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# **Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera)**

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phylogenetic contrasts

**Running title:** Brain adaptation to habitat complexity in bats.

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## **Abstract**

Vertebrate brains are organised in modules, which process information from sensory inputs selectively. Therefore they are probably under different evolutionary pressures. We investigated the impact of environmental influences on specific brain centres in bats. We showed in a phylogenetically independent contrast analysis that wing area of species corrected for body size correlated with estimates of habitat complexity. We subsequently compared wing area, as an indirect measure of habitat complexity with the size of regions associated with hearing, olfaction and spatial memory, while controlling for phylogeny and body mass. The inferior colliculi, the largest sub-cortical auditory centre, showed a strong positive correlation with wing area in echolocating bats. The size of the main olfactory bulb did not increase with wing area suggesting that the need for olfaction may not increase during the localisation of food and orientation in denser habitat. As expected, larger wing area was linked to a larger hippocampus in all bats. Our results suggest that morphological adaptations related to flight and neuronal capabilities as reflected by the sizes of brain regions co-evolved under similar ecological pressures. Thus, habitat complexity presumably influenced and shaped sensory abilities in this mammalian order independently of each other.

## **Introduction**

Animals are moulded by their environment. This is true within orders, families and even genera at large ecological scales (e.g. aquatic versus terrestrial organisms), to closely related species occupying narrow niches (e.g. Darwin's finches, Grant & Grant 1989; Lack 1969). Morphology reflects the environment an organism inhabits, and consequently much about ecological niche can be deduced from the way animals are shaped. Parts of the mammalian brain are adapted to solving different tasks and respond to selective regimes, including environmental influences (Barton et al. 1995; Eisenberg & Wilson 1978; Hutcheon et al. 2002). One well-investigated example showing that brain centres do vary in size under selective pressure is the hippocampus, which becomes larger with increasing demands on spatial memory (e.g. birds, Krebs et al. 1989; rodents, Jacobs et al. 1990; London taxi-drivers, Maguire et al. 2000). The extent to which mammalian brain regions develop independently has been the subject of a controversial debate. While some authors argue that the setup of a common ancestor's brain constrains development (Finlay & Darlington 1995) others think that selection acts on brains and brain regions independently of phylogeny ("mosaic theory": e.g. (Barton & Harvey 2000; Barton et al. 1995; Harvey & Krebs 1990). The following scenarios can be imagined. Either the whole brain of an organism changes in size or selection operates on individual neuro-cognitive systems. In the latter case, the ancestral blueprint may limit changes in brain size, according to the phylogenetic constraint hypothesis (Harvey & Krebs 1990). Or, according to the mosaic theory (Barton & Harvey 2000), selection should act on parts of the brain independently of the rest and of phylogenetic constraints (Barton & Harvey 2000; Harvey & Krebs 1990).

Bats (Chiroptera) are an exceptionally species-rich and widely distributed order and are particularly fascinating, as far as morphological adaptations are concerned (Swartz et al. 2003). The ability to fly in connection with the use of echolocation for orientation (in the suborder microchiroptera) is generally viewed as a prerequisite for the manifold niche differentiations (Altringham 1996; Neuweiler 1993). Wing measures and especially wing area reflect flight performance and ecological niche of flying animals in general (e.g. (Altshuler & Dudley 2002; Hoffmann et al. 2002; Tobalske et al. 2003) and of bats in particular (Fenton & Bogdanowicz 2002; Norberg 1986; Norberg 1994; Norberg & Rayner 1987). At one extreme of morphological adaptations, species hunt insects in open space relying on speed. Such fast flying bats have small wing areas relative to body mass, resulting in low agility and manoeuvrability (Norberg 1994; Norberg & Rayner 1987). At another extreme, bats typically forage in highly structured habitat while flying slowly or perching, detecting their food (animals or fruit) at short range through echolocation calls, olfaction or passive listening. Their wings are broad and large, rendering them highly manoeuvrable (Neuweiler 1990; Norberg & Rayner 1987). Although the study of wing morphology in bats and their adaptation

to habitat complexity represents one of the best documented examples of functional ecology a proper phylogenetic analysis of the correlation of wing morphology with habitat complexity was lacking. Thus, we validated the reliability of this measure in a comparative approach using appropriate statistical methods of phylogenetically independent contrasts.

Habitat should not only influence morphological adaptation to flight, but also sensory requirements. Previous comparative studies on the neurobiology of bats dealt with taxonomy, echolocation and dietary specialisation (Barton et al. 1995; Eisenberg & Wilson 1978; Hutcheon et al. 2002; Jolicoeur & Baron 1980; Jolicoeur et al. 1984; Neuweiler 1989; Neuweiler 1993; Pirlot & Jolicoeur 1982). Preferences of the two main dietary subgroups, plant- and animal-eating bats, were found to correlate with sensory specialization, reflected by size changes of the corresponding brain centres (Hutcheon et al. 2002). However, this may at least partially be a consequence of the underlying effect of sensory adaptations to habitat, and only indirectly connected with diet (Harvey & Krebs 1990).

Here, we aimed to correlate the influence of ecological factors with the evolution of sensory adaptations to the environment. We associated wing morphology as an indirect measure of the complexity of a bat's foraging habitat and the brain centres connected with three sensory channels (hearing: auditory nuclei and inferior colliculi; smell: main olfactory bulb; and spatial memory: hippocampus), while controlling for phylogeny and body mass.

We made the following predictions regarding the influence of wing area on the size of the investigated brain parts:

(1) Bats foraging in complex habitats must distinguish prey from background clutter, while simultaneously recognising and avoiding obstacles. This puts higher demands on hearing abilities, than detection of prey and orientation in open space. Consequently, we expected an increase in the size of auditory nuclei and/or inferior colliculi along with increasing wing area (= habitat complexity) in all echolocating bats (animal-eating species and phytophagous Phyllostomidae), but no association in the exclusively frugivorous suborder Megachiroptera with the single family Pteropodidae, whose members do not echolocate. Hearing ability influences the size of the inferior colliculi in bats (Baron et al. 1996). They are the main switchboard for all incoming auditory information, incorporating the acoustic fovea (Neuweiler 1993)

(2) The main olfactory bulb is assumed to be of importance for phytophagous bats for the detection of food sources and the determination of the ripeness of fruit (Baron et al. 1996). However, whether olfaction alone is sufficient for the localization of food is controversial (Baron et al. 1996; Hutcheon et al. 2002), and we did not expect an influence of habitat complexity on the size of this brain part.

(3) Finally, hippocampus size is directly related to spatial memory (Krebs et al. 1989). We expected a positive correlation of wing area with hippocampus size. Dense habitats

contain many obstacles and changes occur relatively frequently, making spatial memory a valuable tool for orientation. While frugivorous bats have bigger hippocampi than animal-eating bats (Hutcheon et al. 2002) we expected an influence of habitat structure in all species.

## **Methods**

Using wing morphology data from Norberg & Rayner (1987), and brain volumes from Baron et al. (1996) we analysed a total of 97 species from 12 families. Data for body mass (in g), wing area (in cm<sup>2</sup>), volume of hippocampus and main olfactory bulb were available for all 97 species. Volume of auditory nuclei was obtained of 75 species and volume of inferior colliculi of 69. Brain components were in mm<sup>3</sup>. Data were log<sub>10</sub> transformed to obtain normal distribution. Dietary information was assigned according to Nowak (1994) and in case of the Genus *Tonatia* according to Reid (1997).

Bat species can be categorized into guilds according to complexity of their foraging habitats (Patterson et al. 2003). We selected 30 species grouped into four categories (1=open aerial foragers; 2=edge and gap foragers; 3=background-cluttered and narrow space habitat; 4=highly cluttered habitat; see Kalko et al. 1996; guilds according to Kalko et al. 1996 and J. Fahr, pers. comm.). We then compared these guilds according to their wing area in order to verify the reliability of this measure for habitat complexity. We treated the four categories as continuous characters. This assumes a continuous spectrum of habitat complexity, representing discrete approximations (for a similar approach see: Purvis et al. 2000; Safi & Kerth in press).

## **Statistical analyses:**

Statistical tests were based on phylogenetically independent contrasts (Felsenstein 1985; Pagel 1999), generated with the software CAIC (Purvis & Rambaut 1995 <http://www.bio.ic.ac.uk/evolve/software/caic/>). Using this approach we acknowledge the fact that species are not independent entities and have a common history represented by a hierarchical and branched phylogeny. We used the recent phylogeny provided by Jones et al. (2002) to infer relationships between the species used in this analysis. Since branch lengths were not known, we set them to equal length (Garland et al. 1992). The plots of the absolute values of the standardized independent contrasts versus the standard deviation showed no correlation for all variables analysed in this study. This suggested that the arbitrarily equalized branch lengths standardized the contrasts and were reasonable for use in our analyses (Diaz-Uriarte & Garland 1996; Diaz-Uriarte & Garland 1998). As all variables represented continuous data, the 'crunch' algorithm of the CAIC package was used (Purvis & Rambaut 1995). The results were tested in GLMs for type 3 sums of squares using SAS

version 6.12 (SAS Institute Inc. 1993). Wing area was the main predictor, and body mass the covariate. Regressions were forced through the origin (Purvis & Rambaut 1995).

In the analysis with CAIC (Purvis & Rambaut 1995) we first tested the data for all species together. As recommended by Garland et al. (Garland et al. 1992) we analysed the data on species level and using phylogenetically independent contrasts. Species level data were assumed to be independent or to stem from a star phylogeny, where all species have the same ancestor and equal branch lengths.

Then we separated the data for CAIC into subgroups according to our predictions. We investigated the effect of increasing wing area on the auditory nuclei and inferior colliculi of echolocators and pteropodids separately, because differences may exist between their hearing brains. We also individually analysed the size of the main olfactory bulb of phyllostomid bats, pteropodid bats and all other bats in association with wing area, as frugivorous bats are thought to rely on their sense of smell very much. Pteropodids and phyllostomids were separated due to fundamental differences in orientation mode (echolocation vs. vision), which might indirectly influence the role of olfaction for orientation. Finally, for the analysis of hippocampus size, phytophagous and non-phytophagous bats were separated. Although we expected an influence of habitat structure in all bats, hippocampus is assumed to play a more important role for frugivores (Hutcheon et al. 2002). We only present the results on subsets of the entire data for the phylogenetically independent contrasts. The data and the tree used are available from the corresponding author upon request.

## **Results:**

### **Verification of wing area as a measure for habitat complexity**

At species level, wing area corrected for body mass showed a significant positive correlation with guild ( $N=30$ ,  $F_{3,0.1}=5.29$ ,  $p=0.006$ ). A significant positive correlation was maintained after correcting for phylogenetic dependence and controlling for body mass ( $N_{\text{contrasts}}=9$ ,  $F_1, 0.12=18.35$ ,  $p=0.004$ ). These analyses justify the use of wing area as a reliable correlate of habitat complexity.

### **Auditory nuclei and inferior colliculi**

At species level, wing area showed a significant positive correlation with the size of the auditory nuclei, both corrected for body mass (table 1). However, after controlling for phylogeny, the effect of wing area on auditory nuclei was no longer significant (table 1).

When we separated the pteropodids from all other bats in a phylogenetically corrected analysis, size of auditory nuclei still did not correlate with wing area in echolocating species, while it increased significantly with wing area in the Pteropodidae (table 2).

Table 1: The effect of log wing area on four different brain regions corrected for body weight (covariate) for all species. Estimate denotes the slope of a given source on the independent variable in the model.

	<u>Species independent</u>					<u>Contrast level</u>				
	Estimate	d.f.	SS3	F	p	Estimate	d.f.	SS3	F	p
<u>Log auditory nuclei<sup>a</sup></u>										
Log wing area	0.19	1	0.10	4.32	0.04	0.03	1	<0.001	0.26	0.61
Log body weight	0.37	1	0.07	2.81	0.10	0.50	1	0.10	46.5	<0.01
Error		71					30			
<u>Log inferior colliculi<sup>b</sup></u>										
Log wing area	0.25	1	0.06	2.28	0.14	0.25	1	0.04	24.6	<0.01
Log body weight	0.28	1	0.11	4.40	0.04	0.37	1	0.05	28.8	<0.01
Error		68					30			
<u>Log main olfactory bulb<sup>c</sup></u>										
Log wing area	-0.29	1	0.08	1.07	0.30	0.04	1	0.002	0.34	0.56
Log body weight	1.20	1	3.50	47.50	<0.01	0.81	1	0.35	72.03	<0.01
Error		94					41			
<u>Log hippocampus<sup>c</sup></u>										
Log wing area	0.40	1	0.14	4.29	0.04	0.43	1	0.18	108.0	<0.01
Log body weight	0.53	1	0.68	20.70	<0.01	0.40	1	0.08	50.7	<0.01
Error		94					41			

<sup>a</sup> N<sub>species</sub>=75; N<sub>contrasts</sub>=32

<sup>b</sup> N<sub>species</sub>=69; N<sub>contrasts</sub>=32

<sup>c</sup> N<sub>species</sub>=97; N<sub>contrasts</sub>=43

There was no correlation between wing area and the size of inferior colliculi at species level (table 1). When using independent contrasts, a strong positive correlation between wing area and the size of the inferior colliculi was found (table 1).

In a separate analysis, both, echolocating and pteropodid bats showed a significant increase in the size of the inferior colliculi with increasing wing area, however, the effect was much stronger for echolocating bats (table 2).

Table 2: The effect of log wing area corrected for body size on A: log auditory nuclei and B: log inferior colliculi for echolocating bats and pteropodid bats using phylogenetically independent contrasts.

	<u>Echolocating bats:</u>					<u>Pteropodid bats:</u>				
	Est.	d.f.	SS3	F	p	Est.	d.f.	SS3	F	p
<u>A: Log auditory nuclei</u>										
Log wing area	0.03	1	<0.01	0.48	0.50	0.68	1	0.01	7.86	0.01
Log body weight	0.64	1	0.08	91	<0.01	0.09	1	<0.01	0.25	0.63
Error		16					12			
<u>B: Log colliculi inferiores</u>										
Log wing area	0.21	1	0.02	20.4	<0.01	0.47	1	<0.01	7.09	0.03
Log body weight	0.52	1	0.05	51.9	<0.01	0.20	1	<0.01	2.47	0.15
Error		20					10			

### Main olfactory bulb

Volume of the main olfactory bulb was not affected by wing area either at species level or using independent contrasts, (table 1).



We analysed three subgroups: pteropodids, phytophagous phyllostomids, and non-phytophagous bats. Only the pteropodids showed a significant relation between wing area and mass of olfactory bulb (table 3). In addition the main olfactory bulb shows a tendency to be reduced in non-phytophagous bats in relation to wing area.

Table 3: Effect of wing area on log main olfactory bulb using phylogenetically independent contrasts.

	Phytophagous bats:					Non-phytophagous bats:										
	Phyllostomids					Pteropodids					All remaining species					
	Est.	d.f.	SS3	F	p	Est.	d.f.	SS3	F	p	Est.	d.f.	SS3	F	p	
<u>Log main olfactory bulb</u>																
Log wing area	-0.02	1	<0.01	0.00	0.96	0.53	1	<0.01	5.36	0.04	-0.16	1	0.02	4.17	0.05	
Log body weight	0.58	1	<0.01	4.54	0.06	0.22	1	<0.01	1.76	0.21	1.02	1	0.32	68.0	<0.01	
Error		9					14					20				

## Hippocampus

There was a correlation between size of hippocampus and wing area at species level (table 1). The independent contrasts also showed a significant increase in size of the hippocampus with increasing wing area (table 1) (figure 1).

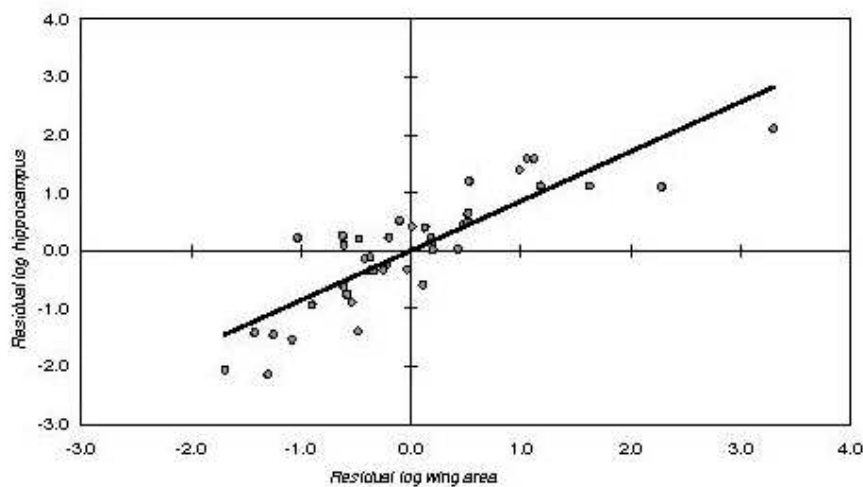


Figure 1: Plot of residual contrasts in log wing area (residuals generated from a least-squares regression of contrasts in log wing area and log hippocampus against log body mass (Garland et al. 1992 )) against contrasts in log hippocampus. Contrasts were generated using CAIC.

When using independent contrasts, wing area was positively correlated to an increase in size of hippocampus in phytophagous and all other bats (table 4).

Table 4: Effect of log wing area on log hippocampus using phylogenetically independent contrasts.

	Phytophagous bats:					Non-phytophagous bats:				
	Est.	d.f.	SS3	F	p	Est.	d.f.	SS3	F	p
<u>Log hippocampus</u>										
Log wing area	0.30	1	<0.01	5.80	0.01	0.47	1	0.07	82.1	<0.01
Log body weight	0.38	1	<0.01	6.88	0.02	0.35	1	0.1	54.9	<0.01
Error		26					20			

### **Phylogenetic inertia**

The independent contrast analyses and the species level analyses substantially deviated in the analyses concerning brain regions associated with hearing. This suggests that phylogenetic inertia is present and that corresponding correction required. A species level ANOVA, with volume of brain regions nested in family, revealed significant differences for all four brain regions, confirming the strong phylogenetic influence (auditory nuclei:  $N_{\text{species}}=74$ ,  $F_{21,5.02}=43.2$ ,  $p<0.001$ ; inferior colliculi:  $N_{\text{species}}=70$ ,  $F_{21,4.62}=36.0$ ,  $p<0.001$ ; main olfactory bulb:  $N_{\text{species}}=102$ ,  $F_{22,1.47}=159.5$   $p<0.001$ ; hippocampus:  $N_{\text{species}}=102$ ,  $F_{22,0.74}=78.6$ ,  $p<0.001$ ).

### **Discussion**

We were able to confirm most predictions concerning the influence of morphological adaptations to structure of foraging habitats measured by wing area on various brain regions. We also showed, that phylogenetic constraints may act on the morphology of closely related species to a certain extent making the use of independent contrasts a useful tool to reveal such effects.

Previous studies on encephalization and brain regions in bats (and other mammals) found an influence of diet on brain size (Barton et al. 1995; Eisenberg & Wilson 1978; Harvey & Krebs 1990; Hutcheon et al. 2002; Jolicoeur et al. 1984; Pirlot & Jolicoeur 1982). It has been speculated that not the nature of the food of animal taxa directly influences brain size, but rather the variation in information storage and retrieval systems associated with diet (Eisenberg & Wilson 1978; Harvey & Krebs 1990). Our findings support these hypotheses and suggest that the surplus of information processing required in complex habitats may have influenced brain evolution (Harvey & Krebs 1990).

The size of the inferior colliculi, reflects the hearing capacity of species better than any other brain structure (Baron et al. 1996). The fact that the inferior colliculi of echolocating bats were correlated with wing area may reflect their improved ability to deal with increasingly difficult acoustic environments. However, there may be additional influences on the size of the inferior colliculi: Passive gleaners, which use prey-generated sounds for the detection of food in addition to echolocation, are closely associated with dense and complex

habitats. Such species have two sensitive frequency ranges possibly resulting in larger inferior colliculi (Baron et al. 1996).

Echolocating bats have larger auditory nuclei than the non-echolocating pteropodids (Hutcheon et al. 2002). However, auditory nuclei were not influenced by habitat complexity. Environmental influences may act differently on each of the several centres summarized under “auditory nuclei”, and their functions may be only partly or not at all related to changes in the environment.

The increase of both, auditory nuclei and inferior colliculi with wing area in the non-echolocating pteropodids is noticeable. It remains unclear whether selective pressure on hearing ability is responsible for this effect. The benefits of improved hearing in increasingly complex habitats despite a lack of echolocation have not been investigated to date.

Brains of pteropodid bats have been characterised as ‘olfactory’ and ‘visual’ whereas those of microchiropteran bats have been described as ‘auditory’ (Barton et al. 1995; Eisenberg & Wilson 1978; Hutcheon et al. 2002). Our results show increasing main olfactory bulb with wing area only in the Pteropodidae. This suggests that, while olfaction may play a role in the localisation of food (Luft et al. 2003; Möhres & Kulzer 1956), the importance of it is likely to increase in denser habitat in this suborder. The reason for the tendency towards reduction in main olfactory bulb size of non-phytophagous bats is unclear. While it may indicate a phylogenetic constraint (Finlay & Darlington 1995), echolocation is unlikely to be the reason for this, since we would then expect the same pattern in the phytophagous phyllostomid bats who also use echolocation. But the phyllostomids, seem to use olfaction only for the detection but not for the localization of food sources in denser habitat.

The hippocampus is responsible for spatial memory in various animal taxa, (Jacobs et al. 1990; Krebs et al. 1989; Maguire et al. 2000). The ability of bats to memorise structures within their foraging area has long been recognised and anecdotal evidence suggests that spatial memory is crucial for orientation in bats (Neuweiler 1993). Dense habitat is not only difficult to move in but changes in vegetation, which require improved spatial learning, occur more often here. Among the Chiroptera, phytophagous bats have the largest hippocampus (Hutcheon et al. 2002). They evidently benefit from enhanced spatial memory by remembering the location of unpredictable but stationary food resources such as flowering trees (Baron et al. 1996; Barton et al. 1995). The correlation with wing area in this group of bats suggests, that at least two mechanisms (location and orientation) act together on hippocampus’ size. Thus the alleged effect of habitat complexity reflected by wing morphology presumably influenced the evolution of spatial memory.

The strong influence of the phylogenetic corrections on practically all of our results indicates that common ancestry influences external as well as brain morphology. The phylogenetic independent analyses of the four brain regions in bats presented here show

that the involved size changes in brain regions differed between specific structures and functional systems. Similarly as shown by Hutcheon et al (2002) in the context of diet, the diverging influence of habitat structure on the two suborders and even within the suborder Microchiroptera, e.g. concerning the size of the olfactory bulb, indicate that specific brain regions can develop in a mosaic pattern (Barton & Harvey 2000; Barton et al. 1995) at least to a large extent when selective pressure necessitates it.

## **Conclusions**

Our study shows that neuronal capacities in bats presumably coevolved with flight morphology, under selection imposed by habitat complexity. This was true for brain parts processing sensory input connected to hearing, and spatial memory, but not for olfaction. Our study on the selective evolution of brain regions reveals a differentiated pattern of size increase in brain regions in relation to habitat complexity. These findings suggest that neuro-cognitive centres are under specific selection pressure according to the “mosaic theory” (Barton & Harvey 2000). The fingerprints of the adaptive radiation in the order of Chiroptera thus cannot only be found on external morphology but also on neuronal units. Both, morphology and brain regions, together with sensory capabilities, seem to be shaped to match the demands of a species' ecology.

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