

Does wing morphology reflect different foraging strategies in sibling bat species *Plecotus auritus* and *P. austriacus*?

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A b s t r a c t. Variability of wing shape of the genus *Plecotus* in Central Europe was studied in 159 individuals of *P. auritus* (n = 109) and of *P. austriacus* (n = 50). Measurements of all metacarpals and phalanges of digit III, IV and V as well as measurements of forearm were taken from live animals (n = 102) and from museum dry specimens (n = 57). Interspecific differences of the relative length of the first phalanges of digits III, IV and V to the total length of corresponding digits were observed. A difference in relative wing tip length to the forearm length (wing tip index) was also found. In *P. austriacus* the wing tip is significantly longer than in *P. auritus*. However the first phalanx of digit III in *P. austriacus* is significantly shorter. An adaptive importance of this morphometric difference is discussed.

Key words: morphometrics, wing tip, metacarpals, digits

Introduction

Bats occupy a wide range of natural habitats and therefore they show diverse morphological adaptations. Wing morphology has been reported to be correlated with habitat use and foraging behaviour (Farnley & Fleharty 1996, Findley et al. 1972, Norberg & Rayner 1987, McKenzie et al. 1995). Therefore predictions regarding habitat use could be made when morphological properties of the wing are known. A significant relationship between wing morphology of individuals of the same species and their habitat preference has been shown in *Myotis lucifugus* and *Miniopterus schreibersii* (Kalcounis & Brigham 1995, Jacobs 1999). Three major variables describe the adaptive design of the wing in flying animals: wing loading, aspect ratio and the relative wing tip length. High values for wing tip index, which could also be described as high ratio of digit III dimension to forearm (Findley et al. 1972), occur together with high aspect ratio among migrants and fast serial hawkers. The high values of wing tip index occur also among bats adapted to hovering flight (tribe Plecotini). These bats have low aspect ratio and wing loading (Norberg & Rayner 1987, McKenzie et al. 1995).

Based on food analysis, *Plecotus auritus* (Linnaeus, 1758) belongs to the group of foliage gleaners (Swift & Racey 1983) and behavioural observations on captive individuals confirmed that it prefers gleaning moths from surfaces (Anderson & Racey 1991, 1993). The ability of hovering flight in *P. auritus* has been described in detail previously (Norberg 1976). This species is adapted for foraging in cluttered vegetation and is unable to forage in open areas because its echo-location calls cannot detect flying prey over long distances (Entwistle et al. 1996). *P. austriacus* (Fischer, 1829) is thought to be able to capture prey in open space. It may forage moths around street lamps

and insects flying about trees but gleaning moths from surfaces is not excluded (B a u e r o v á 1982, B e c k 1995). Radio-tracked individuals of *P. austriacus* foraged in forest as well as above fields and meadows (F l u e c k i n g e r & B e c k 1995).

The present paper discusses whether the differences between the foraging behaviour of the two sibling species are reflected also in their wing design.

Material and Methods

A total of 159 individuals were investigated; 102 of them alive and 57 as dry museum specimens. Species were preliminary identified (S c h o b e r & G r i m m b e r g e r 1998); the former group included 77 individuals of *Plecotus auritus* (44 of them were males) and 25 of *Plecotus austriacus* (16 males). The latter group included 32 specimens of *P. auritus* (11 males) and 25 of *P. austriacus* (15 males). All samples originated from Central Europe: 105 from Moravia, 32 from Bohemia (both within the Czech Republic), 15 from West Pomerania (Germany) and 7 from Slovakia. All animals were either adult or subadult.

The lengths of the following skeletal parts integrated in the wing membrane were measured (abbreviations are the same as in Table 1): forearm, M-III, III-1, III-2, III-3, M-IV, IV-1, IV-2, M-V, V-1 and V-2. In live animals M-IV, IV-1 and IV-2 were not measured to avoid too long manipulation with them. The wing length was computed as the sum of forearm length and length of metacarpal and phalanges of digit III, and the wing width as the sum of the length of metacarpal and phalanges of digit V. Aspect ratio, wing area, wing loading and wing tip were estimated based on these dimensions. Computed were: i) wing tip index as the sum of the lengths of metacarpal and phalanges of digit III / forearm, ii) aspect ratio index as (tip + forearm) / length of digit V, iii) area index as (tip + forearm) x length of digit V x 2 and iv) wing loading index as area index / body mass (F i n d l e y et al. 1972). This method enabled comparison of wing shape of large number of investigated living animals. Preliminary results of wing loading computation carried out in 57 dry museum skins allowed the exclusion of body mass recording in live animals. This further reduced the manipulation time.

The Wilcoxon test was used for comparison of computed wing indexes. T-test served for comparison of basic morphometric data, component scores calculated in the frame of a principal component analysis (PCA) and for the evaluation of correlation between investigated characters. PCA was used for description of the correlation among observed characters (B e n d a & H o r á č e k 1995, B i r c h 1997). All statistics were computed with SPSS 10.0 statistical software.

Results

Comparison of live individuals and dry skins

Recorded data were initially evaluated regarding the origin of the animals. Due to significantly higher values for most of the characters in live animals, all samples were categorised into two groups. Individuals investigated alive were placed into group 1 whereas museum dry skins into group 2. They were then processed separately.

Intraspecific comparison

Intraspecific variability of studied populations was controlled before starting to investigate the interspecific differences. Sexual dimorphism was well expressed in studied populations.

Wing length, wing width and wing area index were significantly higher in females than in males in both species ($p < 0.01$). However, wing loading index, aspect ratio index and wing tip index were not affected by sex. No significant difference was found between adult and subadult animals in these characters. *P. auritus* showed no significant difference among populations from Moravia, Bohemia and West Pomerania. For *P. austriacus*, comparison between geographical populations was not possible due to insufficient number of individuals coming from different areas in each studied group.

Interspecific differences of the wing shape

For *P. austriacus*, wing length, wing width as well as the length of digit IV were significantly higher than in *P. auritus* (3-6 percent, $p < 0.01$). Most characters measured contributed to these differences. Significantly higher in *P. austriacus* were: M-III, III-2, M-V, and V-2 in both groups, forearm and III-3 only in group 1 and M-IV and IV-2 only in group 2 (Table 1). However, some exceptions included: III-1 was significantly higher in *P. auritus* in both groups (8 and 3 percent respectively, $p < 0.01$, $p = 0.023$) and V-1 in group 1 (7 percent, $p < 0.01$). The lengths of the forearm, IV-1 and V1 of group 2 were not significantly different between studied species ($p > 0.05$). Wing area index and wing tip index were significantly higher in *P. austriacus* ($p < 0.01$, Table 1). However, aspect ratio index and wing loading index were not significantly different between species.

Results of PCA

The first two principal components (PCs) explained about 70 percent of total variance in both investigated groups. PC-I, explaining the largest amount of variation (50 percent of total variance for group 1 and 57 for group 2), was strongly correlated with all examined wing

Table 1. Interspecific comparison of characters and indexes measured and computed for the wing of *P. auritus* and *P. austriacus*. Data from live animals (group 1) and museum dry skins (group 2) were compared separately. Wing dimensions were compared by unpaired t-test and wing indexes by Wilcoxon test. M-III, M-IV and M-V are metacarpals of digit III, IV and V, III-1, III-2 and III-3 are 1st, 2nd and 3rd phalanges of digit III etc. WTI stands for wing tip index, ARI - aspect ratio index, AI - area index and WLI is wing loading index.

Character	Group 1					Group 2				
	<i>P. auritus</i> N=77		<i>P. austriacus</i> N=25		Sig.	<i>P. auritus</i> N=32		<i>P. austriacus</i> N=25		Sig.
Mean	SD	Mean	SD	Mean		SD	Mean	SD		
Forearm	39.56	1.27	40.37	1.12	0.005	39.07	1.50	39.80	1.35	>0.05
M.III	35.98	1.14	37.63	1.04	<0.001	35.26	1.50	37.10	1.31	<0.001
III-1	14.24	0.89	13.51	0.48	<0.001	13.78	0.72	13.40	0.47	0.023
III-2	12.89	0.75	13.90	0.55	<0.001	12.38	1.20	13.28	0.54	0.001
III-3	7.68	0.53	8.03	0.65	0.007	6.24	0.78	6.85	0.87	>0.05
M-IV						34.71	1.36	36.79	1.15	<0.001
IV-1						9.33	0.55	9.25	0.36	>0.05
IV-2						9.45	0.73	10.26	0.74	<0.001
M-V	34.45	1.23	36.18	0.96	<0.001	33.90	1.52	35.63	1.27	<0.001
V-1	10.13	0.54	9.67	0.31	<0.001	9.71	0.62	9.64	0.67	>0.05
V-2	9.94	0.61	10.34	0.54	0.004	9.01	0.76	9.46	0.69	0.024
WTI	1.791	0.040	1.810	0.028	0.008	1.736	0.050	1.778	0.034	>0.001
ARI	2.024	0.039	2.020	0.031	>0.05	2.032	0.038	2.016	0.038	>0.05
AI.10 ³	12.044	0.770	12.754	0.669	<0.001	11.268	0.970	12.085	0.817	0.002
WLI.10 ³						0.724	0.082	0.748	0.084	>0.05

characters: forearm, M-III, III-1, III-2, III-3, M-IV, IV-1, IV-2, M-V, V-1 and V-2 ($p < 0.01$, Fig. 1). PC-II explaining 19 and 13 percent of total variance, respectively, was strongly correlated with III-1, IV-1, IV-2 and V-1 ($p < 0.01$) and also correlated with III-2 (only in group 1) and with M-IV ($p < 0.05$, Fig. 1). Thus these six variables were correlated with both PCs. Significant interspecific differences were found both for PC-I and PC-II ($p < 0.01$, Fig 2).

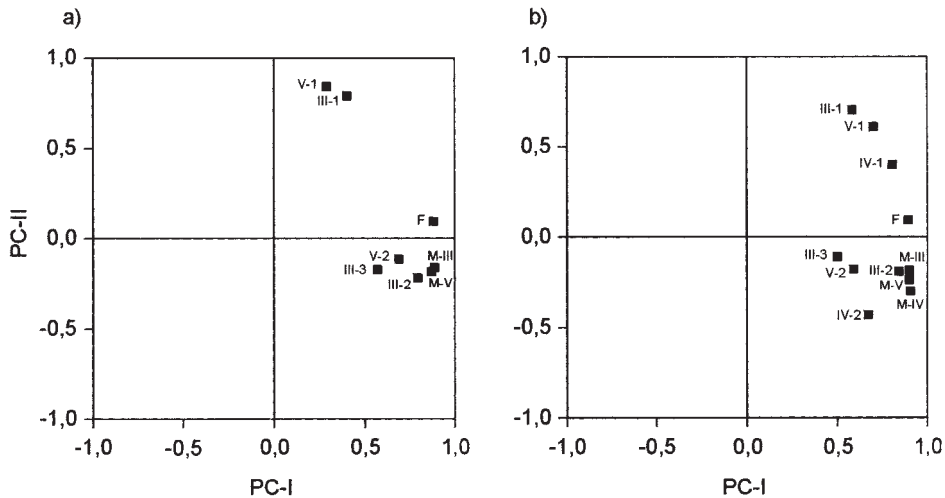


Fig. 1. Component weights plot for each wing measurement taken from live animals (a) and museum dry skins (b) on the first two principal components (PC). Two PCs explain 69 percent of wing characters variance (a) and 71 percent (b) respectively. Graph a) shows high degree of positive correlation of all wing characters with PC-I while III-1, V-1 and to lesser extent III-2 are correlated with PC-II. Correlation with PCs in b) is weaker (III-1, V-1, IV-1 and IV-2 are in an intermediate position between PC-I and PC-II). F - forearm, other abbreviations are the same as in Table 1.

Discussion

Previous morphological studies comparing wing shape in large numbers of bat species reported main ecomorphological adaptations of the wing in bats (Findley et al. 1972, Lawlor 1973, Norberg & Rayner 1987). Nevertheless, fine differences of a wing design between two sibling species have not been studied in detail. In order to arrange it in the studied species, first the relevance of the data was to be considered regarding differences between dry museum specimens and live animals. Dimensions of bones from dry museum specimens were smaller than those from live bats, as previously has been published (Araña 1968). A similar effect of liquid preservation on bat wing dimensions has also been described (Binda-Emonds & Russell 1994).

In contrast to clear sexual dimorphism found in this study, no differences of wing dimensions between males and females have been found in populations of the genus *Plecotus* in Spain (Paz 1994).

The analysis of the wing shape showed significant interspecific differences of the wing tip index and wing area index. The wing morphology is influenced by foraging behaviour, size of prey, migratory habits as well as flight performance (Norberg 1995), which are not well known in *P. austriacus*. In contrast, clearly different flight styles in two species are not always coupled with changes of the wing shape (Richmond et al. 1998). Higher

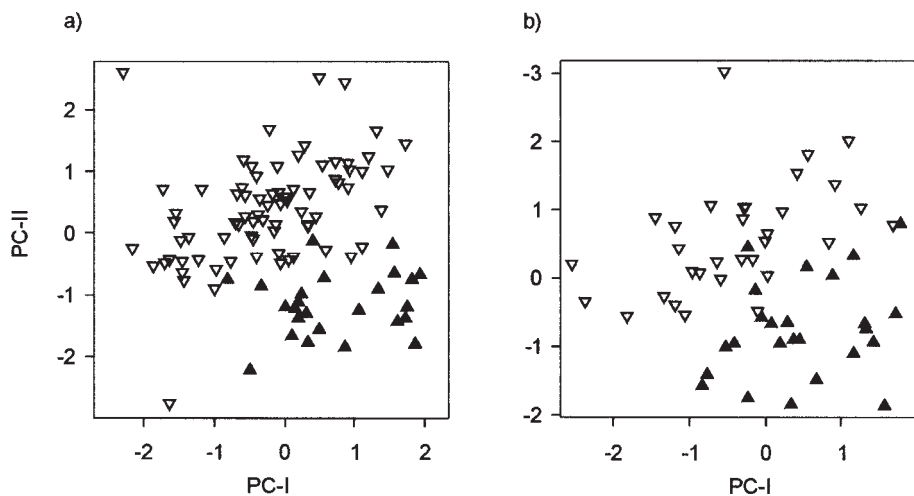


Fig. 2. Component scores plot for individual bats on the first two principal components computed for wing dimensions of 102 investigated live bats (a) and 57 museum dry skins (b). Graphs show relatively clear clusters of individual component scores for both species. ▼ *P. auritus*, ▲ *P. austriacus*.

value of wing area index in *P. austriacus* is probably related to slightly bigger body dimension reported for this species (Strelkov 1988, Schöber & Grimberger 1998). However, higher wing tip index in *P. austriacus* might be responsible for different flight performance. Different wing shape would enable these species to occupy different niches. *P. austriacus* is thought indeed to forage more in open spaces than *P. auritus*. This assumption is supported by its prey composition (Bauerová 1982, Beck 1995). The presence of a high wing tip index simultaneously with a low aspect ratio and wing loading is thought to be an adaptation for hovering flight. Generally, this supports the ability to move close to the complex surfaces of stems and leaves (Norberg & Rayner 1987, Aldridge & Rautenbach 1987). Then, the significant increase in wing tip index could be a result of an adaptation to hovering flight and foraging in open space together.

Why are the lengths of the first phalanges of digits III and V less in *P. austriacus* whereas the total lengths of its wing tip and of digit V are even higher than in *P. auritus*? Could the flight pattern be influenced by change, such as eight percent shorter phalanx of a digit? Probably, it could. This change may support adaptation of wing tip shape and may serve to stretch out the membrane, for example (Norberg 1972). In addition, this difference seems to be stable among populations from different geographical regions. It supports the existence of a kind of selection pressure on this character. Nevertheless, explanation of changes in dimensions of individual phalanges as well as of the wing tip shape of genus *Plecotus* will require further behavioural study of both species, in particular *P. austriacus*.

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LITERATURE

- ALDRIDGE H. & RAUTENBACH I. 1987: Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* 56: 763–778.
- ANDERSON M. & RACEY P. 1991: Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* 42: 489–493.
- ANDERSON M. & RACEY P. 1993: Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* 46: 1151–1155.
- ARATA A. 1968: Discrepancy between “dry” and “fresh” forearm measurements in bats. *J. Mammal.* 49: 155–156.
- BAUEROVÁ Z. 1982: Contribution to the trophic ecology of the grey long-eared bat, *Plecotus austriacus*. *Folia Zool.* 31: 113–122.
- BECK A. 1995: Fecal analyses of European bat species. *Myotis* 32–33: 109–119.
- BENDA P. & HORÁČEK I. 1995: Geographic variation in three species of *Myotis* (Mammalia: Chiroptera) in South of the Western Palearctics. *Acta Soc. Zool. Bohem.* 59: 17–39.
- BININDA-EMONDS O. & RUSSELL P. 1994: Flight style in bats as predicted from morphometry: the effects of specimen preservation. *J. Zool. Lond.* 234: 275–287.
- BIRCH J. 1997: Comparing wing shape of bats: The merits of principal-components analysis and relative-warp analysis. *J. Mammal.* 78: 1187–1198.
- ENTWISTLE A., RACEY P.A. & SPEAKMAN J.R. 1996: Habitat exploitation by a gleaning bat, *Plecotus aurtus*. *Phil. Trans. R. Soc. Lond. B* 351: 921–931.
- FARNEY J. & FLEHARTY E. 1969: Aspect ratio, loading, wing span, and membrane areas of bats. *J. Mammal.* 50: 362–367.
- FINDLEY J., STUDIER H. & WILSON D. 1972: Morphologic properties of bat wings. *J. Mammal.* 53: 429–444.
- FLUECKINGER P. & BECK A. 1995: Observations on the habitat use for hunting by *Plecotus austriacus* (Fischer 1829). *Myotis* 32–33: 121–122.
- JACOBS D. 1999: Intraspecific variation in wingspan and echolocation call flexibility might explain the use of different habitats by the insectivorous bat, *Miniopterus schreibersii* (Vespertilionidae; Miniopterinae). *Acta Chiropterol.* 1: 93–103.
- KALCOUNIS M. & BRIGHAM M. 1995: Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). *Can. J. Zool.* 73: 89–95.
- LAWLOR T. 1973: Aerodynamic characteristics of some neotropical bats. *J. Mammal.* 54: 71–78.
- MCKENZIE N., GUNNELL A., YANI M. & WILLIAMS M. 1995: Correspondence between flight morphology and foraging ecology in some palaeotropical bats. *Aust. J. Zool.* 43: 241–257.
- NORBERG U. 1972: Bat wing structures important for aerodynamics and rigidity (Mammalia, Chiroptera). *Z. Morph. Tiere* 73: 45–61.
- NORBERG U. 1976: Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. *J. Exp. Biol.* 65: 170–212.
- NORBERG U. 1995: How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* 9: 48–54.
- NORBERG U. & RAYNER J. 1987: Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* 316: 335–427.
- PAZ O. 1994: Systematic position of *Plecotus* (Geoffroy, 1818) from the Iberian Peninsula (Mammalia : Chiroptera). *Mammalia* 58: 423–432.
- RICHMOND J., BANACK S. & GRANT G. 1998: Comparative analysis of wing morphology, flight behaviour, and habitat use in flying foxes (genus: *Pteropus*). *Aust. J. Zool.* 46: 283–289.
- SCHOBER W. & GRIMMBERGER E. 1998: Die Fledermäuse Europas. *Verlag Franckh-Kosmos, Stuttgart*.
- STRELKOV P. 1988: Brown (*Plecotus auritus*) and grey (*P. austriacus*) bats (Chiroptera, Vespertilionidae) in the USSR, 1. *Zool. Zh.* 67: 90–100.
- SWIFT S. & RACEY P. 1983: Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool., Lond.* 200: 249–259.