D. petechia* | 0 | 2 | 2 | 0 | 0 | 1 | 0.5 | 1.5 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 1 | 0.5 | TF, GAL |
| *D. pinus* | 2 | 1.5 | 2 | 0.5 | 0.5 | 1.5 | 0.5 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1.5 | 1 | TF |
| *D. striata* | 1 | 2 | 1 | 0 | 0 | 1 | 0.5 | 0 | 0.5 | 0.5 | 1 | 0.5 | 1 | 0.5 | 1.5 | 0 | CR, SL |
| *D. tigrina* | 2 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 2 | 2 | 2 | 2 | 1 | 1 | FK, li |
| *D. virens* | 2 | 2 | 1 | 0 | 0 | 0.5 | 1 | 0.5 | 0.5 | 0 | 0.5 | 1.5 | 1 | 1 | 1 | 0.5 | RS, MAV |
| *Parula [1]ame.* | 1 | 2 | 2 | 1 | na | 1 | na | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | JK |
| *Parus ater* | 2 | 0 | 2 | 0 | 0 | 1.8 | 1.5 | 2 | 2 | 0.5 | 2 | 0 | 0.5 | 0.5 | 2 | 1.8 | FK, PK |
| *P. atricap.* | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | FK |
| *P. caerul.* | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | FK |
| *P. carolin.* | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | li |
| *P. cristatus* | 2 | 0.3 | 2 | 0.5 | 1.5 | 0.5 | 1 | 0.5 | 0.3 | 0 | 1.5 | 1.3 | 0.5 | 0 | 0.5 | 0.3 | PK, FK |
| *P. inornat.* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | li |
| *P. major* | 0 | 0 | 2 | 0 | 1.5 | 1 | 0.5 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | FK, BT |
| *P. montan.* | 1.5 | 0.5 | 1.5 | 0 | 0 | 2 | 1 | 1.5 | 1.5 | 1 | 1 | 1 | 0 | 0 | 1.5 | 1.5 | WF, FK |
| *P. palustris* | 0.8 | 0.8 | 2 | 0 | 1 | 1.3 | 0.5 | 0.8 | 0.5 | 0 | 0.8 | 0.3 | 0 | 0 | 0.8 | 0.5 | FK, PK |
| *P. rufonu.* | 1 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | li |
| *Regulus cale.* | 2 | 2 | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | li |
| *R. ignicap.* | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | FK |
| *R. regulus* | 2 | 1 | 2 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | FK |
| *R. satrapa* | 2 | 1.5 | 2 | 1 | 1 | 2 | 1 | 1 | 1.5 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | DS, li |

[1] The genus *Parula* is genetically not separable from the genus *Dendroica* and therefore treated as *Dendroica* in this study (Lovette and Bermingham 2001).