

The brains of woodpeckers

Hans WINKLER & Viola WINKLER

Abstract: The brains of woodpeckers are among the relatively largest in birds. Differences in brain size among species correlate with foraging behavior and migration: species that hammer a lot tend to have bigger brains, while those of migrants are smaller. Extractive foraging and use of anvils may be associated with well-developed brains. Brain size is also related to the stress on the brain during pecking. Our analyses based on microCT scans support the findings of GIBSON (2006) that woodpeckers, because of their small absolute brains, can withstand accelerations without suffering from injuries about 16 times than can humans. We discuss the relationships between brain size and cognition, and speculate on the possible advantages of large brains in the context of reserve capacity as insurance against the consequences of brain injuries.

Key words: Woodpecker, Picidae, brain size, concussion, phylogeny, cognition

Introduction

A quick search through the internet reveals a clear public interest in the question why woodpeckers do not suffer from serious brain or eye injuries, a question that has held even the attention of scientists working in various fields for quite a while and continues to do so (BECHER 1953; GORDON 1976; GIBSON 2006; ODA et al. 2006; WYGNANSKI-JAFFE et al. 2007; WANG et al. 2011; LIZHEN et al. 2013; ZHU et al. 2014; LIU et al. 2015). This topic, while interesting and dealt with in the contribution by Bock (this volume), distracts from other intriguing facts about the brains of woodpeckers.

Overall brain size in birds has received some attention in the past two decades, with attempts to relate it to certain cognitive abilities. In particular Louis LEFEBVRE and his co-workers stressed the positive relationship between relative forebrain size and behavioral flexibility, measured mainly as the frequency at which new and/or unusual feeding techniques had been reported of a species in the ornithological literature (LEFEBVRE et al. 1997, 2004). Actually it was PORTMAN and his students who pioneered this type of research. He was particularly intrigued by the extraordinary forebrain development of woodpeckers (1951). Another consistent correlation emerged a bit later when researchers discovered that the (fore)brain size of long-distance migrants is smaller than that of closely related residents both in birds and bats (WINKLER et al. 2004; SOL et al. 2005, 2010; PRAVOSUDOV et al. 2007; MCGUIRE & RATCLIFFE 2010; FUCHS et al. 2014).

Here we will summarize briefly what is known about the brains of woodpeckers with respect to gross

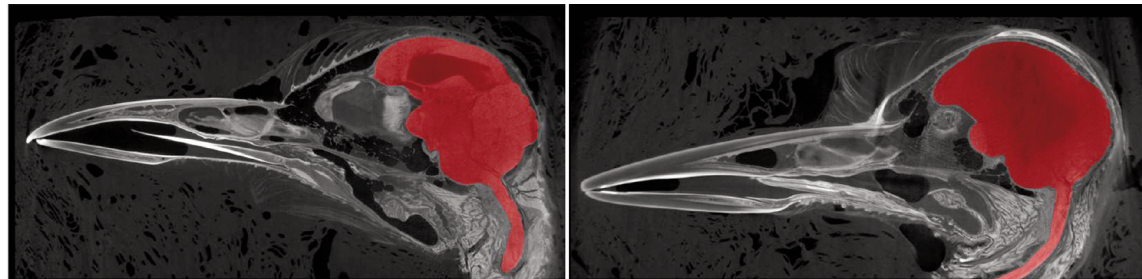
morphology and neurobiology, and then focus on the size of woodpecker brains and its implication for behavior, comparative studies, and also, impact injuries.

Some characteristics of woodpecker brains

Figure 1 gives a general impression of the size and position of woodpecker versus songbird brains. DENNLER (1919) and BECHER (1953) characterize the brain of woodpeckers as follows: The dorsal surface is rather round, with a groove at the nasal end. The sagittal groove is not very deep, the bulbous olfactorius cannot be seen from above. The frontal parts are strongly arched, and the cerebellum is broad, and so is the medulla. The cranium fits closely around the brain, so endocasts very much look like real brains (cf. KAWABE et al. 2013) and the cortex is small and rudimentary as in all modern birds, with no cortical areas on the surface that faces in the direction of the impact forces generated when excavating (BECHER 1953). While the cortical development is poor, the basal ganglia are big leaving little room for the ventricles which are thin slits or completely reduced. However, birds do not possess a six-layered cortex like mammals do, and these statements need to be contrasted with the current views on the homologies between mammalian and avian brains (The Avian Brain Nomenclature Consortium 2005; ABOITIZ & ZAMORANO 2013). According to BECHER (1953), the histological structure of the woodpecker brain does not differ from the general avian condition.

Woodpeckers are altricial and thus possess all the features of the brain typical for birds with that type of

Fig. 1: Sagittal sections of the heads of a Blackbird (left) and a Great Spotted Woodpecker (right). Brains and spinal cords are shown in red. Pictures were generated on the basis of microCT scans.



Turdus merula

Dendrocopos major

development: late differentiation of the myelin sheaths and a relatively large (fore)brain (PORTMANN 1946, 1947, 1962; BENNETT & HARVEY 1985; RICKLEFS & STARCK 1998; IWANIUK & NELSON 2003). The cerebralization index used by PORTMANN (1951) for his comparative studies in vertebrate brains is rather high in woodpeckers (4.62 for the wryneck and 11.04-19.35 in the Picinae).

The olfactory bulb comprises 8-14.3 % of the cerebral hemispheres' diameter. This is about the relation found in starlings, but substantially higher than in finches and sparrows, and about half of that found in Procellariiformes (Petrels and albatrosses) and the Kiwi (BANG & COBB 1968).

BRANDIS (1896) published a comparative study of avian cerebella in which he found, among other things, clear differences between the cerebellum of the wryneck and the true woodpeckers, of which his sample had five species. Both groups were also found to differ in this respect from the barbets. In his judgement, the wryneck

had a more primitive cerebellum than the other picids (see also DENNLER 1919). At that time the sister-group relationship between the honeyguides and the woodpeckers was not yet established, and BRANDIS therefore was surprised to find more similarities between the cerebella of the woodpeckers and honeyguides than between the former and the barbets. Taken all this together, he came to the conclusion that the honeyguides and woodpeckers have the most differentiated cerebellum of the Pici, in which (along with FÜBRINGER (1888) he had included the barbets, toucans, honeyguides, and woodpeckers. Within the cerebellum, the trigeminal and visual parts are particularly enlarged, a condition also found in parrots and crows (SULTAN 2005).

It is also interesting to note that certain pathological conditions in the brain of ageing humans have also been discovered in woodpeckers, whereas little is known in other birds (NAKAYAMA et al. 1999).

Brain size Introduction

Brain size generally correlates with body size. This relationship is allometric with coefficients 0.574 to 0.609 (NEALEN & RICKLEFS 2001). This means that brains get relatively smaller as body size increases (RENSCH 1958). It is important to realize that slopes are more or less similar among groups of birds and mammals and that the differences are mainly found in the multiplier in the allometric function, or in the intercept in the log-log relationships between body mass and other morphological or physiological variables. To find relationships between brain size and other variables, one has therefore always to take the body-brain size relationship into account. One way is to take the residuals from a body-brain size regression; another is to apply multivariate regression techniques.

Researchers have repeatedly noticed the surprising fact that woodpeckers are among the birds with the relatively biggest brains (e.g. PORTMANN 1962; LEFEBVRE et al. 2004; RICKLEFS 2004; CNOTKA et al. 2008; Figure 2). The Great Spotted Woodpecker has a brain about 1.6 times larger (2.7 ml) than the similarly sized blackbird

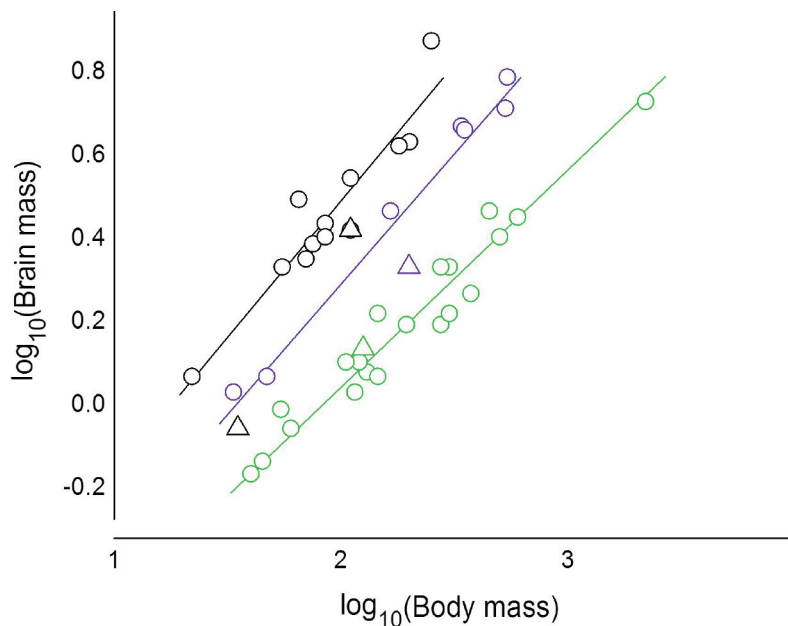


Fig. 2: Brain size – body size regressions in woodpeckers (black), barbets and toucans (blue), and pigeons and doves (green). Data from MLÍKOVSKÝ (1989). Triangles denote long distance migrants; these species were not included when computing the regression parameters.

(*Turdus merula*; 1.4 ml). The brain of a Black Woodpecker, for instance, is as large as the one of the exceedingly intelligent New Caledonian Crow (*Corvus moneduloides*), or even larger (CNOTKA et al. 2008). Most researchers would agree that relative brain size is correlated with behavioural complexity. However, to actually operationalize “behavioural complexity” is not a simple matter. Likewise, the problem of how different parts of the brain contribute to cognitive performance is not easily solved. Even the role of absolute versus relative brain size for cognitive abilities is still not clear. For instance, DEANER et al. (2007) found that absolute brain size may be a better predictor of cognitive abilities than its relative size.

Several studies in passeriform birds had claimed that birds that cache food extensively and exhibit astonishing abilities to recover individually stored food items also possess a comparatively large hippocampus. This region in the forebrain is known to be involved in forming long-term memories. Strange discrepancies between European and American tits (LUCAS et al. 2004) illustrated some methodological difficulties that arise from the fact that the various parts of the avian brain are often difficult to separate in practice. To cut a long story short, published differences in the size of the hippocampus not only reflected biological differences, but also trans-Atlantic differences in lab procedures. With respect to woodpeckers, brain size differences could be related to differences in caching behavior only within *Melanerpes*; otherwise no obvious such relations were found (VOLMAN et al. 1997; GARAMSZEGI & EENS 2004; SHERRY 2006), and woodpeckers have a slightly smaller hippocampus than the otherwise relatively small-brained honeyguides (CORFIELD et al. 2013).

We provide here some more data on total brain sizes of woodpeckers and their relationship with some aspects of their behavior and ecology.

Methods

Brain sizes were measured by filling crania with small (0.397 mm diameter) steel balls (ISOMETALL Handelsgesellschaft Schmidt. u. Co., Pleidelsheim, Germany) instead the lead shot used in other studies (e.g. MLÍKOVSKÝ 1989; IWANIUK & NELSON 2001). These volumetric measures were adjusted to mass using a brain density value of $1.03\text{g}\cdot\text{cm}^{-3}$ (MLÍKOVSKÝ 1989a). These data were used to augment the data presented by MLÍKOVSKÝ (1989b), KAWABE et al. 2013 and Andrew IWANIUK (pers. comm.).

To determine other dimensions of the brain, 3D size-calibrated images based on microCT scans of three specimens one Great Spotted Woodpeckers, one Eurasian Green Woodpecker, and one Blackbird (*Tur-*

us merula) from the Natural History Museum Vienna were obtained at the the MicroCT Imaging Lab of the University of Veterinary Medicine, Vienna.

Results

Allometric relation with body size

Figure 3 shows the relationship between body size and brain size in 67 species of woodpeckers using a standard log-log regression. The allometric coefficient was 0.72 or approximately $\frac{3}{4}$. Reduced major axis analysis (WARTON et al. 2006) yielded a coefficient of 0.76.

Relations with behavior

Woodpecker brain size is not related to simple measures of sociality. Neither published nor our own analyses indicate a relationship (BURISH et al. 2004; BEAUCHAMP & FERNÁNDEZ-JURICIC 2004). Often woodpeckers are considered to be aggressive and solitary. This may be true for some northern species, but cannot be generalized because many species, especially in the subtropics and tropics, maintain pair and family bonds throughout the year and over years (see chapter on behavior, this volume). Hence, the ideas on social bonds put forward by EMERY et al. (2007) and SHULTZ & DUNBAR (2010) should be considered seriously as an explanation for the generally large size of woodpecker brains.

WINKLER (2008) suggested that extractive foraging associated with strong hammering and great skill in manipulating objects, and using anvils as tools may explain brain size differences among woodpeckers. Indeed, some of the cognitive abilities of the Great Spotted Woodpecker, a species that uses hammering a lot (Fig. 4), are astounding (GAJDON, this volume). A comparison between species that excavate extensively

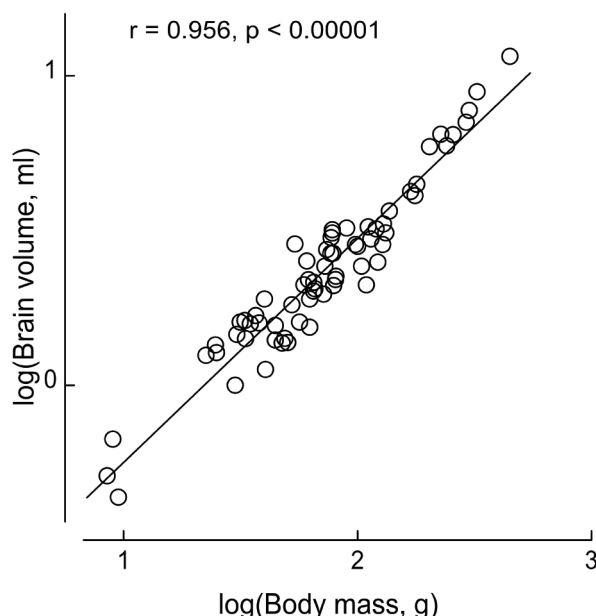
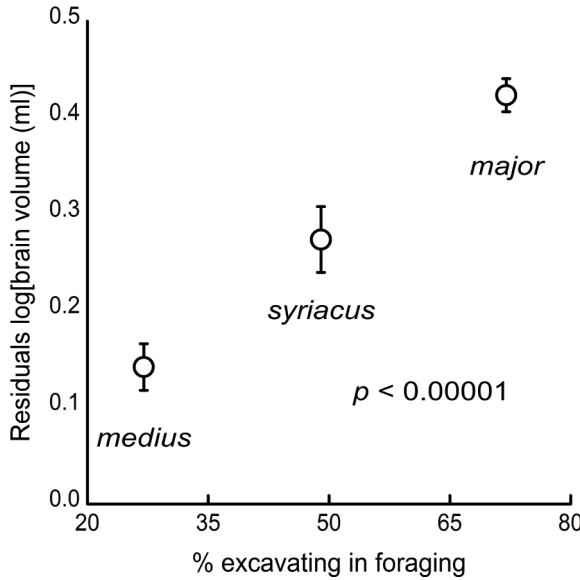


Fig. 3: Brain size – body size regressions in 67 species of woodpeckers.

Fig. 4: Relationship between the role of excavating in foraging and brain size (corrected for body size) in three pied woodpeckers (*Leiopicus medius*, *Dendrocopos syriacus*, *D. major*). Foraging data from Winkler 1973. Based on brain volumina of 10 *major*, 3 *syriacus* and 4 *medius* specimens. Adapted from WINKLER 2008.



when foraging and those that do not showed a highly significant difference, with a larger brain being associated with excavating. Comparing three sympatric pied woodpeckers for which quantitative foraging data are available (WINKLER 1973, Fig. 4) also showed a significant relationship with brain size ($p < 0.00001$, ANOVA). A multiple regression analysis revealed that body size, excavating, and migratory behavior together explain 96% of the variation in brain volume among 66 species of woodpeckers ($p < 0.00001$, $F_{3,62} = 474$). Excavating as an important foraging technique correlates positively with brain size ($p < 0.00001$), and, as expected, negatively ($p < 0.05$) with migration (we included also short-distance migrants).

Scaling and brain injury

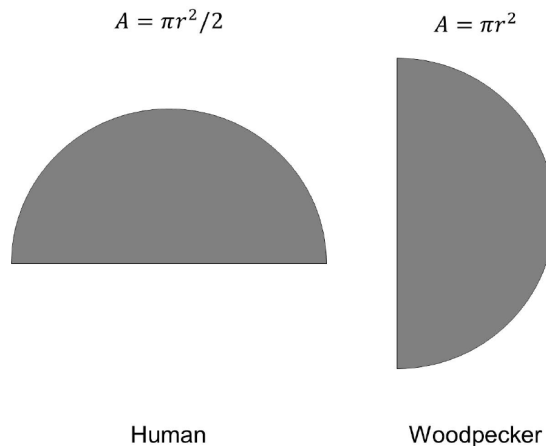
GIBSON (2006) made an important contribution to the problem of brain injury by pointing out that size does matter in this context. In other words, by the laws of physics the effects of impacts decrease with mass and affected area. Research on humans showed that the

damage to the brain depends on acceleration and duration of the impacts (e.g. OMMAYA & HIRSCH 1971; ONO et al. 1980; GREENWALD et al. 2008; VIANO 2012). GIBSON (2006) approximated the shape of the brain by a hemisphere and assumed that the woodpecker brain is oriented differently from the human brain by an angle of 90° resulting in half of the projected contact area of the woodpecker brain against the skull. As Figure 5 shows, this approximation looks rather coarse. By measuring the area of brain cross-sections normal to the axis of the upper bill we found that the area of contact would be 256 mm^2 in the Great Spotted Woodpecker (only one specimen measured) and 335 mm^2 in the Eurasian Green Woodpecker. A sphere corresponding to a brain of 1400 g (assumed for humans, GIBSON loc. cit.) and a density of $1.03 \text{ g} \cdot \text{cm}^{-3}$ (see methods) would have the radius of 7.56 cm . The corresponding calculations for a Great Spotted Woodpecker would yield a radius of 0.958 cm . According to GIBSON (2006) on impact a brain area of roughly 148 cm^2 would be exposed in the case of the human brain, and 2.37 cm^2 in the Great Spotted Woodpecker, given a brain volume of 2.745 cm^3 (mean of 10 volumetric measurements). However, shape and orientation of the woodpecker's brain differ from these assumptions. The actual area exposed in the case of the Great Spotted Woodpecker according to our measurements was 2.56 cm^2 , 8% more than in the simple estimate. The value for the Eurasian Green Woodpecker would be 3.28 cm^2 for the hemispheric approximation, and 3.35 cm^2 (2% more) for the measured value. Let us finish with a few comparisons of stress values on those brains. Assuming that a human brain can tolerate an acceleration of 15.7 g/s^2 for the duration of a millisecond (GIBSON 2006), we would calculate according to standard mechanics and from the figures given above a stress value of about $296 \text{ g/cm} \cdot \text{s}^2$. This is compared with the stress of $21.5 \text{ g/cm} \cdot \text{s}^2$ on a Eurasian Green Woodpecker's or $17.3 \text{ g/cm} \cdot \text{s}^2$ on a Great Spotted Woodpecker's brain at the same acceleration and using the empirically found values for the exposed areas. Thus, the translational acceleration the brains of these woodpeckers could withstand without injury is 14 to 17 times that of a human due to the mass differences alone.

Discussion

„The effect of increased relative brain size on behavior is one of the thorniest issues in comparative neurobiology”. There is little to add to this statement of Glenn NORTH CUTT (2002). Our analyses, too, are correlational and can only serve as first indication of relevant causal relationships. Total brain size may reflect both the size of the telencephalon and the cerebellum which may more important for certain cognitive abili-

Fig. 5: Brains of humans (left) and woodpeckers (right) modeled as hemispheres according to Gibson (2006). Formulae for the area of impact when the hitting force is horizontal are given above the schematic representations of the hemispheres. See text for further explanations.



ties than generally thought (e.g. SULTAN 2005). The relationship with migration found here is dominated by the small brain of the Eurasian Wryneck. A comparison with the sedentary Rufous-throated Wryneck would clearly be desirable in this case. Reasons why migrants have smaller brains are discussed extensively in the literature (WINKLER et al. 2004; SOL et al. 2005, 2010, PRAVOSUDOV et al. 2007; MCGUIRE & RATCLIFFE 2010; FUCHS et al. 2014; see also SAFI et al. 2005) and need not to be repeated here.

It remains an open question whether the clearly different brain structure and size of wrynecks (BRANDIS 1896; DENNLER 1919) are due to adaptations to drilling in the Picinae. IWANIUK et al. (2007) found a strong phylogenetic signal in cerebellum development within birds and a weak positive correlation with strong hindlimbs. Their study included two woodpecker species and no wrynecks

Another project would be to confirm the results found for parrots, namely that larger brains occur in species that live in areas with greater climatic instability (SCHUCK-PAIM et al. 2008)

Hammering and drilling are clearly related to brain size, a fact that BURT already mentioned in passing in his paper on woodpecker functional morphology (BURT 1930, p. 471, Fig. 2). This may be related to the cognitive skills of those species of woodpeckers that use these foraging techniques (GAJDON & WINKLER this volume); anvil use should be mentioned here particularly (LEFEBVRE et al. 2002; YI et al. 2014). It remains to be shown that the density of neurons remains the same in big-brained versus smaller-brained species. The vague statement of BECHER (1953) that he found no histological differences between woodpeckers and other birds needs to be confirmed.

As already discussed by Bock (this volume), studies of woodpeckers as models for protecting humans from brain injury fail to acknowledge some basic biological facts. One is brain size and has been referred to first by GIBSON (2006) and elaborated on as well in our analyses. In the light of our empirical measurements, the hemispheric model presented by GIBSON (2006) seems to constitute an acceptable first approximation for biomechanical considerations. We consider modeling the brain as a sphere as in ODA et al. (2006) as obsolete. All the other adaptations to hammering found in woodpeckers are mainly to withstand the forces on the bones. The cranium of woodpeckers does not provide more protection to the brain than in any other bird and cannot serve as a prominent model for biomimicry research. The claims by YOON & PARK (2011) or YOON et al. (2009), for instance, are not justified.

In closing, we offer a speculation that incorporates both cognition and the problem of brain injuries. It rests partially on the assumption that in the long run hammering does have some negative consequences, and also on the observation of a woodpecker brain with amyloid angiopathy (NAKAYAMA 1999). The latter has to our knowledge not been studied or found yet in other birds. Coping with damage to complex structures depends on the number of critical elements involved, and the relation with age follows a function that drops off sharply towards the end of the life-span (WITTEN 1985). A brain that starts big and unharmed thus provides reliable functioning for the whole life span. With this reserve capacity (cf. GRAVES et al. 1996; MORI et al. 1997; STERN 2003) as an adaptation in long-lived species, brain capacity for cognitive performance is made available that may incur further selective advantages for larger brains. This hypothesis could be tested with studies on brain histology of ageing birds with different risks of brain injury.

Acknowledgements

We thank Dr. Anita GAMAUF, Natural History Museum Vienna, for providing the specimens for the brain scans. The latter would have not been possible without the instructions and help given by Dr. Brian METSCHER at the University of Vienna Theoretical Biology Department and Stephan HANDSCHUH at the University of Veterinary Medicine, Vienna. Volumetric measurements were carried out at the American Museum of Natural and the Natural History Museum Vienna. Christine NÖSTLER helped to measure the skulls at the Vienna Museum, Brian Metscher, Gulya Gajdon and Walter Bock made valuable suggestions to an earlier draft of the manuscript.

References

- ABOITIZ F. & F. ZAMORANO (2013): Neural progenitors, patterning and ecology in neocortical origins. — *Frontiers in Neuroanatomy* **7**: 38.
- BALANOFF A.M., BEVER G.S., ROWE T.B. & M.A. NORELL (2013): Evolutionary origins of the avian brain. — *Nature* **501**: 93-97.
- BANG B.G. & S. COBB (1968): The size of the olfactory bulb in 108 species of birds. — *The Auk* **85**: 55-61.
- BEAUCHAMP G. & E. FERNÁNDEZ-JURICIC (2004): Is there a relationship between forebrain size and group size in birds? — *Evolutionary Ecology Research* **6**: 833-842.
- BECHER F. (1953): Untersuchungen an Spechten zur Frage der funktionellen Anpassungen an die mechanische Belastung. — *Zeitschrift für Naturforschung* **8b**: 192-203.
- BENNETT P.M. & P.H. HARVEY (1985): Relative brain size and ecology in birds. — *Journal of Zoology* **207**: 151-169.
- BRANDIS F. (1896): Das Kleinhirn der Vögel in Beziehung zur Systematik. — *Journal für Ornithologie* **54**: 274-304.

- BURISH M.J., KUEH H.Y. & S.S.H. WANG (2004): Brain architecture and social complexity in modern and ancient birds. — *Brain, Behavior and Evolution* **63**: 107-124.
- BURT W.H. (1930): Adaptive modifications in the woodpeckers. — *University California Publications in Zoology* **32**: 455-524.
- CNOTKA J., GÜNTÜRKÜN O., REHKÄMPER G., GRAY R.D. & G.R. HUNT (2008): Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). — *Neuroscience Letters* **433**: 241-245.
- CORFIELD J.R., BIRKHEAD T.R., SPOTTISWOODE C.N., IWANIUK A.N., BOOGERT N.J., GUTIÉRREZ-IBÁÑEZ C., OVERINGTON S.E., WYLIE D.R. & L. LEFEBVRE (2013): Brain size and morphology of the brood-parasitic and cerophagous honeyguides (Aves: Piciformes). — *Brain, Behavior and Evolution* **81**: 170-186.
- DEANER R.O., ISLER K., BURKHART J. & C.P. VAN SCHAIK (2007): Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. — *Brain, Behavior and Evolution* **70**: 115-124.
- DENNLER G. (1919): Die hirnanatomisch begründete Sonderstellung von *Jynx Torquilla*. — *Falco* **15**: 7-10.
- EMERY N.J., SEED A.M., BAYERN A.M.P. VON & N.S. CLAYTON (2007): Cognitive adaptations of social bonding in birds. — *Philosophical Transactions of the Royal Society B Biological Sciences* **362**: 489-505.
- FÜBRINGER M. (1888): Untersuchungen zur Morphologie und Systematik der Vögel: zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. Band 2: Allgemeiner Theil, Resultate und Reflexionen auf morphologischem Gebiete, systematische Ergebnisse und Folgerungen. — TJ van Holkema, Amsterdam. 1717 pp.
- FUCHS R., H. WINKLER, BINGMAN V.P., ROSS J.D. & G. BERNROIDER (2014): Brain geometry and its relation to migratory behavior in birds. — *Journal of Advanced Neuroscience Research* **1**: 1-9.
- GARAMSZEGI L.Z. & M. EENS (2004): The evolution of hippocampus volume and brain size in relation to food hoarding in birds. — *Ecol. Letters* **7**: 1216-1224.
- GIBSON L.J. (2006): Woodpecker pecking: how woodpeckers avoid brain injury. — *Journal of Zoology (London)* **270**: 462-465.
- GORDON D. (1976): Woodpeckers, gannets, and head injury. — *The Lancet* **307**: 801-802.
- GRAVES A.B., MORTIMER J.A., LARSON E.B., WENZLOW A., BOWEN J.D. & W.C. McCORMICK (1996): Head circumference as a measure of cognitive reserve. Association with severity of impairment in Alzheimer's disease. — *British Journal of Psychiatry* **169**: 86-92.
- GREENWALD R.M., GWIN J.T., CHU J.J. & J.J. CRISCO (2008): Head impact severity measures for evaluating mild traumatic brain injury risk exposure. — *Neurosurgery* **62**: 789-798.
- IWANIUK A.N., HURD P.L. & D. R.W. WYLIE (2007): Comparative morphology of the avian cerebellum: II. Size of folia. — *Brain, Behavior and Evolution* **69**: 196-219.
- IWANIUK A.N. & J.E. NELSON (2001): A comparative analysis of relative brain size in waterfowl (Anseriformes). — *Brain, Behavior and Evolution* **57**: 87-97.
- IWANIUK A.N. & J.E. NELSON (2003): Developmental differences are correlated with relative brain size in birds: a comparative analysis. — *Canadian Journal of Zoology* **81**: 1913-1928.
- KAWABE S., SHIMOKAWA T., MIKI H., OKAMOTO T., MATSUDA S., ITOU T., KOIE H., KITAGAWA M., SAKAI T., HOSOJIMA M. & H. ENDO (2013): Relationship between brain volume and brain width in mammals and birds. — *Paleontological Research* **17**: 282-293.
- LEFEBVRE L., NICOLAKAKIS N. & D. BOIRE (2002): Tools and brains in birds. — *Behaviour* **139**: 939-973.
- LEFEBVRE L., READER S.M. & D. SOL (2004): Brains, innovations and evolution in birds and primates. — *Brain, Behavior and Evolution* **63**: 233-246.
- LEFEBVRE L., WHITTLE P., LASCARIS E. & A. FINKELSTEIN (1997): Feeding innovations and forebrain size in birds. — *Animal Behaviour* **53**: 549-560.
- LIU Y., QIU X., ZHANG X. & T.X. YU (2015): Response of woodpecker's head during pecking process simulated by material point method. — *PLoS ONE* **10**: e0122677.
- LIZHEN W., SHAN L., XIAOYU L., XUFENG N., CHAO W., YIKUN N., MEIYA Z., CHENGLONG F., MING Z. & F. YUBO (2013): Biomechanism of impact resistance in the woodpecker's head and its application. — *Science in China Series C: Life Sciences* **56**: 715-719.
- LUCAS J.R., BRODIN A., DE KORT S.R. & N.S. CLAYTON (2004): Does hippocampal size correlate with the degree of caching specialization? — *Proceedings of the Royal Society of London, Series B Biological Sciences* **271**: 2423-2429.
- MCGUIRE L.P. & J.M. RATCLIFFE (2010): Light enough to travel: migratory bats have smaller brains, but not larger hippocampi, than sedentary species. — *Biology Letters* : .
- MLIKOVSKÝ J. (1989a): Brain size in birds: 1. Tinamiformes through Ciconiiformes. — *Vstník eskoslovenské Spole nosti zool. Acta societatis zoologicae bohemoslovenicae* **53**: 33-47.
- MLIKOVSKÝ J. (1989b): Brain size in birds: 3. Columbiformes through Piciformes. — *Vstník eskoslovenské Spole nosti zool. Acta societatis zoologicae bohemoslovenicae* **53**: 252-264.
- MORI E., HIRONO N., YAMASHITA H., IMAMURA T., IKEJIRI Y., IKEDA M., KITAGAKI H., SHIMOMURA T. & Y. YONEDA (1997): Premorbid brain size as a determinant of reserve capacity against intellectual decline in Alzheimer's disease. — *Am. J. Psychiatry* **154**: 18-24.
- NAKAYAMA H., KATAYAMA K.I., IKAWA A., MIYAWAKI K., SHINOZUKA J., UETSUKA K., NAKAMURA S.I., KIMURA N., YOSHIKAWA Y. & K. DOI (1999): Cerebral amyloid angiopathy in an aged great spotted woodpecker (*Picoides major*). — *Neurobiology of Aging* **20**: 53-56.
- NEALEN P.M. & R.E. RICKLEFS (2001): Early diversification of the avian brain:body relationship. — *Journal of Zoology* **253**: 391-404.
- NORTHCUTT R.G. (2002): Understanding vertebrate brain evolution. — *Integrative and Comparative Biology* **42**: 743-756.
- ODA J., SAKAMOTO J. & K. SAKANO (2006): Mechanical evaluation of the skeletal structure and tissue of the woodpecker and its shock absorbing system. — *Japan Society of Mechanical Engineers International Journal Series A* **49**: 390-396.
- OMMAYA A.K. & A.E. HIRSCH (1971): Tolerances for cerebral concussion from head impact and whiplash in primates. — *Journal of Biomechanics* **4**: 13-21.
- ONO K., KIKUCHI A., NAKAMURA M., KOBAYASHI H. & N. NAKAMURA (1980): Human head tolerance to sagittal impact reliable estimation deduced from experimental head injury using

- subhuman primates and human cadaver skulls. — In , (Eds.): 24th Stapp Car Crash Conference, Tory, Michigan, 1980. SAE Technical Paper 801303. — , : 101-160.
- PORTMANN A. (1946): Études sur la cérébralisation chez les oiseaux. I. — *Alauda* **14**: 2-20.
- PORTMANN A. (1947): Études sur la cérébralisation chez les oiseaux. III. Cérébralisation et mode ontogénétique. — *Alauda* **15**: 161-171.
- PORTMANN A. (1951): Ontogenesetypus und Cerebralisation in der Evolution der Vögel und Säuger. — *Revue Suisse de Zoologie* **58**: 427-434.
- PORTMANN A. (1962): Zerebralisation und Ontogenese. — *Medizinische Grundlagenforschung* **4**: 1-62.
- PRAVOSUDOV V.V., SANFORD K. & T.P. HAHN (2007): On the evolution of brain size in relation to migratory behaviour in birds. — *Animal Behaviour* **73**: 535-539.
- RENSCH B. (1958): Die Abhängigkeit der Struktur und der Leistung tierischer Gehirne von ihrer Größe. — *Die Naturwissenschaften* **45**: 145-154.
- RICKLEFS R.E. (2004): The cognitive face of avian life histories: The 2003 Margaret Morse Nice Lecture. — *Wilson Bulletin* **116**: 119-133.
- RICKLEFS R.E. & J.M. STARCK (1998): The evolution of the developmental mode in birds. — In STARCK, J.M. & R.E. RICKLEFS (Eds.): *Avian growth and development. Evolution within the altricial precocial spectrum*. — Oxford University Press, New York: 366-380.
- SAFI K., SEID M.A. & D.K.N. DECHMANN (2005): Bigger is not always better: when brains get smaller. — *Biology Letters* **1**: 283-286.
- SCHUCK-PAIM C., ALONSO W.J. & E.B. OTTONI (2008): Cognition in an ever-changing world: climatic variability is associated with brain size in neotropical parrots. — *Brain, Behavior and Evolution* **71**: 200-215.
- SHERRY D.F. (2006): Neuroecology. — *Annual Review of Psychology* **57**: 167-197.
- SHULTZ S. & R.I.M. DUNBAR (2010): Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. — *Biological Journal of the Linnean Society* **100**: 111-123.
- SOL D., LEFEBVRE L. & J.D. RODRIGUEZ-TEJERO (2005): Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. — *Proceedings of the Royal Society B* **272**: 1433-1441.
- SOL D., GARCIA N., IWANIUK A., DAVIS K., MEADE A., BOYLE W.A. & T. SZÉKELY (2010): Evolutionary divergence in brain size between migratory and resident birds. — *PLoS ONE* **5**: e9617.
- STERN Y. (2003): The concept of cognitive reserve: a catalyst for research. — *Journal of Clinical and Experimental Neuropsychology* **25**: 589-593.
- SULTAN F. (2005): Why some bird brains are larger than others. — *Current Biology* **15**: R649-R650.
- The Avian Brain Nomenclature Consortium (2005): Avian brains and a new understanding of vertebrate brain evolution. — *Nature Reviews Neuroscience* **6**: 151-159.
- VIANO D.C. (2012): Biomechanics of brain injury. — In ZASLER N.D., KATZ D.J. & R.D. ZAFONTE (Eds.): *Brain Injury Medicine. Principles and Practice*. 2nd edition. — Demos Medical Publishing, New York: 124-136.
- VOLMAN S.F., GRUBB T.C. Jr. & K.C. SCHUETT (1997): Relative hippocampal volume in relation to food-storing behavior in four species of woodpeckers. — *Brain, Behavior and Evolution* **49**: 110-120.
- WANG L., CHEUNG J.T.M., PU F., LI D., ZHANG M. & Y. FAN (2011): Why do woodpeckers resist head impact injury: A biomechanical investigation. — *PLoS ONE* **6**: e26490.
- WARTON D.I., WRIGHT I.J., FALSTER DANIEL S & M. WESTOBY (2006): Bivariate line-fitting methods for allometry. — *Biological Reviews* **81**: 259-291.
- WINKLER H. (1973): Nahrungserwerb und Konkurrenz des Blutspechts, *Picooides (Dendrocopos) syriacus*. — *Oecologia* **12**: 193-208.
- WINKLER H. (2008): Kognition und Hirngröße bei Spechten. — *Die Vogelwarte* **46**: 273-274.
- WINKLER H., LEISLER B. & G. BERNROIDER (2004): Ecological constraints on the evolution of avian brains. — *Journal für Ornithologie* **145**: 238-244.
- WITTEN M. (1985): A return to time, cells, systems, and aging: III. Gompertzian models of biological aging and some possible roles for critical elements. — *Mechanisms of Ageing and Development* **32**: 141-177.
- WYGNANSKI-JAFFE T., MURPHY C.J., SMITH C., KUBAI M., CHRISTOPHERSON P., ETHIER C.R. & A.V. LEVIN (2007): Protective ocular mechanisms in woodpeckers. — *Eye* **21**: 83-89.
- YI X., STEELE M.A. & Z. SHEN (2014): Manipulation of walnuts to facilitate opening by the great spotted woodpecker (*Picooides major*): is it tool use? — *Animal Cognition* **17**: 157-161.
- YOON S.H., ROH J.E. & K.L. KIM (2009): Woodpecker-inspired shock isolation by microgranular bed. — *Journal of Physics D: Applied Physics* **42**: 035501.
- YOON S.H. & S. PARK (2011): A mechanical analysis of woodpecker drumming and its application to shock-absorbing systems. — *Bioinspiration & Biomimetics* **6**: 016003.
- ZHU Z.D., ZHANG W. & C. WU (2014): Energy conversion in woodpecker on successive peckings and its role on anti-shock protection of brain. — *Science China. Technological Sciences* **57**: 1269-1275.

Addresses of the authors:

Prof. Dr. Hans WINKLER
Konrad-Lorenz-Institute of Ethology
Department of Integrative Biology and Evolution
Veterinary University Vienna
Savoyenstraße 1A
A-1160 Wien
E-Mail: hans-christoph.winkler@oeaw.ac.at

Viola WINKLER, BSc
Dept. of Theoretical Biology
University of Vienna
Althanstraße 14
A-1090 Wien
E-Mail: viola.winkler@gmx.at

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Denisia](#)

Jahr/Year: 2015

Band/Volume: [0036](#)

Autor(en)/Author(s): Winkler Hans Christoph, Winkler Viola

Artikel/Article: [The brains of woodpeckers 55-61](#)