

Neuroecology and diet selection in phyllostomid bats

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ABSTRACT

For many birds and mammals relative brain and hippocampus volume are positively related to enhanced behavioral flexibility and spatial memory. I tested for correlations between species-specific diet selection and relative brain and hippocampus volumes in the New World leaf-nosed bats (Phyllostomidae). To this end, I classified each of 53 species from this ecologically diverse family as one of the following: (i) predatory, (ii) omnivorous, (iii) frugivorous, or (iv) nectivorous. Species-level analyses and the comparative method (i.e. phylogenetically independent contrasts) revealed that relative hippocampus volume was greater in predatory species than in frugivorous and nectivorous species and that relative brain size was greater in frugivorous species than in predatory species. As previously reported, specialized frugivory appears to be associated with increased relative brain volume suggesting these two traits evolve together. I suggest some plausible functional explanations for variation in hippocampus volume in light of our current understanding of the acquisition of spatial information and its use by echolocating bats.

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1. Introduction

Neuroecology involves the comparative study of adaptive variation in brain and behavior. It is based on the premise that ecological demands on particular cognitive, motor and perceptual functions influence the size of brain structures that support these functions. This is illustrated in food-storing birds that retrieve their caches by remembering the locations of cache sites (e.g., Sherry et al., 1981; Shettleworth and Krebs, 1982), a behavior that places demands on spatial memory. The hippocampus, a telencephalic structure that plays a role in spatial memory (e.g., O'Keefe and Nadel, 1978), is larger in food-storing birds than in non-food-storing birds (Krebs et al., 1989; Pravosudov and Clayton, 2002; Sherry et al., 1992; Sherry, 2006). The strong link between spatial memory and hippocampal function in birds (e.g., Hampton and Shettleworth, 1996; Sherry and Vaccarino, 1989) and mammals (Morris et al., 1982; Wilson and McNaughton, 1993), including humans (Ekstrom et al., 2003; Maguire et al., 2000), suggests that comparative studies may lead to new insights about the neurobiological bases of natural spatial behaviors. For example, bats appear to be an especially relevant group for investigating potentially meaningful relationships between relative brain and hippocampal volume and habitat complexity (Ratcliffe et al., 2006; Safi and Dechmann, 2005; Shumway, 2008).

Amongst mammals, and vertebrates in general, bats are long-lived and for a variety of reasons presumably face extraordinary

demands on spatial information processing. Maternity colonies of the insectivorous free-tailed bat *Tadarida brasiliensis* can number in the millions and mothers must relocate their single, non-volant pup amongst countless others after returning from the night's foraging (McCracken, 1993). Other bats migrate thousands of kilometers each year – both predatory bats (e.g., *Pipistrellus nathusii*, Hutterer et al., 2005) and Old World fruit bats (e.g., *Eidolon helvum*, Richter and Cumming, 2006) – while the flower bat *Glossophaga soricina* is able to remember from what flowers it has fed and depleted and thus ascertain what flowers might still contain nectar (Winter and Stich, 2005). *G. soricina* belongs to the family Phyllostomidae (the New World leaf-nosed bats), one of the most species rich families of bats alive today (Jones et al., 2002).

The phyllostomids are found only in consistently warmer parts of the Americas but are the most ecologically diverse group of bats with respect to diet. It is comprised not only of predatory bats (including vampires), but also of omnivorous species, frugivores, and bats that include in their broad diet the nectar of flowers, a specialization reflected in morphology, behavior and sensory systems (von Helversen and Winter, 2003). Compared to other families of echolocating bats, the phyllostomids exhibit little variation in either wing morphology or echolocation call design. Among laryngeal echolocators, it is these bats that most obviously use non-auditory sensory information for the detection and discrimination of food (e.g., olfactory information: *Carollia castanea*, *C. perspicilata*, Thies et al., 1998; visual information: *G. soricina*, Winter et al., 2003). However, what information is used in foraging, and to what extent, has been studied in only a very few phyllostomid bat species. Here I investigate potential relationships between brain and hippocampus size and diet in phyllostomid bats. I predicted that frugivorous

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phyllostomids would have relatively larger brains than species relying primarily on insects and other small animals because of greater requirements for acquiring spatially distributed food, assessing its ripeness and its efficient and effective handling. Together, these demands might be correlated to an enlargement of several areas of the brain involved with sensory information processing, integration, and motor control and, thus, on a coarse scale an overall larger brain. I also predicted that the hippocampuses of phyllostomids specialized (i) for feeding on the nectar of flowers and/or (ii) for hunting animal prey from perches would be relatively larger than in frugivorous and omnivorous species. I hypothesize that the demands on spatial memory are greater for bats that would do well to remember (i) where and when a nectar resource was last visited and/or depleted or (ii) where a previously used hunting perch is located and when it might again be productive. This as opposed to the demands faced by frugivores and omnivores, which might better rely on the phenology of different fruits and nightly inspection of their foraging range.

2. Materials and methods

Body mass and brain volume data were available for 53 phyllostomid species in Baron et al. (1996) and all were used in the following analyses. Based only on diet information taken from two books (Nowak, 1994; Reid, 1997) and available mammalian species accounts, I assigned each bat species to one of four categories. Bats were classified as being (a) predatory, (b) omnivorous, (c) frugivorous, or (d) nectivorous (Fig. 1 and Table 1). All analyses were carried out as previously described (Ratcliffe et al., 2006). Briefly, I log transformed species-specific data on body mass, brain volume, and hippocampus volume and brain remainder volume (i.e. species' brain volume minus species' hippocampus volume). I then took the standardized residuals from log–log regressions of (i) brain volume

versus body mass and (ii) hippocampus volume versus brain volume remainder as species-specific measures of (i) relative brain and (ii) hippocampus volume. I compared standardized residuals at the species level and, to control for the potential effects of shared evolutionary histories (Felsenstein, 1985), calculated standardized independent linear contrasts based on these residuals using the program CAIC v. 2.6.9 (Purvis and Rambaut, 1995). Based on the phylogeny for the Phyllostomidae found in Jones et al. (2002), including relevant polytomies, I used the Crunch procedure and dummy variables to map and analyze these data (Dunn et al., 2001; Ratcliffe et al., 2006).

3. Results

Brain volume was highly dependent upon species' body mass; similarly species-specific hippocampus volume was dependent on brain volume remainder. Log brain volume was positively related to log body mass ($F_{1,51} = 904.1$, $R^2 = 0.95$, $P < 0.001$). Log hippocampus volume was positively related to log brain volume remainder ($F_{1,51} = 286.7$, $R^2 = 0.85$, $P < 0.001$). Standardized residuals from these log–log regressions were compared using traditional statistics and standardized independent contrasts.

Among species and for independent contrasts, relative brain size was significantly greater in frugivorous species than in predatory species (species data—ANOVA: $F_{3,49} = 3.27$, $P = 0.029$; independent contrasts—ANOVA: $F_{3,49} = 3.37$, $P = 0.0195$; Tukey HSD post hoc tests; Fig. 2a). At the species level and for independent contrasts, relative hippocampus volume was significantly greater in predatory species than in frugivorous and nectivorous species and significantly greater in omnivorous species than in frugivorous species (species data—ANOVA: $F_{3,49} = 7.95$, $P = 0.0002$; independent contrasts—ANOVA: $F_{3,49} = 7.13$, $P = 0.0001$; Tukey HSD post hoc tests; Fig. 2b).



Fig. 1. (a) *Tonatia saurophilus*, a predatory species; (b) *Phyllostomus discolor*, an omnivorous species; (c) *Artibeus jamaicensis*, a frugivorous species; (d) *Anoura geoffroyi*, a nectivorous species. Photographs taken by Marco Tschapka.

Table 1

Diet, brain and hippocampus volume, and body mass for each of the 53 phyllostomid species considered here (brain volume = brain mass/1.036, Baron et al., 1996). *Mesophylla* (= *Ectophylla*) *macconnelli*, not included in the phylogeny of Jones et al. (2002) was substituted for *Ectophylla alba* for which brain volume data was not available.

Species	Diet category	Hippocampus volume (mm ³)	Brain volume (mm ³)	Body mass (g)
<i>Diphylla ecaudata</i>	Predatory	41	770.3	30.9
<i>Desmodus rotundus</i>	Predatory	42.4	964.3	36.3
<i>Macrophyllum macrophyllum</i>	Predatory	19.6	309.8	8.6
<i>Micronycteris brachyotis</i>	Predatory	22.6	393.8	14.7
<i>Micronycteris megalotis</i>	Predatory	14.1	264.5	6.5
<i>Micronycteris minuta</i>	Predatory	17.3	276.1	6.9
<i>Micronycteris schmidtorum</i>	Predatory	14.4	297.3	7.8
<i>Trachops cirrhosus</i>	Predatory	50.6	968.1	36.9
<i>Vampyrum spectrum</i>	Predatory	110.4	2497.1	173
<i>Tonatia bidens</i>	Predatory	41.7	760.6	29.4
<i>Tonatia schulzi</i>	Predatory	16.1	492.3	21.3
<i>Tonatia silvicola</i>	Predatory	27.1	729.7	32.3
<i>Mimon crenulatum</i>	Predatory	18.2	314.7	11.8
<i>Phylloderma stenops</i>	Omnivorous	91.7	1291.5	46.1
<i>Phyllostomus discolor</i>	Omnivorous	67.9	1052.1	36.6
<i>Phyllostomus hastatus</i>	Omnivorous	79.8	1464.3	90.1
<i>Phyllostomus elongatus</i>	Omnivorous	49.1	854.2	44.9
<i>Sturnira lilium</i>	Frugivorous	23.2	596.5	20.2
<i>Sturnira ludovici</i>	Frugivorous	24.3	652.5	25.9
<i>Sturnira tildae</i>	Frugivorous	27.8	676.6	24.4
<i>Sphaeronycteris toxophyllum</i>	Frugivorous	20.5	505.8	18.4
<i>Artibeus hartii</i>	Frugivorous	21.3	493.2	16.1
<i>Artibeus cinereus</i>	Frugivorous	20	450.8	12.6
<i>Artibeus concolor</i>	Frugivorous	25.3	611	19.4
<i>Artibeus jamaicensis</i>	Frugivorous	44.1	980.7	41
<i>Artibeus lituratus</i>	Frugivorous	49.5	1190.2	56
<i>Mesophylla macconnelli</i>	Frugivorous	13.5	332	7.5
<i>Chiroderma salvini</i>	Frugivorous	27.6	785.7	26.1
<i>Chiroderma villosum</i>	Frugivorous	22.8	681.5	24.8
<i>Chiroderma trinitatum</i>	Frugivorous	17.2	518.3	13.7
<i>Vampyressa pusilla</i>	Frugivorous	14.9	364.9	8.6
<i>Uroderma bilobatum</i>	Frugivorous	28.4	590.7	16.2
<i>Vampyrodes caraccioli</i>	Frugivorous	30.2	914.1	39.7
<i>Platyrrhinus brachycephalus</i>	Frugivorous	20.7	562.7	12.9
<i>Platyrrhinus helleri</i>	Frugivorous	19.4	501	13.8
<i>Platyrrhinus infuscus</i>	Frugivorous	36.4	1071.4	50.2
<i>Platyrrhinus lineatus</i>	Omnivorous	26	715.3	22.6
<i>Platyrrhinus vittatus</i>	Frugivorous	46.8	1134.2	36.6
<i>Rhinophylla pumilio</i>	Frugivorous	12.7	343.6	8.9
<i>Carollia castanea</i>	Frugivorous	16.9	436.3	13.1
<i>Carollia perspicillata</i>	Frugivorous	20	527	17.8
<i>Brachyphylla cavernarum</i>	Omnivorous	36.8	1154.4	44.5
<i>Lionycteris spurrelli</i>	Nectivorous	13.6	339.8	7.55
<i>Lonchophylla mordax</i>	Nectivorous	15.6	417	10.7
<i>Lonchophylla thomasi</i>	Nectivorous	13.5	325.3	6.9
<i>Leptonycteris curasoae</i>	Nectivorous	23.1	588.8	24.5
<i>Leptonycteris nivalis</i>	Nectivorous	22.4	565.6	22.8
<i>Monophyllus plethodon</i>	Omnivorous	15.3	429.5	15
<i>Glossophaga soricina</i>	Nectivorous	14.9	379.3	9.9
<i>Glossophaga longirostris</i>	Nectivorous	17	419.9	11.3
<i>Anoura caudifer</i>	Nectivorous	15.7	390.9	10.6
<i>Anoura geoffroyi</i>	Nectivorous	24.1	565.6	16
<i>Choeroniscus minor</i>	Nectivorous	16.5	375.5	9.6

4. Discussion

At both the species level and when controlling for the potential effects of a shared evolutionary history, I found that the relative brain volume of frugivorous species was greater than that of predatory species within the family Phyllostomidae (see also Eisenberg and Wilson, 1978; Safi and Dechmann, 2005). This relationship between brain size and frugivory mirrors that found for frugivorous primates and those more reliant upon insects as food (Barton et al., 1995). The phyllostomid adaptive radiation may be at least partially explained by this group's exploitation of fruit and may have depended on the evolution of larger brains (see Sol et al., 2005 for a potentially analogous situation in birds). Insectivory is believed to be the ancestral state of the Order Chiroptera and with the exception of the phyllostomids and the Old World fruit bats (family Pteropodidae), all other families consist solely of predatory species. Indeed,

insectivory appears to have been the ancestral state of the New World fruit bats (Fenton, 1992; Jones et al., 2002). That only frugivorous species – and not also omnivorous and nectivorous species – have relatively larger brains than predatory species might be a reflection of the cognitive demands of specializing solely on fruit rather than taking what is immediately available in the form of small animals, fruit, pollen, nectar and seeds.

At both the species level and for independent contrasts predatory species' hippocampuses were relatively larger than the hippocampuses of frugivorous and nectivorous species. Those of omnivores were also larger than those of frugivorous species at both levels of analysis. Prior to discussing the possible implications of the correlation between diet and hippocampus volume, a number of caveats are in order. First, this gross morphological approach does not control for potential species-specific differences in neuronal density and connectivity. Second, we do not yet understand

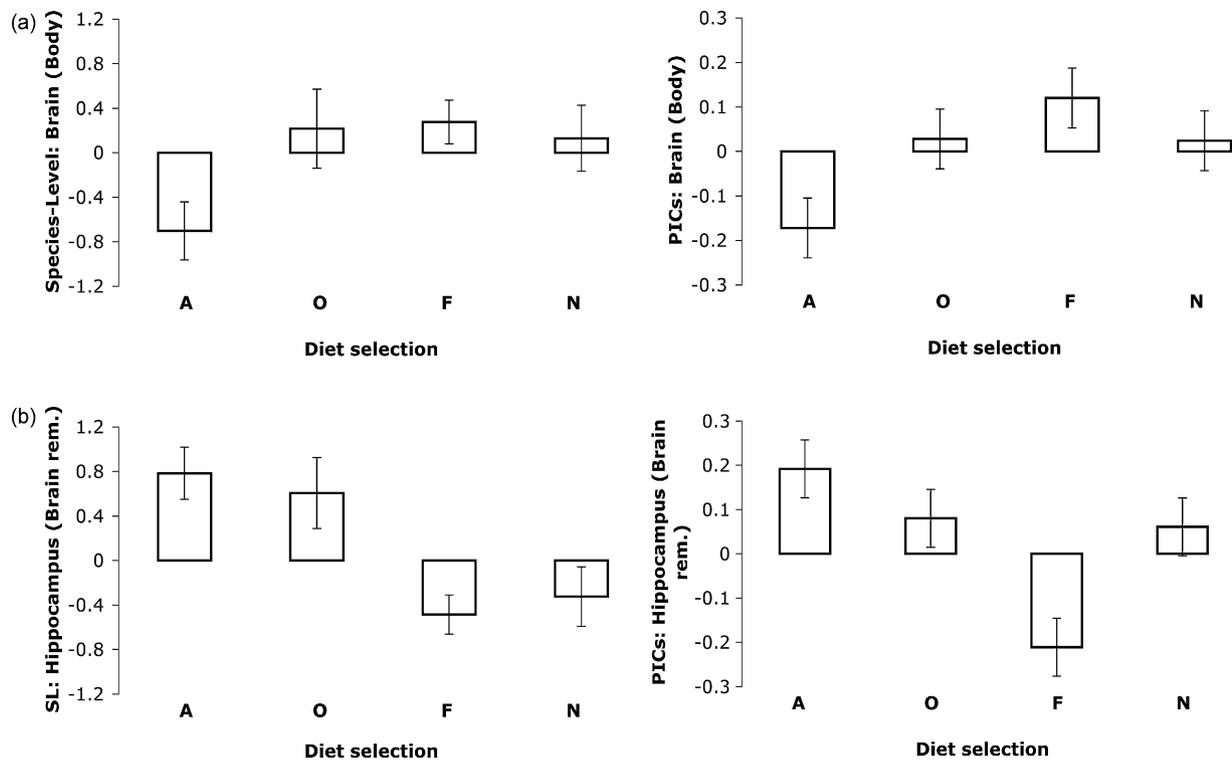


Fig. 2. (a) Relative brain size in phyllostomid bats in relation to four diet categories; (b) relative hippocampus volume in phyllostomid bats in relation to these same four categories (A=Predatory; O=Omnivorous; F=Frugivorous; N=Nectivorous; mean \pm S.D.). Left panel: based on species-level analysis (SL); right panel: based on phylogenetically independent contrasts (PICs). See text for details of statistically significant relationships.

the adaptive function(s) of the hippocampus in bats as well as we do for some rodents and birds (Neuweiler, 2000). For example, while preliminary results suggest that echolocating bats in general exhibit low adult hippocampal neurogenesis relative to rats (Amrein et al., 2007), Ulanovsky and Moss (2007) have shown that big brown bats *Eptesicus fuscus* have hippocampal place cells that fire in a manner similar to those of rodents. Third, my categories reflect diet selection and not necessarily the ways that phyllostomid bats go about finding and relocating nutritious food resources (that is, I have used reported diet from the secondary literature as a proxy for behavior). Last, I recognize that more detailed species-specific diet information exists for a subset of the species considered here but have elected to take information from three sources in an effort to standardize the data. These caveats acknowledged, given what is understood about this group of bats as a whole and the importance of brain and hippocampus size for adaptive behavior and spatial memory in other mammals and birds, I offer the following preliminary analysis.

Anecdotal reports and past research findings suggest that bats possess exceptional spatial memories (Griffin, 1958; Fleming, 1988; Schnitzler et al., 2003). Examples include the use of acoustic landmarks for spatial orientation (Jensen et al., 2005) and associations of specific structural cues with prey capture (Siemers, 2001). Three of the four diets I consider have been suggested to be demanding with respect to resource location (e.g., perch hunting: Ratcliffe et al., 2005; fruit finding: Fleming, 1988; flower visiting: Thiele and Winter, 2005; Winter and Stich, 2005). However, little experimental work has been undertaken at the behavioral level on spatial memory in bats (for a rare example see Jensen et al., 2005) and even less at the neurobiological level on hippocampus function (Neuweiler, 2000; Ulanovsky and Moss, 2007). Omnivorous species, as a result of their broad diet, may not rely heavily on spatial memory for relocating specific resources. Similarly, frugivorous and nectivorous species are able to detect and localize preferred

resources at some distance through fruit and flower olfactory cues (Mikich et al., 2003; Thies et al., 1998; von Helversen and Winter, 2003). Ratcliffe et al. (2006) found that among predatory species, substrate-gleaning and behaviorally flexible species (i.e., species able both glean and aerially hawk prey) trend towards having relatively larger hippocampuses than species that capture only airborne prey, seemingly irrespective of habitat use and home range. Among phyllostomid bats, excepting water trawling *Macrophyllum macrophyllum*, predatory species (including vampires) primarily employ a gleaning strategy for prey capture. Using the relationship between wing area and body mass as a proxy for behavior, Safi and Dechmann (2005) found that species expected to forage in cluttered habitats had larger hippocampuses than those expected to forage in more open spaces. It is among these cluttered habitat foragers that most gleaning and behaviorally flexible species are found (Ratcliffe et al., 2006). Taken together these results suggest that one way to interpret the finding that predatory phyllostomids have larger hippocampuses than do frugivorous and nectivorous species would be through an overdue consideration of the role of spatial memory for perch hunting. It appears that at least some of the time all predatory species of bat take airborne prey on the wing, however of those that also take prey from surfaces, many may use familiar perches for hunting (e.g., *Megaderma lyra*, Audet et al., 1991). This sit-and-wait strategy, during which time the bats are passively listening for low-intensity, prey-generated sounds, may be augmented by the ability to remember when and where patches of prey were discovered over and between seasons. And so, while monitoring spatiotemporal fluctuations in fruit phenology and recalling the depletion of nectar in flowers are undoubtedly cognitively taxing (Fleming, 1988; Thiele and Winter, 2005; Winter and Stich, 2005), the demands of remembering where a perch is located within a cluttered habitat and when that perch might again be a good place to listen for prey may be more taxing still.

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References

- Amrein, I., Dechmann, D.K.N., Winter, Y., Lipp, H.P., 2007. Absent or low rate of adult neurogenesis in the hippocampus of bats (Chiroptera). *Public Library of Science ONE* 2, e455.
- Audet, D., Krull, D., Marimuthu, G., Sumithran, S., Balasingh, J., 1991. Foraging behavior of the Indian false vampire bat, *Megaderma lyra* (Chiroptera: Megadermatidae). *Biotropica* 23, 63–67.
- Baron, G., Stephan, H., Frahm, H.D., 1996. Comparative Neurobiology in Chiroptera. Birkhäuser, Basel, CH.
- Barton, R.A., Purvis, A., Harvey, P.H., 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philosophical Transactions of the Royal Society of London B* 348, 381–392.
- Dunn, P.O., Whittingham, L.A., Pitcher, T.E., 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55, 161–175.
- Eisenberg, J.F., Wilson, D.E., 1978. Relative brain size and feeding strategies in the Chiroptera. *Evolution* 32, 740–751.
- Ekstrom, A.D., Kahana, M.J., Caplan, J.B., Isham, E., Fields, T.A., Isham, E., Newman, E., Fried, I., 2003. Cellular networks underlying human spatial navigation. *Nature* 425, 184–187.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *American Naturalist* 125, 1–15.
- Fenton, M.B., 1992. Wounds and the origin of blood-feeding in bats. *Biological Journal of the Linnean Society* 47, 161–171.
- Fleming, T.H., 1988. *The Short-Tailed Fruit Bat: A Study in Plant–Animal Interactions*. University of Chicago Press, Chicago, IL.
- Griffin, D.R., 1958. *Listening in the Dark: The Acoustic Orientation of Bats and Men*. Yale University Press, New Haven, CT.
- Hampton, R.R., Shettleworth, S.J., 1996. Hippocampal lesions impair memory for location but not color in passerine birds. *Behavioral Neuroscience* 110, 831–835.
- Hutterer, R., Ivanova, T., Meyer-Cords, C., Rodrigues, L., 2005. Bat migrations in Europe: a review of banding data and literature. *Naturschutz und Biologische Vielfalt* 28, 1–176.
- Jensen, M.E., Moss, C.F., Surlykke, A., 2005. Echolocating bats can use acoustic landmarks for spatial orientation. *Journal of Experimental Biology* 208, 4399–4410.
- Jones, K.E., Purvis, A., MacLarnon, A., Bininda-Emonds, O.R.P., Simmons, N.B., 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews* 77, 223–259.
- Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H., Vaccarino, A.L., 1989. Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences of the United States of America* 86, 1388–1392.
- Maguire, E.A., Gadian, D.G., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S.J., Frith, C.D., 2000. Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America* 97, 4398–4403.
- McCracken, G.F., 1993. Locational memory and female–pup reunions in Mexican free-tailed bat maternity colonies. *Animal Behaviour* 45, 811–813.
- Mikich, S.B., Bianconi, G.V., Maia, B.H.L.N.S., Teixeira, S.I., 2003. Attraction of the fruit-eating bat *Carollia perspicillata* to *Piper gaudichaudianum* essential oil. *Journal of Chemical Ecology* 29, 2379–2383.
- Morris, R.G., Garrud, P., Rawlins, J.N., O'Keefe, J., 1982. Place navigation impaired in rats with hippocampal lesions. *Nature* 297, 681–683.
- Neuweiler, G., 2000. *The Biology of Bats*. Oxford University Press, Oxford, UK.
- Nowak, R.M., 1994. *Walker's Bats of the World*. Johns Hopkins University Press, Baltimore, MD.
- O'Keefe, J., Nadel, L., 1978. *The Hippocampus as a Cognitive Map*. Clarendon Press, Oxford, UK.
- Pravosudov, V.V., Clayton, N.S., 2002. A test of the adaptive specialization hypothesis: population differences in caching, memory and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience* 116, 515–522.
- Purvis, A., Rambaut, A., 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications for the Biosciences* 11, 247–251.
- Ratcliffe, J.M., Raghuram, H., Marimuthu, G., Fullard, J.H., Fenton, M.B., 2005. Hunting in unfamiliar space: echolocation in the Indian false vampire bat, *Megaderma lyra*, when gleaning prey. *Behavioral Ecology and Sociobiology* 58, 157–164.
- Ratcliffe, J.M., Fenton, M.B., Shettleworth, S.J., 2006. Behavioural flexibility positively correlated with relative brain volume in predatory bats. *Brain, Behavior, and Evolution* 67, 165–176.
- Reid, F.A., 1997. *A Field Guide to the Mammals of Central America and Southeast Mexico*. Oxford University Press, Oxford.
- Richter, H.V., Cumming, G.S., 2006. Food availability and the annual migration of the straw-coloured fruit bat (*Eidolon helvum*) at Kasanka National Park, Zambia. *Journal of Zoology*, London 268, 35–44.
- Safi, K., Dechmann, D.K.N., 2005. Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). *Proceedings of the Royal Society of London B* 272, 179–186.
- Schnitzler, H.-U., Moss, C.F., Denzinger, A., 2003. From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology and Evolution* 18, 386–394.
- Sherry, D.F., 2006. Neuroecology. *Annual Review of Psychology* 57, 167–197.
- Sherry, D.F., Vaccarino, A.L., 1989. Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience* 103, 308–318.
- Sherry, D.F., Krebs, J.R., Cowie, R.J., 1981. Memory for the location of stored food in marsh tits. *Animal Behaviour* 29, 1260–1266.
- Sherry, D.F., Jacobs, L.F., Gaulin, S.J.C., 1992. Spatial memory and the adaptive specialization of the hippocampus. *Trends in Neuroscience* 15, 298–303.
- Shettleworth, S.J., Krebs, J.R., 1982. How marsh tits find their hoards: the roles of site preference and spatial memory. *Journal of Experimental Psychology Animal Behavior Processes* 8, 354–375.
- Shumway, C.A., 2008. Habitat complexity, brain, and behavior. *Brain, Behavior, and Evolution* 72, 123–134.
- Siemers, B.M., 2001. Finding prey by associative learning in gleaning bats: experiments with a Natterer's bat *Myotis nattereri*. *Acta Chiropterologica* 3, 211–215.
- Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P., Lefebvre, L., 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America* 102, 5460–5465.
- Thiele, J., Winter, Y., 2005. Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. *Animal Behaviour* 69, 315–327.
- Thies, W., Kalko, E.K.V., Schnitzler, H.-U., 1998. The roles of echolocation and olfaction in two neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on piper. *Behavioral Ecology and Sociobiology* 42, 397–409.
- Ulanovsky, N., Moss, C.K., 2007. Hippocampal cellular and network activity in freely moving echolocating bats. *Nature Neuroscience* 10, 224–233.
- von Helversen, O., Winter, Y., 2003. Glossophagine bats and their flowers: costs and benefits for plants and pollinators. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. University of Chicago Press, Chicago, IL, pp. 348–397.
- Wilson, M.A., McNaughton, B.L., 1993. Dynamics of the hippocampal ensemble code for space. *Science* 261, 1055–1058.
- Winter, Y., Stich, K.P., 2005. Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology* 208, 539–548.
- Winter, Y., López, J., von Helversen, O., 2003. Ultraviolet vision in a bat. *Nature* 425, 612–614.