Cognition in woodpeckers

Gyula K. Gajdon & Hans Winkler

Abstract: Despite their large telencephalons, not much is known about cognition in woodpeckers. The hypothesis that large brains evolved in the context of a complex social life seems not to hold for most woodpeckers because many large brained species are rather solitary. Nevertheless, woodpeckers show signs of flexible communicative skills. Recently, the social brain hypothesis has been challenged by broader concepts of the relevance of behavioral flexibility for the evolution of large brains. Especially in the context of extractive foraging, woodpecker may require a good spatial memory and sophisticated technical skills. Woodpeckers rank high among birds with respect to feeding innovations. The extractive foraging style of woodpeckers may require high motivation to explore what in turn could positively affect cognitive performance.

Key words: Animal cognition, social brain hypothesis, extractive foraging, technical intelligence, sensorimotor intelligence, anvils, reversal learning, Picidae.

Introduction

Birds provide especially interesting subjects for studying cognition, the brain and their adaptive variation because large brains evolved independently more often in birds, and in fact other sauropsids, than in mammals (Nealen & Ricklefs 2001; Isler & Van Schaik 2009; Balanoff et al. 2013). This seems to be linked with an altricial breeding style that evolved several times in birds and that helps to buffer the costs of developing a large brain (Bennett & Harvey 1985; Ricklefs & Starck 1998; Iwaniuk & Nelson 2003). Because brain and body size are correlated, most authors postulate that brain size has to be related to body size for comparing brains and other traits across species. For instance, residuals obtained from a log-log regression of brain size on body size provide a useful measure of relative brain size (see Winkler & Winkler, this volume). Regression analyses indicate that crows, ravens, and jays (Corvidae), parrots (Psittacidae), hornbills (Bucerotidae), owls (Strigidae), and the true woodpeckers (Picinae) have larger than average brains (Mlíkovský 1989; see Winkler & Winkler, this volume). For example the Great Spotted Woodpecker has about 1.6 times more brain volume than the about equally sized blackbird (*Turdus merula*) (see Winkler & Winkler, this volume).

The purposes of this paper are to review our current knowledge about the cognitive performance of woodpeckers, to consider some of the factors selecting for high cognitive performance and brain size and, finally, present some results of a pilot study on reversal learning.

The evolution of ideas on animal cognition

Cognition, learning, tool use

The topic of cognition, especially in birds, has a long and complicated history in the behavioral sciences (Delius et al. 2000). This will be outlined in this, and examples from the research on woodpeckers will illustrate it further. Although it has been known for some time that woodpecker have relatively large brains, relatively little is known about their cognitive performance when compared to corvids, parrots, and even the small brained pigeons or chickens. Only recently the evolutionary ecologist Robert Ricklefs seemed to have become aware of this fact. When reviewing the evidence on the association between certain aspects of life history and brain size in birds, he wrote “I must have underestimated woodpeckers in the past …” Ricklefs (2004, p. 123).

This complex history of cognition research is also partially grounded in the nomenclature of the avian brain because brain regions considered to process cognitively more demanding tasks in mammals were wrongly homologized (The Avian Brain Nomenclature Consortium 2005). Previously, it was believed that these areas are relatively small in birds compared to mammals. Cortical areas are not as easily identified in avian brains as in mammals due to a different cytoarchitecture in birds. The unique mammalian cortex consists of six layers and thus differs clearly from other brain areas; while in birds comparable structures exhibit only three layers if any (Jarvis 2009). In 2005,

Denisia **36**,
zugleich Kataloge des
oberösterreichischen
Landesmuseums
Neue Serie **164** (2015):
63-76

a large consortium of authors published a revised nomenclature of the avian brain, rendering the bird telencephalon on par with that of mammals (The Avian Brain Nomenclature Consortium 2005). And recent reviews indicate not only some important differences, but also surprising similarities in the neural circuits in birds and mammals and discuss the consequences for understanding their cognitive processes (EMERY & CLAYTON 2004; BUTLER & COTTERILL 2006, BUTLER et al. 2005; DUGAS-FORD et al. 2012). These recent anatomical and neurological findings contributed to a general change in attitude from a pejorative "bird brain" to "brainy birds".

Comparative neuroanatomy and the comparative study of behavior have long histories reaching back to DARWIN (1872). In particular animal learning is one of the oldest topics studied in animal behavioral sciences because learning was of major interest in the psychological sciences right from their beginning (MACKINTOSH 1974). Psychologists have traditionally used rats as the main model species. Ethology, behavioral and evolutionary ecology, as well as behavioral biology, neuroecology and affective neuroscience, became flourishing disciplines later on, and accordingly the main emphasis about the nature of cognition changed as these disciplines evolved. Thus, while at first animal cognition largely referred to learning mechanisms investigated by psychologists (THORPE 1956), its concepts widened and evolved. According to Sara SHETTLEWORTH, a behavioral ecologist, cognition refers to ways in which animals (including humans) retain, process, and act on information taken in through the senses (SHETTLEWORTH 2001; DUKAS 2004). It includes processes such as perception, learning, memory, and problem solving. This broad definition refers to the interest in the modularity of information processing. Anthropologist Duane RUMBAUGH and colleagues provide a definition in the narrower sense by which cognition refers to "knowing, the creative capacity to reorganize perception and past learning to generate new solutions to problems" (RUMBAUGH et al. 1996) Thus, this proposal, despite being aware of the importance of perception, restricts cognition to some forms of problem solving by the reorganization of mental representations of the environment in the tradition of the cognitive revolution as a counter movement to the models of associative learning that behaviorists had developed in their theory of stimulus/response learning (SKINNER 1974).

There seems to be a growing interest in a notion of animal intelligence that stresses the importance of behavioral flexibility (BUTLER & COTTERILL 2006), ignoring such narrower definition as provided by RUMBAUGH et al. (1996). Along with this development, researchers increasingly regard cognition as an adaptive response to rather specific ecological problems. Among other things, scientists tested the hypothesis that large brains evolved to find adaptive answers to rather novel and unusual challenges; what Daniel SOL called the cognitive buffer hypothesis (SOL et al. 2007, SOL 2009).

Interestingly, this shift of emphasis is linked with discussions between those scientists interested in primates and those in birds and their respective interpretation of research results. For example, primates' primacy in tool using was challenged by the sophisticated way New Caledonian Crows (*Corvus moneduloides*), use and modify tools in the wild (ORENSTEIN 1972; HUNT 1996, 2003). One captive New Caledonian crow was found to spontaneously bend a piece of wire in order to form a hook for solving a new problem (WEIR et al. 2002). It seems that physical cognition in New Caledonian Crows may have become adapted to tool-using behavior. But later on it was found that captive Rooks (*Corvus frugilegus*) that do not use tools commonly in the wild, solved the same task of bending a wire into a hook with a high level of consistency (BIRD & EMERY 2009). This raised the yet unsolved question of whether tool-using behavior in New Caledonian Crows, rather than being an adaptive cognitive specialization, is a result of general intelligence in large brained crows (CNOTKA et al. 2008; KACELNIK 2009; LIND et al. 2009).

The Social Brain Hypothesis

The Social Brain Hypothesis (SBH) dominated the field of animal cognition for some decades. It claims that intelligence evolved in response to social rather than ecological problems in primates in particular (DUNBAR 1998; ADOLPHS 1999; PÉREZ-BARBERÍA et al. 2007). The rationale of the SBH is that social life in larger primate groups is especially demanding because social partners are complex agents in terms of how they will interact and how they can be exploited, alone or together with allies, against other allied individuals (DE WAAL 2007). Keeping track of what all dyads did, where and with whom, rapidly increases computational demands as group size increases. Accordingly, there was much interest in the scientific community to demonstrate and dissect mechanisms of social learning, that is the modification of behavior by witnessing what others are doing (WHITEN, et al. 2004). Imitation, the ability to copy the form of a complete action on the same object types, was regarded as the most demanding process of social learning. This mechanism is distinguished from just achieving the same result as the model had achieved or only mimicking the movements with some inappropriate object (CALL & CARPENTER 2002; WHITEN et al. 2004). Thus, scientists focused on the question of whether and how novel behavior is spread by social learning (ZENTALL & GALEF 1988; HEYES & GALEF 1996; ZENTALL 2004).

The SBH was also investigated in birds, with some conflicting outcomes in some analyses (BUGNYAR et al. 2004; EMERY 2007; RICKLEFS 2004). For example, it was found that the highly social Pinyon Jay (*Gymnorhinus cyanocephalus*) is able to infer a complete linear hierarchy from the outcomes of an incomplete number of dyadic interactions more rapidly and more accurately than the relatively non-social Western Scrub Jay (*Aphelocoma californica*) (BOND et al 2003). However, support for this hypothesis in other birds is mixed (cf. BEAUCHAMP & FERNÁNDEZ-JURICIC 2004) and probably related to the notion of "sociality". However, even studies that claimed to have found evidence for this hypothesis in birds, woodpeckers, despite their large telencephalons, seem to be the exception as their brain size seems not to be related to sociality (BURISH et al. 2004). The strong pair bond found in woodpeckers may be a better predictor of brain size (see EMERY et al. 2007; SHULTZ & DUNBAR 2010; see also LIGON 1970; KELLAM 2003; PECHACEK et al. 2005; WINKLER & WINKLER, this volume).

Nevertheless, the woodpeckers' communicative skills, that are social by definition, should not be underestimated. CHAUVIN-MUCKENSTURM (1974) showed that three Great Spotted Woodpeckers, brought to captivity as nestlings, learned two different drumming codes for requesting different types of food at the age of 11 to 12 weeks: one strike with the beak for a pistachio nut and two strikes for a house cricket. The experimenter produced the referential code on a xylophone and a diversity of food items was offered in Perspex boxes that were only opened after the corresponding referential code was given. The repertoire of codes was successfully enlarged to three strikes for a mealworm, two double strikes separated by a pause for a chafer, and three double strikes separated by two pauses for a locust. When the experimenter opened a box that did not contain the food referred to by a given code, the birds usually rejected it. When a new experimenter signaled, the woodpeckers immediately used the code with him. In a later study (CHAUVIN 1987) with two of the Great Spotted Woodpeckers that had learned those codes, the author investigated their spontaneous reaction when a picture of a pistachio was shown. Both birds produced the code for "pistachio nut" on the picture when it was shown the first time and flew to the corresponding box containing the pistachio. When they were shown the pistachio picture once again immediately thereafter (the woodpeckers never ate two pistachio nuts in succession), they rejected the card or tapped the code of another food type on the hand of the experimenter or on another substrate, but never on the pistachio picture. After a while, the birds stopped producing the percussion signal and directly went to the feeders after seeing the picture. These results strongly indicate that the birds spontaneously perceived a picture-object correspondence and integrated sensory information of two different modalities for one type of object without confusing the picture with the real object (BOVET &VAUCLAIRE 2000; WEIN et al. in press).

Food storing, foraging and hippocampus size

A classic topic in neuroecology is the relationship between food storing in birds and size of the hippocampus. The hippocampus is involved in spatial memory which is important in order to relocate scattered food caches. Several bird species store food including shrikes, some hawks, owls, parids, and most corvids (SMITH & REICHMAN 1984). There is little information about memory for food caches and relative size of the hippocampus in most of these birds, but some data seem to indicate that food storing chickadees and tits do develop larger hippocampi than close relatives do (GARAMSZEGI & EENS 2004; LUCAS et al. 2004; SHERRY & HOSHOOLEY 2006; BRODIN & BOLHUIS 2008).

A few woodpeckers cache food as well, and VOLMAN et al. (1997) compared two species in the genus *Melanerpes* that both cache food but in a different way. The Red-headed Woodpecker stores food concentrated in a "larder" that it defends against other animals, while the Red-bellied Woodpecker is a "scatter-hoarder", rather like food-storing chickadees and jays. Thus the former do not need to remember a large number of storage sites, while the latter most likely uses memory to find its caches when moving through the home range. This is not corroborated by available behavioral data, but is indicated by comparing to the Red-headed Woodpecker's larger hippocampus, to the size of the rest of the brain (VOLMAN et al. 1997). However, the relative size of the hippocampus is no smaller in Hairy and Downy Woodpecker's that do not store food (VOLMAN et al. 1997). Thus, data of *Melanerpes* woodpeckers conform to the pattern observed in passerine food hoarders, whereas the data for these two species of pied woodpeckers do not.

Interestingly, we still have little information on how woodpeckers manage to locate their prey in the substrate. Several authors have reported that Black and Eurasian Green Woodpeckers locate the colonies of ants in the ground after probing a few times with their beak, and that the birds seem to relocate these spots later even when they are covered with snow (BLUME 1966; LÖHRL 1977). These authors suggest that some olfactory cues might be involved, but accurate spatial memory is likely to play a greater role. The latter is probably also the case with the Ground Woodpecker. Groups of these birds harvest ant hills in their homerange in a systematic fashion allowing the ants to recover from the raids upon their nests (OATLEY et al. 1989). Further research is required in this respect, and the need for spatial memory in routine foraging might actually mask differences in the size of the hippocampus between woodpeckers that are scatter hoarders and those that are not.

Innovation reports and brain size

In the nineties, studies by Louis LEFEBVRE and colleagues showed that there are numerous innovation reports published on bird orders that have large brains (LEFEBVRE et al. 1997; 1998; NICOLAKAKIS & LEFEBVRE 2000; TIMMERMANS et al. 2000). For this analysis, the authors searched ornithological journals for short notes describing unusual behavior in a bird species that was not described before or that was described for the first time. Examples of innovations considered were American Robins (*Turdus migratorius*) capturing and eating smolts at a salmon hatchery (BAYER 1980) or house sparrows searching radiator grilles of cars for insects (SIMMONS 1984). Piciform birds ranged in the top quarter of innovation frequencies reported for the different bird orders. The topic of innovation received increasing attention as researchers became aware of the fact that before an innovation can spread by social learning, it it first has to be invented by some individuals. Primatologists analyzed innovation reports in the same way LEFEBVRE and colleagues did with conventional statistics and by correcting for phylogenetic relationships (species level values do not provide independent data), and verified the findings of previous studies (READER & LALAND 2002). As by definition, innovations are novel behavior, they might not be predisposed in a way suggested by the hypothesis of adaptive specialization of cognition for phylogenetically old and specific demands (see the example of tool-use in rooks described above or spatial memory in food caching birds), although an innovation might not only be a solution for a new problem but also a new solution for an old problem (KUMMER & GOODALL 1985). The simplicity of operationalizing innovation by searching for short notes containing particular key words, might surprise (RAMSEY et al. 2007) because there is considerable variation in the degree the described behavior deviates from a species' normal behavioral repertoire. But the advantage is that these are data from free ranging birds and the frequency of reports were corrected in different ways (LEFEBVRE et al. 2001), for example for a bias that might have resulted because some bird orders received more attention by observers than others.

A number of studies on innovation and meta-analyses of field and lab data of different cognitive domains, seem increasingly to confirm that the SBH has not played the pivotal role in driving the evolution of large brains as suggested earlier. READER et al. (2011) performed a meta-analysis on the interrelation of eight cognitive and socio-ecological measures in 62 primate species: reported frequencies of innovation, social learning, using tools, extracting concealed or embedded food (extractive foraging; GIBSON 1986), and engaging in tactical deception were used as five ecologically relevant measures of behavioral flexibility. Diet breadth, percentage of fruit in the diet, and measures of social group size are thought to reflect the cognitive demands of exploiting / locating foods and tracking social relationships. Principal component analysis revealed two components in which all measures loaded significantly. Component 2 had strong positive associations with diet breath, percentage fruit, and social group size, while the other measures had strong positive associations with component 1. A composite measure of general intelligence of the different species co-varied with both brain volume and measures of learning performance in captivity. The authors concluded that their "analyses suggest that ecologically relevant cognitive abilities, from multiple domains, have coevolved in primates, revealing an across-species general intelligence, with general rather than purely social intelligence probably driving brain evolution" (READER et al. 2011, p. 1022).

Extractive foraging and technical intelligence

Extracting concealed or embedded food is especially relevant for woodpeckers because they are renowned for their extractive foraging behavior. Recently, Sue Taylor PARKER (2015) referred to the analysis of READER et al. (2011) in favor of a reconsideration of the extractive foraging hypothesis (EFH). Forty years earlier, PARKER & GIBSON (1977, 1979) had postulated that complex cognition in apes evolved as an adaptation for extracting embedded high energy food through intelligent tool use and its social transmission. PARKER stressed that extractive foraging in READER'S et al. (2011) analysis as a measure of technical flexibility correlated with most of the other measures including tool use, innovation, social leaning, tactical deception and diet breadth. Thus, the EFH in its original form is not a strictly technical, but also a socio-ecological hypothesis. Yet it is plausible that extracting cryptic food without social learning provides some cognitive challenges because it requires manipulative and motor skills, and the location of food has to be inferred by other means than direct observation. It is in this respect that several studies refer to the EFH as a base for technical intelligence.

OVERINGTON et al. (2009) did so when they examined the relationship between innovation and brain size in the context of two classical hypothesis for the evolution of cognition: the aforementioned technical intelligence hypothesis (PARKER & GIBSON 1977; BYRNE 1997; HUBER & GAJDON 2006) and the hypothesis that "a generalist lifestyle, especially in the feeding domain, should favor an enhanced learning capacity (DALY et al. 1982; DOMJAN & GALEF 1983; SCHUCK-PAIM et al. 2008)" (OVERINGTON et al. 2009, p. 1002). They classified the above mentioned innovations reported in the short notes of ornithological journals in twelve categories, taking into consideration the variation in how the innovations deviated from normal behavior. Three categories were lumped and classified as 'food type innovations'. These contained reports where innovations involved a novel food item, but no departure from the usual foraging techniques of the species (e.g. Wilson's storm-petrels, *Oceanites oceanicus*, feeding on the fat of a whale carcass). The other categories were classified as 'technical innovations' were the authors of the reports described the foraging technique as novel, regardless of whether the food type was novel or not (e.g. Cetti's warbler, *Cettia cetti*, catching insects in mid-air like a flycatcher; HILL 1993). It turned out that the diversity of technical innovations displayed by bird families was a much better predictor of residual brain size than was the number of food type innovations, providing support for the technical intelligence hypothesis. With respect to the diversity of technical innovations, corrected for research effort, woodpeckers were second only to grassland and forest-dwelling kingfishers (Dacelonidae), and followed by the ground cuckoos (Neomorphidae). Woodpeckers might innovate also in the communicative domain. Many species use artificial structures to produce especially loud drumming signals (WINKLER & CHRISTIE 2002). The diversity of technical innovations in woodpeckers might seem surprising because the beak of the woodpeckers can be considered as highly specialized for hacking and pecking, in contrast to the beak of Keas (*Nestor notabilis*) that may be employed in various ways when these parrots investigate an object by pushing, pulling, pealing, scraping, levering, and so forth, and thus was likened to a Swiss army knife by HUBER & GAJDON (2006). A recent study showed that birds that display a high diversity of investigatory behaviors most likely solve mechanical problems (GRIFFIN et al. 2014). Nevertheless, the woodpeckers outperformed the parrots in terms of the above mentioned diversity of reported technical innovations, indicating that large brained birds can be very innovative even when constrained by a highly specialized morphological structure.

CHAUVIN-MUCKENSTURM (1973) presented a good example of the problem solving capacities of woodpeckers. She showed that Great Spotted Woodpeckers quickly solved the new problem of retrieving a reward from inside a glass tube they could not pierce by pecking and which the experimenter had firmly stuck in a support. The woodpeckers used their bill in a combination of wedging, pushing and pulling to remove the glass tube. Similarly, we observed a variation of extracting food without breaking its substrate for access (GAJDON, unpublished data): when a captive Great Spotted Woodpecker was confronted with a metal bowl that contained a few wax moth larvae and that was covered with a wire mesh so that it was difficult for the bird to reach the larvae directly, it started to peck the rim of the metal bowl so firmly that the larvae were catapulted out of the rocked bowl.

Despite the plausibility of the interrelation between extractive foraging and brain size, only the junior author has tested this hypothesis so far. WINKLER & WINKLER (this volume) measured and analyzed the brain volumes of more than 60 species of woodpeckers. Multiple regression analysis with log body size, migration behavior, and excavation dominated foraging as independent and log brain size as dependent variable revealed that beside body size, foraging by excavation and migration significantly contributed to the interspecific variation of brain volumes.

In terms of technical intelligence, the wedging behavior or anvil use of woodpeckers is especially interesting. Woodpeckers wedge food items too difficult to consume immediately in tree forks, crevices, and the like so they can be processed further. Such sites are called "anvils" (MEIJERING 1967; KEDRA & MAZGAJSKI 2001; BONDO et al. 2008). Woodpeckers seem to have anvils they re-use for years, but also show considerable flexibility in finding crevices for wedging when there is need at a new place. Wedging behavior has been described to be analogous to tool-use behavior, although it is not tool-use behavior in the strict definition which requires that a loose object is used to alter a target item in order to achieve a goal (BECK 1980). This definition seems at first to be restrictive, but such tool-use behavior develops later in children than inserting objects into holes (UZGIRIS & HUNT 1975). Thus, there is some justification from developmental psychology for such a stricter definition of tool-use behavior. Nevertheless, when wedging a seed, a nut, or a cone into a crevice, a spatial relation is produced between the object and the crevice. And this is a core feature of tool use behavior (VISALBERGHI & FRAGASZY 2006) and can be considered as proto-tool use at least.

Nuts are often inserted in a specific orientation, exposing the fissure between the shells for easy opening by pecking (MUCKENSTURM 1971). Considering that the orientation of objects when inserting them into a hole increases the number of spatial relations that have to be taken into account, is considered to be cognitively

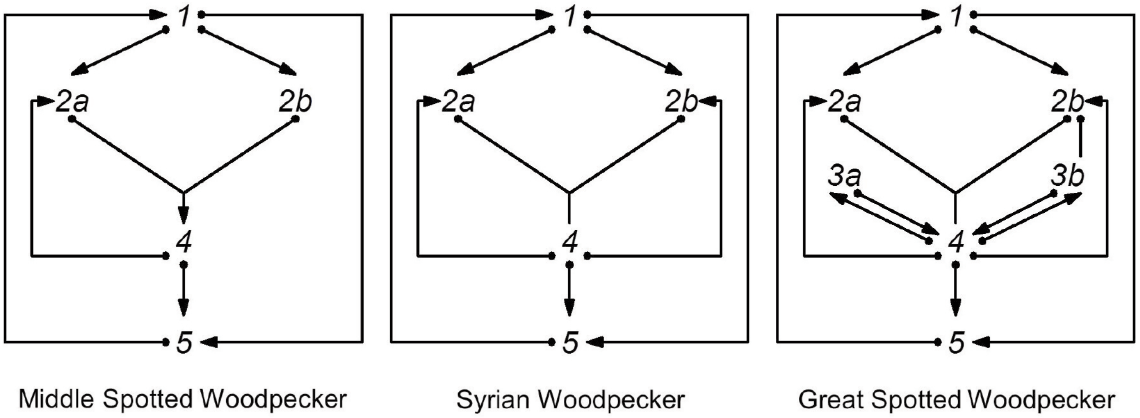

Fig. 1. A comparison of the behavioral sequences during anvil use in three pied woodpeckers (after MEIJERING 1967 and WINKLER 1967). 1 Harvest of the item; 2a transport to an occasional anvil, 2b transport to a proto-anvil or true anvil; 3a modification of a true anvil, 3b cleaning of an anvil; 4 fixing item; 5 manipulation and feeding.

rather demanding (FRAGASZY et al. 2011). YI et al. (2014) investigated how wild White-backed Woodpeckers (which they mistook for Great Spotted Woodpeckers) considered proper orientation when they attempted to crack nuts of *Juglans mandshurica*. The woodpeckers consistently reoriented the nuts when the experimenter removed the nuts and reinserted them in an inappropriate orientation, but birds did not reorient them when the experimenter re-inserted the nuts in an orientation feasible for opening. MUCKENSTURM (1971) offered a few captive Great Spotted Woodpeckers pistachio nuts (18-20 mm in length and 12-14 mm in diameter) close to a randomly arranged array of 13 holes, measuring between 13 and 20 mm in diameter, that were drilled in a vertical board. The birds ignored the holes that were too small for inserting the nuts. These tests were done in two periods separated by a three month interval. In the second testing period, the birds increasingly preferred some particularly sized holes in the range of sizes that were suitable for inserting nuts. This and the fact that woodpeckers also insert small seeds into tiny crevices indicate that the hole sizes chosen in MUCKENSTURM'S study did not correspond to an innate preference for holes of a specific diameter. Rather the birds matched the diameter of the nut and the hole like the commonly tool-using New Caledonian Crows match the diameter of a stick with the diameter of the hole they will probe with the stick (CHAPPELL & KACELNIK 2002). Acorn Woodpeckers insert acorns so neatly into holes that is hard to remove them and drill differently sized holes to accommodate different sizes of acorns or nuts (RITTER 1922; ROBERTS 1979).

MUCKENSTURM (1971; see also MEIJERING 1967) observed that Great Spotted Woodpeckers cleaned the preferred crevices for wedging. But there is no systematic investigation whether and how woodpeckers do modify the crevices/holes in order that they fit for their purposes. An elaborated behavior in this respect could be on par with cognition in tool-use behavior.

Anecdotal observations suggest, however, that at least Great Spotted Woodpeckers may enlarge the excavation used as anvil according to the size of the food item "at hand" (SIELMANN 1958). MEIJERING (1967) classified anvils into three types: (1) occasional anvils – any hard surface where a food item is pounded, (2) proto-anvils – any natural crevice where a food item is wedged and held firm for hammering, and (3) true anvils – anvils created by the bird in vertical branches or trunks to hold food items for consumption. He suggested that true anvils are constructed mainly for larger cones, while smaller nuts and seeds may be wedged into existing crevices. He reported that Great Spotted Woodpeckers invaded the Island Spikeroog for feeding on pine cones and that building anvils took place mainly in the beginning of a cone feeding season. After a sufficient variety of anvils had been created, the woodpeckers focused on using and cleaning them and cones were transported up to fifty meters to these anvils. However in order to clarify how woodpeckers consider the size of cones when constructing and modifying anvils ahead of actually using them, experimental investigations are needed. There is large variation between populations and between species regarding the number of nuts and cones processed in anvils (reviewed in MEIJERING 1967; see also KEDRA & MAZGAJSKI 2001): While Middle Spotted Woodpeckers seem not to clean anvils and wedge small items one on top of another until a crevice is full and abandoned, some populations of Great Spotted Woodpeckers in Scandinavia in particular, and in contrast to woodpeckers in Spain for example, may process thousands of cones in a season. Woodpeckers in these populations depend to a substantial part on constructing and using anvils. Accordingly we can assume that there are sufficient inter-specific differences suitable for conducting comparative studies on how woodpeckers take features of food items into account when constructing and modifying anvils (Fig. 1). Modification of anvils might be an interesting analogy to tool modification that is much rarer in animals than tool use as such (HUNT 1996). In due course, studying anvil use might help in understanding relations between brain size, extractive foraging and technical skills and intelligence.

Motivation and Cognition

Extractive foraging behavior may require some very specific motivations (WINKLER & LEISLER 1999), and there is an increasing agreement that cognition research should be done in a more multidimensional way that incorporates aspects of motivation and temperament (often also subsumed under the term animal personality) (DUCATEZ et al. 2015; SIH & DEL GIUDICE 2012). Extractive foragers may have to work hard and long before they can claim the reward. Especially for young subjects that still have to improve their foraging skill, this may require high persistence, resistance to failure, or tolerating frustration (HOLZHAIDER et al. 2010). This may be achieved with an intrinsic motivation to engage in extracting foraging activity so that the behavior is not dependent on immediate rewards. PARKER (2015) stressed that the sensorimotor intelligence series of PIAGET's (1952, 1954) model of cognitive development plays a central role in their extractive foraging hypothesis. In Piaget's notion of the development of sensorimotor intelligence, subjects first explore the possible relations between objects and themselves, and become more and more interested in the relationships they can produce between objects later. But the basic nature of this model is one of intrinsically motivated exploration in a playful way. This may enlarge the horizon of events taken into consideration and thus such intrinsically motivated behavior may be regarded as cognitively powerful (THORPE 1956).

There are reasons to believe that sociality imposes some constraints on innovative behavior. Among other things, individuals may refrain from exhibiting novel behavior to conform to group standards, or because of competition (BROSNAN & HOPPER 2014). Socially low ranking individuals may also be hindered to benefit from innovations (KOTHBAUER-HELLMANN 1990). A comparison between social and more solitary woodpecker species could test these hypotheses.

Several authors addressed the relation of play behavior and brain size (DIAMOND & BOND 2003; RICKLEFS 2004). There are not many observations reported about play behavior in woodpeckers, but KILHAM (1974) described different types of play behavior in Hairy and Downy Woodpeckers as well as in Red-bellied Woodpecker. For the latter he described an especially interesting form of play behavior, the storing of miscellaneous objects of no apparent value. "When I gave one female a bent, 3-inch nail, she spent five minutes trying to insert it into various holes" (KILHAM 1974, p. 39). At another occasion, KILHAM observed a similar behavior in a Yellow-bellied Sapsucker. Inserting odd objects (pebbles) has been described for the Acorn Woodpeckers as well, and was interpreted as a misdirected acorn storing instinct (RITTER 1921). We observed similar behavior in several captive Great Spotted Woodpeckers (GAJDON, unpublished data). In our case, the juvenile woodpeckers inserted gravel stones very tightly into holes the observer had drilled into trunks some time before (see Fig. 2). These holes were rarely used as holes for wedging food. We also observed captive Great Spotted Woodpeckers carrying around long sticks and putting them in various places, a behavior not related to any natural activities we know of (WINKLER, pers. obs.). Thus, it might well be that this kind of manipulative behavior is an expression of playfully exploring the spatial relations that can be produced with objects in a way described as an advanced stage of sensorimotor development in Piaget's model. PEPPERBERG & SHIVE (2001), GAJDON et al. (2014), AUERSPERG et al. (2014) reported similar behavior of parrots, and (TORIGOE 1985) of primates. Both of these groups are known for their advanced technical skills.

Fig. 2. a and b: Gravel stones wedged into holes by a Great Spotted Woodpecker at the Haidlhof Research Station (Lower Austria) in 2011 (University of Veterinary Medicine, Vienna and University of Vienna). The holes were drilled by GKG; pictures taken on 31 July 2011.

Reversal learning

Reversal learning provides a frequently used measure of behavioral flexibility (HERNDON et al. 1997; BOND et al. 2007; BERAN et al. 2008; FLORESCO et al. 2008; KLOO et al. 2008; GAJDON et al. 2011). In this task, subjects are required to discriminate between two

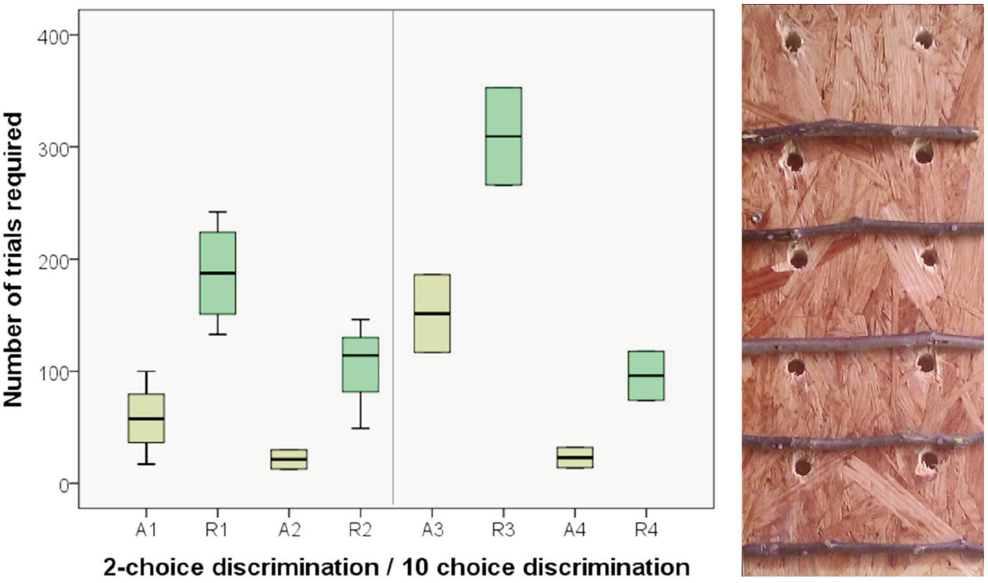

Fig. 3. Left: Number of trials required to reach different discrimination criterions in acquisition (brown box-plots) and reversal learning (green box-plots; left) in one Syrian and five Great Spotted Woodpeckers. The birds were offered one pair of choice options per trial only (2-choice discrimination; 4 subjects) or five pairs of choice options (10-choice discrimination; 2 subjects; right) (see body text for further explanation; Tockner 2015). 'A' below the horizontal axis indicates data for acquisition and 'R' for reversal learning. Numbers in the scale of the x-axis indicate the criteria the birds had to meet: A/R1: at least 85% correct first choices in two consecutive blocks of 20 trials each. A/R2: first trial from which on a subject sampled holes on the less preferred side for a longer run of trials only when the color of the seal correctly indicated that there was food. A/R3: significant preference to first chose all five holes that were sealed with the correct color in 4 successive blocks of the 10-choice trials, according to a permutation test (Gajdon et al. 2014). This requires less than 85% correct first choices as requested in criterion 1. A/R4: preference to choose the correct color first on a new row in two successive blocks of 20 trials, significant according to binomial test. Right: Board used for the 10-choice-trials.

options, one of which is always food rewarded. When the subjects reached a learning criterion, reward contingencies are reversed so that the formerly negative option becomes the rewarded one and the formerly positive the negative option. Despite the suggestion that extractive foragers have large brains and thus should flexibly react to such reversed reward contingencies, it is believed that persistence in extractive foragers may mask a quick reversal of the acquired discrimination (Teschke & Tebbich 2011; O'Hara 2015; see McNamara & Houston 1985 for a theoretical treatment in the context of optimal foraging). A student of ours (Tockner, 2015) tested this in two female and three male Great Spotted Woodpeckers and one female Syrian Woodpecker that were received from a veterinarian clinic after recovering from wing injuries before being released again. Four of these birds were trained to discriminate between two holes that were sealed with crumbled paper balls of two different colors. One of these hole types was loaded with a mealworm, pinky or wax moth larva, depending on the food preference of the subjects, in a semi-random fashion. The rewarded hole was sealed with a paper ball of a particular color (always orange, pink, blue or green, depending on the subjects), and the alternative with a different one (always green yellow pink or orange, depending on the subject). Thus, in order to access the reward, the subject had to remove the paper ball of the correct color irrespective of its position. Depending on the motivation of the subjects to participate in the trials, a maximum of 20 trials a session and one session per day were held for each subject. Holes were reloaded out of sight of the birds and no attempts were made to prevent the birds pulling out both paper balls. Because most of the subjects were disturbed when a human remained close by, the experimenter just put the board with the sealed holes in position, started a video camera for data recording and left. When the subjects pulled the ball of the correct color in at least 85% of the trials in two consecutive blocks of 20 trials, the learning criterion was considered to be achieved. Reward contingencies were reversed thereafter in the next session until this new learning criterion was met again. This procedure corresponds to that used in the study of O'Hara et al. (2015) with Keas. As Fig. 3 shows, the number of trials needed to reach the learning criterion was much larger in reversal than in acquisition learning. This difference was similar in Keas that are also extractive foragers O'Hara et al. (2015), but was much smaller in corvids that do not extract food to the same degree (Bond et al. 2007). This confirms the suspected effect of an extractive foraging style on reversal learning. There was a tendency that a win/shift-loose/stay strategy concerning the position (left or right) of the hole first checked in successive trials had more priority than a win/stay-loose/shift strategy before the birds started to perform their choices according to the color of the paper balls. Spatial relations seemingly had priority over color cues. As a result, upon having found food at the left side of a row they checked the right side of the next row encountered first,

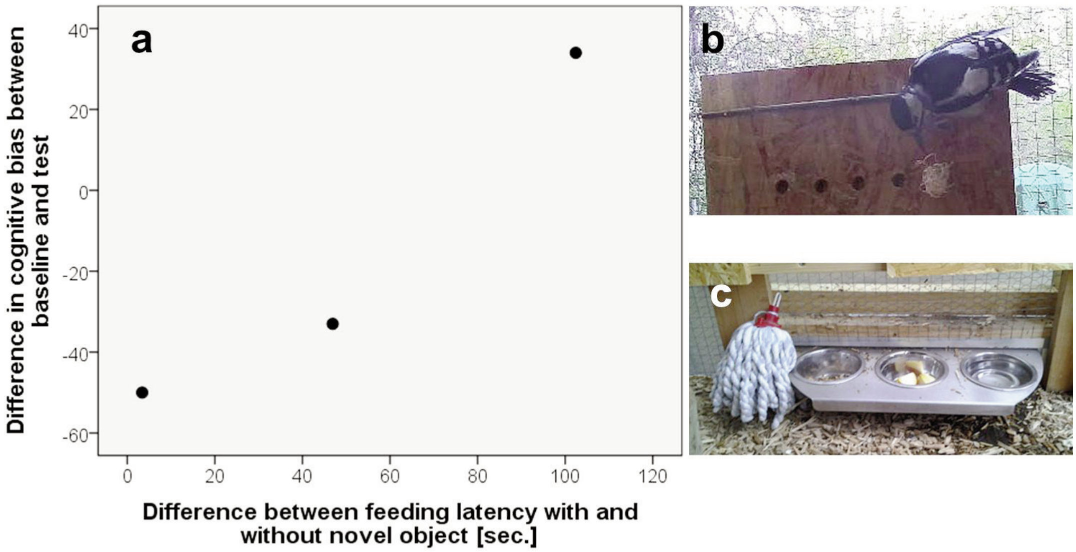

Fig. 4. a: The relation between a neophobia score (X-axis: time difference in feeding latency with and without a novel object beside the feeding dishes) and the difference between the proportion of seals pulled from ambiguous holes located between a positive and negative training hole after and before environmental enrichment in one Syrian and two Great Spotted Woodpeckers. b A Great Spotted Woodpecker pulling the seal at one of the two training locations. c The novel object beside the food dishes used to score neophobic reactions.

irrespective of plug color. This may make sense on a microscale for a woodpecker when several larvae of wood beetles are found in one patch. Once a grub is found, the bird should slightly shift its position of investigatory extraction, but it should persist in thoroughly investigating other locations in the same food patch. Interestingly, three of the four birds showed long sequences of trials with side preferences: they started to pull all paper balls at one side irrespective of the ball's color. But when they pulled the ball on the less preferred side, they always correctly chose the rewarded color. Thus they knew which color cued a reward well before they actually reached the formal learning criterion (Fig. 3).

With two of the remaining captive subjects, a different methodology of reversal learning was employed that, we think, should be more feasible for future investigations with free ranging woodpeckers. In this procedure, five rows of two holes each were drilled in a board. Hence the experimenter did not have to interrupt the foraging birds with re-baiting and sealing the holes so often. The woodpeckers required more trials to reach the learning criterion in this testing procedure than when offered only one pair of holes in each trial (Fig. 4). However, when only the first choice in a row was considered, the number of trials required to reach the learning criterion matched the two choice discrimination task (Fig. 3). Thus in the first period of the trials, on the 10-choice discrimination board, the birds pulled the correct plug in a row, continued, however, with opening the alternative in the same row before proceeding to another row. This is well in line with the strategy described above to systematically search through all positions in a food patch. And this strategy may also explain some of the results of Lima (1984) who investigated the sampling efficiency in free-ranging Downy Woodpeckers that could exploit artificial food patches consisting of twigs with 24 holes that were covered with strips of masking tape. He created three different "environments" each of which had 60 patches, with about half of the patches empty. Depending on the environment, a full hole contained 24, 12, or 6 seeds. The woodpeckers did not strictly follow a simple, theoretically optimal foraging strategy. Instead, they engaged in some sampling to gather information. They had obviously learned that there are completely empty patches. They gave up a full patch with fewer seeds per hole later than one with holes that held the full reward of 24 seeds. Interpreting the experimental results, Lima (1984) also concluded that the woodpeckers have a "weak counting ability". Our results regarding the patches with holes sealed with differently colored plugs indicate that Great Spotted Woodpeckers react to micro-local conditions in a food patch, but only after having systematically sampled all holes. This may be a good strategy under natural conditions because most hidden food items there are distributed in a clumped fashion. This interpretation could be tested with offering woodpeckers concealed as well as scattered and openly presented food.

Based on the suggestion that extractive foragers should be especially motivated to explore, it can be assumed that environmental enrichment will improve well-being in captive woodpeckers. One way to evaluate this is by testing their cognitive bias (Harding et al. 2004). The rationale of testing cognitive bias is that subjects in emotionally negative states judge ambiguous stimuli more likely as negative than subjects in a positive mood. In a particular cognitive bias task, birds are trained to recognize that there is always food in a particular hole when this hole is sealed, and that a hole in a particular position beside the positive location is never rewarded when sealed. When the bird has learned this discrimination task, a hole in various positions in between the positive and negative hole is sealed, and the researcher records whether the bird samples it. A cognitively more biased bird will continue to sample sealed holes in positions closer to the negative hole while a cognitively less biased bird will restrict its sampling to holes that are sealed close by the positive location if at all. Students of GKG tested cognitive bias in this way in two Great Spotted Woodpeckers and one Syrian Woodpecker before and after their 8 m^3 aviaries were enriched with additional branches. In cognitive bias studies, tests are usually performed after a prolonged period of environmental enrichment or impoverishment (MENDL et al. 2009). We expected that in woodpeckers cognitive bias will be affected already shortly after the environmental enrichment, but still in a way related to the individual's degree of reactive behavioral disposition. For this aim, we also tested the subjects' neophobia: a novel object (a cotton mop) was offered together with a feeding bowl at the birds' usual feeding place and the latency in the birds' feeding (time between arrival and actual feeding) was recorded. This latency is compared with feeding latency when there is no new object presented at the feeding place (GREENBERG & METTKE-HOFMANN 2001). In other animal studies it was found that neophobic individuals that showed a high feeding latency when there was a new object, showed a reactive behavioral style in general (CARERE et al. 2005; METTKE-HOFMANN et al. 2005). That is that they are more sensitive to changes than more proactive birds. Thus, when a novel object was presented in a neutral place in the aviary, this time it was the birds that reacted more neophobic to the change at the food dish that were the first to explore the object in the neutral place (METTKE-HOFMANN et al. 2005). Accordingly, we assumed that the enrichment cognitively biased those woodpeckers more that were neophobic at the food dish. As Figure 4 shows, the preliminary results of these few subjects are in line with the expectation. This indicates that motivational and ecological disposition have to be carefully taken into account when designing experimental investigations in woodpeckers.

Conclusion

Although only preliminary and suggestive studies of cognition in woodpeckers are currently available, the few authors that reported these results agree that there is a fascinating potential for cognitive research in these large brained birds. One problem for investigating cognition in woodpeckers is that many of them are relatively aggressive and cannot be kept in groups. This makes experimental work logistically more demanding in terms of the size of aviaries needed to conduct studies on a reasonable number of subjects. In our experience, Great Spotted Woodpeckers are especially shy when housed in small aviaries. This might be one reason why there are almost no zoos that keep woodpeckers. For a few seasons, GKG kept four Great Spotted Woodpeckers in succession in a 520 m^2 large aviary designed for behavioral research with a group of twenty Keas. Four other woodpeckers were kept close by in 8 m^3 aviaries, each. It was remarkable to see how fast the woodpeckers habituated to particular people in the large Kea aviary (they remained afraid of new visitors), how neophilic and cooperative the woodpeckers reacted when experimental tasks were offered, and what diverse behaviors could be observed. The woodpeckers in the smaller aviaries on the other hand remained wary and this constrained their behavior and the tasks an experimenter could present. Most likely, woodpeckers remained shy in the smaller aviaries because they could not control the distance to the observer. Reading CHAUVIN-MUCKENSTURM's writings, we feel that she would agree. This was different in the large Kea cage, where the birds approached voluntarily, sometimes coming as close to the observer as in the forced situation in a small aviary. As shown by LIMA (1983, 1984) and YI et al. (2014), it is possible to work experimentally with free ranging woodpeckers, and this line of research should be intensified, along with cooperation between several research stations that run bigger aviaries for other bird species where woodpecker could be kept too, so that a reasonable number of woodpeckers can be investigated at the same time. On the other hand, there are social woodpeckers, especially in the genus *Melanerpes*, that have been kept successfully in zoos. These species would be ideal for studying the interactions between sociality and innovative behavior, for example. We are certain that the great diversity of life-styles that woodpeckers exhibit constitutes a great opportunity for comparative studies in animal cognition.

Acknowledgements

We thank especially Tilmann LANGE and Tamara TOCKNER, but also Claudia HABERL, Doris KÖBRUNNER, Astrid LENGAUER, and Denis REITER for collecting the data in the pilot studies described here (testing reversal learning and testing cognitive bias in Great Spotted Woodpeckers) and Raoul SCHWING, Wolfgang VOGL, Mark O'HARA and Martin SCHLUMPP for practical support. We are especially thankful to Annett HÄBICH for veterinarian supervision of the woodpeckers. Gerard Gorman helped in improving our English. The pilot studies described here were approved by the institutional ethics committee in accordance with GSP guidelines and national legislation.

References

Adolphs R. (1999): Social cognition and the human brain. — Trends in Cognitive Sciences **3**: 469-479.

Auersperg A.M.I., N. Oswald, M. Domanegg, G.K. Gajdon, T. Bugnyar (2014): Unrewarded object combinations in captive parrots. — Animal Behavior and Cognition **1:** 470-488.

Balanoff A.M., G.S. Bever, T.B. Rowe & M.A. Norell (2013): Evolutionary origins of the avian brain. — Nature **501**: 93-97.

Bayer R.D. (1980): Novel use of an unusual food: American Robins eating parts of fish. — Journal of Field Ornithology 51:74–75.

Beck B.B. (1980): Animal tool behavior: the use and manufacture of tools by animals. — Garland Publ. INC, New York.

Blume D. (1966): Schwarzspecht - Grünspecht – Grauspecht. — Franckh'sche Verlagshandlung, Stuttgart.

Beauchamp G. & E. Fernández-Juricic (2004): Is there a relationship between forebrain size and group size in birds? — Evolutionary Ecology Research **6**: 833-842.

Bennett P.M. & P.H. Harvey (1985): Relative brain size and ecology in birds. — Journal of Zoology **207**: 151-169.

Beran M.J., E.D. Klein, T.A. Evans, B. Chan, T.M. Flemming, E.H. Harris, D.A. Washburn & D.M. Rumbaugh (2008): Discrimination reversal learning in capuchin monkeys (*Cebus apella*). — The Psychological Record **58**: 3–14.

Bird C.D. & N.J. Emery (2009): Insightful problem solving and creative tool modification by captive nontool-using rooks. — Proceedings of the National Academy of Sciences of the United States of America **106**: 10370-10375.

Bond A.B., A. Kamil & R.P. Balda (2003): Social complexity and transitive interference in corvids. . — Animal Behaviour **65**: 479-487.

Bond A.B., A.C. Kamil & R.B. Balda (2007): Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). — Journal of Comparative Psychology **121**: 372-379.

Bondo K.J., L.N. Gilson & R. Bowman (2008): Anvil use by the Red-cockaded Woodpecker. — The Wilson Journal of Ornithology **120**: 217-221.

Bovet D. & J. Vauclair (2000): Picture recognition in animals and humans. — Behavioural Brain Research **109**: 143-165.

Brodin A. & J.J. Bolhuis (2008): Memory and brain in food-storing birds: Space oddities or adaptive specializations? — Ethology **114**: 633-645.

Brosnan S.F. & L.M. Hopper (2014): Psychological limits on animal innovation. — Animal Behaviour **92**: 325-332.

Bugnyar T., M. Stöwe & B. Heinrich (2004): Ravens, Corvus corax, follow gaze direction of humans around obstacles. . — Proceedings of the Royal Society B **271**: 1331–1336.

Burish M.J., H.Y. Kueh & S.S.H. Wang (2004): Brain architecture and social complexity in modern and ancient birds. — Brain, Behavior and Evolution **63**: 107-124.

Butler A.B. & R.M.J. Cotterill (2006): Mammalian and avian neuroanatomy and the question of consciousness in birds. — Biological Bulletin **211**: 106-127.

Butler A. B., P. R. Manger, B.I.B. Lindahl & P. Århem (2005): Evolution of the neural basis of consciousness: a bird-mammal comparison. — BioEssays **27**: 923-936.

Byrne R.W. (1997): The Technical Intelligence hypothesis: An additional evolutionary stimulus to intelligence?, — In A. Whiten and R.W. Byrne (Eds.): Macchiavellian Intelligence II. Extensions and evaluations. — Cambridge University Press, Cambridge: 289-311.

Call J. & M. Carpenter (2002): Three sources of information in social learning. — In Dautenhahn, K. & C.L. Nehaniv (Eds.): Imitation in animals and artefacts. — The MIT Press, Cambridge, Massachusetts, London: 211-228.

Carere C., P.D. Drent, J.M. Koolhaas & T.G.G. Groothuis (2005): Epigenetic effects on personality traits: early food provisioning and sibling competition. — Behaviour **142**: 1329-1355.

Chappell J. & A. Kacelnik (2002): Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). — Animal Cognition **5**: 71-78.

Chauvin-Muckensturm B. (1973): Solution brusque d'un probleme nouveau chez le pic épeiche. — Rev. Comp. Animal **7**: 163-168.

Chauvin-Muckensturm B. (1974): Y a-t-il utilisation de signaux appris comme moyen de communication chez le pic épeiche? — Revue du Comportement Animal **9**: 185–207.

Chauvin B. (1987): Association spontanée d'un signal appris et de la représentation pictographique d'un objet chez le pic épeiche (*Dentrocopos mayor).* — Cahiers d'Ethologie Appliquée **7**: 39-48.

Cnotka J., O. Güntürkün, G. Rehkämper, R.D. Gray & G.R. Hunt (2008): Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). — Neuroscience Letters **433**: 241-245.

Daly M., J. Rauschenberger & P. Behrends (1982): Food aversion learning in kangaroo rats: a specialist-generalist comparison. — Animal Learning & Behavior **10**: 314–320.

Darwin C. (1872): The expression of the emotions in man and animals. — John Murray, London. 374 pp.

del Hoyo J., J. Elliott & J. Sargatal (1992): Handbook of the Birds of the World. — Lynx Edicions, Barcelona.

Delius J. D., M. Siemann, J. Emmerton & L. Xia (2000): Cognition of birds as products of evolved brains. — In Roth, G. & M.F. Wullimann (Eds.): Brain evolution and cognition. — Wiley-Spektrum, New York, Heidelberg: 451-490.

de Waal F. (2007): Chimpanzee Politics. Power and Sex among Apes. 25th edition. — John Hopkins University Press, Baltimore. 256 pp.

Diamond J. & A. Bond, (2003): A comparative analysis of social play in birds. — Behaviour **140**: 1091-1115.

Domjan M. & B.G. Galef (1983): Biological constraints on instrumental and classical conditioning: retrospect and prospect. — Animal Learning & Behavior **11**: 151–161.

Dugas-Ford J., J.J. Rowell & C.W. Ragsdale (2012): Cell-type homologies and the origins of the neocortex. — Proceedings of the National Academy of Sciences of the United States of America **109**: 16974–16979.

Dukas R. (2004): Evolutionary biology of animal cognition. — Annual Review of Ecology, Evolution and Systematics **35**: 347-374.

Ducatez S., J.N. Audet & L. Lefebvre (2015): Problem-solving and learning in Carib grackles: individuals show a consistent speed–accuracy trade-off. — Animal Cognition **18**: 485-496.

Dunbar R.I.M. (1998): The social brain hypothesis. — Evolutionary Anthropology: Issues, News, and Reviews **6**: 178-190.

Emery N.J. & N.S. Clayton (2004): Comparing the complex cognition of birds and primates. — In Rogers, L.J. & G. Kaplan (Eds.): Comparative vertebrate cognition. — Kluwer Academic / Plenum Publishers, New York: 3-55.

Emery N.J., A.M. Seed, A.M.P. von Bayern & N.S. Clayton (2007): Cognitive adaptations of social bonding in birds. — Philosophical Transactions of the Royal Society B Biological Sciences **362**: 489-505.

Floresco S.B., A.E. Block & M.T.L. Tse (2008): Inactivation of the medial prefrontal cortex of the rat impairs strategy set-shifting, but not reversal learning, using a novel, automated procedure. — Behavioural Brain Research **190:** 85–96.

Fragaszy D.M., B.W. Stone, N.M. Scott & C. Menzel (2011). How tufted capuchin monkeys *(Cebus apella spp)* and common chimpanzees *(Pan troglodytes)* align objects to surfaces: insights into spatial reasoning and implications for tool use. — American Journal of Primatology **73**: 1-19.

Gajdon G.K., L. Amann & L. Huber (2011): Keas rely on social information in a tool use task but abandon it in favour of overt exploration. — Interaction Studies **12**: 304-332.

Gajdon G.K., M. Lichtnegger & L. Huber (2014): What a parrot's mind adds to play: the urge to produce novelty fosters tool use acquisition in kea. — Open Journal of Animal Sciences **4**: 51-58.

Garamszegi L.Z. Eens M. (2004): The evolution of hippocampus volume and brain size in relation to food hoarding in birds. — Ecology Letters **7**: 1216 – 1224.

Gibson K.R. (1986): Cognition, brain size and the extraction of embedded food resources. — In Else, J.G. (Ed.): Primate evolution — Cambridge University Press, New York: 95–103.

Greenberg R. & C. Mettke-Hofmann (2001): Ecological aspects of neophobia and neophilia in birds. — Current Ornithology **16**: 119-178.

Griffin A.S., M. Diquelou & M. Perea (2014): Innovative problem solving in birds: a key role of motor diversity. — Animal Behaviour **92**: 221-227.

Harding E.J., E.S. Paul & M. Mendl (2004): Animal behavior—cognitive bias and affective state. — Nature **427**: 312.

Herndon J.G., M.B. Moss, D.L. Rosene & R.J. Killiany (1997): Patterns of cognitive decline in aged rhesus monkeys. — Behavioural Brain Research **87**, 25–34.

Heyes C.M. & B.G. Galef (1996): Social learning in animals: the roots of culture. — Academic Press, London.

Hill B.J. (1993): Cetti's warbler flycatching. — British Birds **86**: 571.

Holzhaider J.C., G.R. Hunt & R.D. Gray (2010) The development of pandanus tool manufacture in wild New Caledonian crows. — Behaviour **147**: 553-586.

Huber L. & G.K. Gajdon (2006): Technical intelligence in animals: the kea model. — Animal Cognition **9**, 295-305.

Hunt G.R. (1996): Manufacture and use of hook-tools by New Caledonian crows. — Nature **379**: 249-251.

Hunt G.R. & R.D. Gray (2003): Diversification and cumulative evolution in New Caledonian crow tool manufacture. — Proceedings of the Royal Society of London, Series B Biological Sciences **270**: 867-874.

Isler K. & C.P. Van Schaik (2009): Why are there so few smart mammals (but so many smart birds)? — Biology Letters **5**: 125-129.

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.

Jarvis E.D. (2009): Bird Brain: Evolution. — In Squire, L.R. (Eds.): Encyclopedia of Neuroscience. — Academic Press, Oxford: 209-215.

Kacelnik A. (2009): Tools for thought or thoughts for tools? — Proceedings of the National Academy of Sciences **106**: 10071-10072.

Kedra A.H. & T.D. Mazgajski (2001): Factors affecting anvils utilization by Great Spotted Woodpecker *Dendrocopos major*. — Polish Journal of Ecology **49**: 79-86.

Kellam J.S. (2003): Pair bond maintenance at roost sites by pileated woodpeckers during autumn. — Wilson Bulletin **115**: 186-192.

Kilham L. (1974): Play in Hairy, Downy, and other woodpeckers. — The Wilson Bulletin **86**: 35-42.

Kothbauer-Hellmann R. (1990): On the origin of a tradition: milk bottle opening by timice (Aves, Paridae). — Zoologischer Anzeiger, Jena **225**: 353-361.

Kloo D., J. Perner, A. Kerschhuber, S. Dabernig & M. Aichhorn (2008): Sorting between dimensions: Conditions of cognitive flexibility in preschoolers. — Journal of Experimental Child Psychology **100**: 115–134.

Kummer H. & J. Goodall (1985): Condidtions of innovative behaviour in primates. — Philosophical Transactions of the Royal Society of London Series B **308**: 203-214.

Lefebvre L., N. Juretic, N. Nicolakakis & S. Timmermans (2001): Is the link between forebrain size and feeding innovations caused by confounding variables? A study of Australian and North American birds. . — Animal Cognition **4**: 91-97.

Lefebvre L., A. Gaxiola, S. Dawson, S. Timmermans, L. Rozsa & P. Kabai (1998): Feeding innovations and forebrain size in Australasian birds. — Behaviour **135**:1077–97.

Lefebvre L., P. Whittle, E. Lascaris, A. Finkelstein (1997): Feeding innovations and forebrain size in birds. — Animal Behaviour **53**:549–560.

Ligon J.D. (1970): Behavior and breeding biology of the Red-cockaded Woodpecker. — The Auk **87**: 255-278.

Lima S.L. (1983): Downy woodpecker foraging behavior: foraging by expectation and energy intake rate. — Oecologia **58**: 232-237.

Lima S.L. (1984): Downy woodpecker foraging behavior: efficient sampling in simple stochastic environments. — Ecology **65**: 166-174.

Lind J., S. Ghirlanda & M. Enquist (2009): Insight learning or shaping? — Proceedings of the National Academy of Sciences **106**: E76.

Lucas J.R., AdK. S.R. Brodin & N.S. Clayton (2004): Does hippocampal size correlate with the degree of caching specialization*?* Proc. R. Soc. Lond. B Biol. Sci. **271**: 2423–2429.

Löhrl H. (1977*):* Zur Nahrungssuche von Grau- und Grünspecht (*Picus canus, P. viridis*) im Winterhalbjahr. — Die Vogelwelt **98**: 15-22.

Mackintosh N.J. (1974): The psychology of animal learning. — Academic Press, London. 730 pp.

McNamara J. & A. Houston (1985): A simple model of information use in the exploitation of patchily distributed food. — Animal Behaviour **33**: 553-560.

Meijering M.P.D. (1967): Werkzeuge der Spechte. — Ardea **55**: 91-111.

Mendl M., O.H.P. Burman, R.M.A. Parker & E.S. Paul (2009): Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. — Applied Animal Behaviour Sciences **118**: 161-181.

Mettke-Hofmann C., C. Ebert, T. Schmidt, S. Steiger & S. Stieb (2005): Personality traits in resident and migratory warbler species. — Behaviour **142**: 1357-1375.

Mlíkovský J. (1989): Brain size in birds: 3. Columbiformes through Piciformes. — Věstník Československé Společnosti zool. Acta societatis zoologicae bohemoslovenicae **53**: 252-264.

Muckensturm B. (1971): Contributation á l'étude de l'utilisation de cavites come „outils" de contention par le pic épeiche (*Dendrocopos major*). — Rev. Comp. Animal, 1971. **4**: p. 227-236.

Nealen P.M. & R.E. Ricklefs (2001): Early diversification of the avian brain:body relationship. — Journal of Zoology **253**: 391-404.

Nicolakakis N. & L. Lefebvre (2000): Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. — Behaviour **137**: 1415–1429.

Oatley T.B., R.A. Earlé & A.J. Prins (1989): The diet and foraging behaviour of the Ground Woodpecker. — Ostrich **60**: 75-84.

O'Hara M., L. Huber & G.K. Gajdon (2015): The advantage of objects over images in discrimination and reversal learning by kea, *Nestor notabilis.* — Animal Behaviour **101**: 51-60.

Orenstein R.I. (1972): Tool-use by the New Caledonian Crow (*Corvus moneduloides*). — The Auk **89**: 674-676.

Overington S.E., J. Morand-Ferron, N.J. Boogert & L. Lefebvre (2009): Technical innovations drive the relationship between innovativeness and residual brain size in birds. — Animal Behaviour **78**: 1001-1010.

Parker S.T. (2015): Re-evaluating the extractive foraging hypothesis. — New Ideas in Psychology **37**: 1-12.

Parker S.T. & K.R. Gibson (1977): Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. — Journal of Human Evolution **6**: 623-641.

Parker S.T. & K.R. Gibson (1979): A developmental model for the evolution of language and intelligence in early hominids. — Behavioral and Brain Sciences **2**: 367-408.

Pechacek P., K.G. Michalek, H. Winkler & D. Blomqvist (2005): Monogamy with exceptions: Social and genetic mating system in a bird species with high paternal investment. — Behaviour **142**: 1093-1114.

Pérez-Barbería F.J., S. Shultz & R.I.M. Dunbar (2007): Evidence for coevolution of sociality and relative brain size in three orders of mammals. — Evolution **61**: 2811-2821.

Pepperberg I.M. & H.R. Shive (2001): Simultanous development of vocal and physical object combinations in a grey parrot (*Psittacus erithacus*): bottles caps, lids and labels. — J. Comp. Psychol. **115:** 376-384.

Piaget J. (1952): The Origins of Intelligence in Children. — International Universities Press, New York, NY. x+419 pp.

Piaget J. (1954): The Construction of Reality in the Child. — Basic Books, New York. xiii+386 pp.

Ramsey G., M.L. Bastian & C.P. van Schaik (2007): Animal innovation defined and operationalized. — Behavioural and Brain Sciences **30**: p. 393-437

Ricklefs R.E. (2004): The cognitive face of avian life histories: The 2003 Margaret Morse Nice Lecture. — The 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.

Reader S.M. & K.N. Laland (2002): Social intelligence, innovation and enhanced brain size in primates. — Proceedings of the National Academy of Sciences of the United States of America **99**: 4436-4441.

Reader S.M., Y. Hager & K.N. Laland (2011): The evolution of primate general and cultural intelligence. — Philosophical Transactions of the Royal Society B Biological Sciences **366**: 1017-1027.

Ritter W.E. (1921): Acorn-storing by California woodpecker. The Condor **23**: 3-14.

Ritter W.E. (1922): Further observations on the activities of the California Woodpecker. — The Condor **24**: 109-122.

Roberts R.C. (1979): The evolution of avian food-storing behavior. — The American Naturalist **114**: 418-438.

Rumbaugh D.M., E.S. Savage-Rumbaugh & D.A. Washburn (1996): Toward a new outlook on primate learning and behavior: complex learning and emergent processes in comparative perspective. — Japanese Psychological Research **38**: 113-125.

Schuck-Paim C., W.J. Alonso & E.B. Ottoni (2008): Cognition in an ever-changing world: climatic variation is associated with brain size in Neotropical parrots. Brain Behavior and Evolution **71**: 200–215.

Shettleworth S.J. (2001): Animal cognition and animal behaviour. — Animal Behaviour **61**: 277-286.

Sherry D.F. & J.S. Hoshooley (2006): The seasonal hippocampus of food-storing birds. — Behavioural Processes **80**: 334-338.

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.

Sielmann H. (1958): Das Jahr mit den Spechten. — Ullstein Verlag, Berlin. 152 pp.

Sih A. & M. del Giudice (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. — Phil. Trans. R. Soc. B **367**: 2762–2772.

Simmons K.E.L. (1984): House sparrows collecting insects from cars. — *Br. Birds* **77**: 121.

Skinner B.F. (1974): About Behaviorism. — Knopf, Random House, New York. 256 pp.

Smith C.C. & O.J. Reichman (1984): The evolution of food caching by birds and mammals. — Annual Review of Ecology and Systematics **15**: 329-351.

Sol D., T. Székely, A. Liker & L. Lefebvre (2007): Big-brained birds survive better in nature. — Proceedings of the Royal Society B **274**: 763-769.

SOL D. (2009): Revisiting the cognitive buffer hypothesis for the evolution of large brains. — Biology Letters **5**: 130-133.

TESCHKE I. & S. TEBBICH (2011): Physical cognition and tool-use: performance of Darwin's finches in the two-trap tube task. — Animal Cognition **14**: 555-563.

TIMMERMANS S., L. LEFEBVRE, D. BOIRE & P. BASU (2000): Relative size of the hyperstriatum ventrale is the best predictor of innovation rate in birds. — Brain, Behavior and Evolution **56**: 196-203.

The Avian Brain Nomenclature Consortium (2005): Avian brains and a new understanding of vertebrate brain evolution. — Nature Reviews Neuroscience **6**: 151-159.

TOCKNER T. (2015): Reversal Learning einer Diskriminierungsaufgabe bei Buntspechten - Eine Pilotstudie mit Arten der Gattung *Dendrocopos*. — Diplomarbeit, Veterinärmedizinische Universität Wien. Wien.

THORPE W.H. (1956): Learning and Instinct in Animals. — Methuen, London. 493 pp.

TORIGOE T. (1985): Comparison of object manipulation among 74 species of non-human primates. — Primates **26**: 182-194.

UŽGIRIS I. . & J.MCV. HUNT (1975): Assessment in Infancy: Ordinal scales of psychological development. — University of Illinois Press, Champaign, IL, US. xi+263 pp.

WEIN A., G.K. GAJDON & R. SCHWING (in press): Picture-object recognition in kea *(Nestor notabilis).* — Ethology.

WEIR A., J. CHAPPELL & A. KACELNIK (2002): Shaping of hooks in New Caledonian crows. — Science **297**: 981.

WHITEN A., V. HORNER, C.A. LITCHFIELD & S. MARSHALL-PESCINI (2004): How do apes ape? — Learning & Behavior **32**: p. 36-52.

WINKLER H. (1967): Das Schmiedeverhalten des Blutspechtes (*Dendrocopos syriacus*). — Egretta **10**: 1-8.

WINKLER H. & D. CHRISTIE (2002): Family Picidae (woodpeckers). — In DEL HOYO, J., A. ELLIOTT & J. SARGATAL (Eds.): Handbook of the Birds of the World. — Lynx Edicions, Barcelona: 296-555.

WINKLER H. & B. LEISLER (1999): Exploration and curiosity in birds: functions and mechanisms. — In ADAMS, N.J. & R.H. SLOTOW (Eds.): Proceedings XXII International Ornithological Congress. — BirdLife South Africa, Durban: 915-932.

VISALBERGHI E. & D.M. FRAGASZY (2006): What is challenging about tool use? The capuchin's perspective. — In WASSERMAN, E.A. & T.R. ZENTALL (Eds): Comparative cognition. Experimental explorations of animal Intelligence. — Oxford University Press, Oxford: 529-552.

YI X., M.A. STEELE & Z. SHEN (2014): Manipulation of walnuts to facilitate opening by the great spotted woodpecker (*Picoides major*): is it tool use? — Animal Cognition **17**: 157-161.

ZENTALL T.R. & B.G. GALEF (1988): Social learning. Psychological and biological perspectives. — Lawrence Erlbaum Associates, Hillsdale.

ZENTALL T.R. (2004): Action imitation in birds. — Learning & Behavior **32**: 15-23.

Addresses of the authors:

Dr. Gyula K. GAJDON
Messerli Research Institute
Unit of Comparative Cognition
University of Veterinary Medicine, Vienna
Veterinaerplatz 1
A-1210 Vienna
E-Mail: gyula.gajdon@vetmeduni.ac.at

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

Zeitschrift/Journal: Denisia

Jahr/Year: 2015

Band/Volume: 0036

Autor(en)/Author(s): Gajdon Gyula K.

Artikel/Article: Cognition in woodpeckers 63-76