TOOLS AND BRAINS IN BIRDS

by

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(Acc. 14-V-2002)

Summary

Tools are traditionally defined as objects that are used as an extension of the body and held directly in the hand or mouth. By these standards, a vulture breaking an egg by hitting it with a stone uses a tool, but a gull dropping an egg on a rock does not. This distinction between true and borderline (or proto-tool) cases has been criticized for its arbitrariness and anthropocentrism. We show here that relative size of the neostriatum and whole brain distinguish the true and borderline categories in birds using tools to obtain food or water. From two sources, the specialized literature on tools and an innovation data base gathered in the short note sections of 68 journals in 7 areas of the world, we collected 39 true (e.g. use of probes, hammers, sponges, scoops) and 86 borderline (e.g. bait fishing, battering and dropping on anvils, holding with wedges and skewers) cases of tool use in 104 species from 15 parvorders. True tool users have a larger mean residual brain size (regressed against body weight) than do users of borderline tools, confirming the distinction in the literature. In multiple regressions, residual brain size and residual size of the neostriatum (one of the areas in the avian telencephalon thought to be equivalent to the mammalian neocortex) are the best predictors of true tool use reports per taxon. Innovation rate is the best predictor of borderline tool use distribution. Despite the strong concentration of true tool use cases in Corvida and Passerida, independent constrasts suggest that common ancestry is not responsible for the association between tool use and size of the neostriatum and whole brain. Our results demonstrate that birds are more frequent tool users than usually thought and that the complex

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Behaviour 139, 939-973 Also available online -

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⁴⁾ We are grateful to Simon Reader for comments on earlier versions and to Sarah Timmermans for alerting us to the existence of Mlikovsky's data. We also thank Simran Kurir, Yutaka Nishioka and Johan Bolhuis for help with the German, Japanese and Dutch-language papers. This work was funded by an NSERC grant to LL and an FCAR fellowship to NN.

cognitive processes involved in tool use may have repeatedly co-evolved with large brains in several orders of birds.

Introduction

When used by humans, hammers, sponges, pokers, anvils and vices are all classified as tools. In other animals, however, only the first three are considered legitimate. This is because the definition of 'true' tools in the literature specifies that they must be detached from the substrate and directly held by the animal in the hand or mouth (van Lawick Goodall, 1970; Beck, 1980; McFarland, 1982). In this view, a vulture breaking an egg by hitting it with a stone is using a tool, but a gull dropping an egg on a rock is not. Several authors have criticised the arbitrariness (Hansell, 1987) and anthropocentrism (Shettleworth, 1998) of this distinction.

Studies of tool use in animals tend to focus on manipulative, largebrained species that are closely related to humans, *e.g.* primates (Fragaszy & Visalberghi, 1989; McGrew, 1992; Whiten *et al.*, 1999). Birds, unlike primates, lack both hands and close hominid parentage and are generally thought to be poor tool users. A review from the 1960's, for example, concludes that the entire class (close to 10 000 species) features only one documented case of true tool use, the insertion of twigs in crevices by the woodpecker finch of the Galapagos Islands (Thomson, 1964). The recent description in *Nature* of leaf tool manufacture in New Caledonian crows (Hunt, 1996) is all the more noteworthy because of the apparent rarity of such reports in birds.

In a series of review papers, Boswall (1977, 1978, 1983a, b) pointed out that cases of tool use in birds may be more numerous that we think. He classified the literature into two categories, 'true' and 'bordeline' cases. Following the traditional definition, borderline cases (called 'proto-tools' by Parker & Gibson, 1977) involve the use of objects that are part of a substrate, *e.g.* anvils on which prey are battered or dropped, wedges and thorns with which food is held, bait that is deposited on water to attract fish. True tools are detached from the substrate, *e.g.* hammers, probes, scoops, sponges and levers held directly in the beak or foot. If true tool use is cognitively more demanding than is borderline tool use (Parker & Gibson, 1977; Hansell, 1987; Vauclair, 1997), relative size of key brain structures could also distinguish the two categories (Gibson, 1986).

In birds, there is large taxonomic variation in the relative size (regressed against body weight or divided by brainstem size) of neural structures thought to underlie cognition. For example, the neostriatum/hyperstriatum ventrale complex (Rehkämper & Zilles, 1991; Dubbeldam, 1989, 1991, 1998) is five and a half times larger in carrion crows than it is in quail (Rehkämper et al., 1991). Reader & Laland (2002; Reader, 1999; see also Gibson, 1986) have shown that the taxonomic distribution of tool use cases is positively correlated with size of the neocortex and striatum in primates. In this study, we look for similar neural correlates of tool use in birds. Volumetric data on the neostriatum, hyperstriatum ventrale and other telencephalic areas (see Fig. 1) are available for 32 avian species covering 17 parvorders (Boire, 1989; Rehkämper et al., 1991; Timmermans et al., 2000; avian taxonomy according to Sibley & Monroe, 1990), while whole brain size is available for 737 species from 35 parvorders (Mlikovsky, 1989a, b, c, 1990). We use both the 737 species data set on whole brains and the 32 species data set on telencephalic areas to test the idea that neural structure size is positively correlated with the taxonomic distribution of tool use reports in birds and provides an independent criterion for distinguishing the true and borderline categories. For the 32 species data set, we compare relative size of the neostriatum and hyperstriatum ventrale with that of two other telencephalic structures that are thought to be less closely involved in cognition, the wulst and the striatopallidal complex. Like the mammalian neocortex, the neostriatum and hyperstriatum ventrale play a crucial role in several kinds of learning (McCabe et al., 1982; Horn, 1990; Nottebohm et al., 1990; MacPhail et al., 1993). In contrast, the wulst is a sensory projection area for visual and somatosensory information (Karten et al., 1973; Shimizu et al., 1995), while the striatopallidal complex is involved in stereotyped, species-specific responses (Reiner et al., 1984; Dubbeldam, 1998). Both the wulst and striatopallidal complex play some role in learned behaviour (wulst: MacPhail, 1976; Shimizu & Hodos, 1989; Deng & Rogers, 1997, 2000; striatopallida1 complex: Parent, 1986; Stewart et al., 1996; Mezey et al., 1999), but they are less specialized in complex integration than are the neostriatum and hyperstriatum ventrale. In a multiple regression, the size of the wulst and striatopallidal complex should consequently be less closely correlated with the number of tool use reports than should size of the neostriatum and hyperstriatum ventrale.



Fig. 1. Coronal sections of the telencephalon of *Alectoris chukar*, illustrating the hyperstriatum ventrale (HV), the neostriatum (Neo), the archistriatum (Archi), the nucleus basalis (n Bas), the wulst (W), and the striatopallidal (Paleo) complex. Top: rostral section; bottom: caudal section. Scale bars in upper left-hand corner represent 1 mm.

We use two data sources for estimating the number of tool use cases. First, we review the specialized literature, starting from Boswall's (1977, 1978, 1983a, b) comprehensive papers and incorporating cases published since then (*e.g.* Andersson, 1989; Marks & Hall, 1992; Hunt, 1996; Caffrey, 2000). Secondly, we use feeding innovation data accumulated for several areas of the world (Lefebvre *et al.*, 1997, 1998, 2001; Nicolakakis & Lefebvre, 2000; Timmermans *et al.*, 2000). At present, this data base includes close

to 1800 cases of new, unusual or rare foraging techniques or food types used by birds, found by exhaustively searching the short note section of 67 ornithology journals over an average of 30 years. Reader & Laland (2002; Reader, 1999) have shown that the number of tool use reports is positively correlated with innovation rate in primates. We look for a similar relationship in birds. According to Wyles *et al.* (1983) and Wilson (1985), innovation, social learning, brain size and cognitively-complex behaviours like tool use are all expected to co-vary in opportunistic taxa that exploit a wide array of rapidly-changing environmental conditions.

Methods

Tool use cases

The specialized literature on tool use was first searched for all true and borderline cases related to feeding and drinking, starting with the classic reviews of van Lawick Goodall (1970), Beck (1980) and Boswall (1977, 1978, 1983a, b). To these were added all cases found in the literature after 1983, the year of Boswall's last exhaustive review. These include Andersson (1989), Hunt (1996) and the review by Switzer & Cristol (1999), as well as papers from the bibliographies of innovation notes (*e.g.* Duyck & Duyck, 1984, found in Clayton and Jollife, 1996) and articles listed under 'tool-using' in *The Zoological Record*. Other tool use functions (*e.g.* grooming: Dubois, 1969; defence: Caffrey, 2001) are sometimes mentioned in the literature, but we focused only on feeding and drinking because these are the only behaviours covered by our other source, innovation reports.

Cases were classified in five categories, true tool use and four sub-categories of borderline tool use (dropping prey on a hard substrate, battering on an anvil, baiting, holding prey with a wedge or skewer). We excluded all cases considered unreliable by Boswall, unless later reports concluded otherwise. For example, egg-breaking with stones in Hamirostra melanosternon is listed in Wilson (1975), excluded by Boswall (1983a), but confirmed by Debus (1991) and Pepper-Edwards & Notley (1991). Use of leaves for grasping nuts in Probisciger aterrimus is also excluded by Boswall (1983a); this negative judgement is confirmed by Bertagnolio (1994). Save for two exceptions, string-pulling was also excluded because van Lawick Goodall (1970) and Boswall (1977) argue that the visual continuity between the food and the string make the latter no different from a stem or branch. The two exceptions we decided to include are the ice fishing cases described by Holmberg (cited by Scott, 1974 and Boswall, 1977). In these cases, Boswall points out that there is no visual continuity between the line and the fish hidden under the ice. The impact of our decision is evaluated later in the results section by comparing inclusion and exclusion of the two cases. The effects of a second decision, inclusion or exclusion of cases from captivity, is also evaluated in a similar way. A total of 71 cases of true or borderline tool use were found in the specialized literature.

The second set of tool use cases was obtained by searching through the innovation data base collected over the years in our laboratory. This data base currently contains 1796 innovations in 6 areas of the world (North America, western Europe, India, Australia, New

Zealand, southern Africa), collected by exhaustively searching the short note sections of 67 ornithology journals over an average of 30 years (see Lefebvre et al., 1997, 1998 and Nicolakakis & Lefebvre, 2000, for examples and details on the collection method). For the purpose of this paper, a 68th journal was also searched, Noticias de Galapagos, which covers a geographical zone outside the six included in our normal data base, but where several tool using cases have been reported (e.g. Hundley, 1963; Curio & Kramer, 1964; Millikan & Bowman, 1967). Innovations are defined as the ingestion of a new food type or the use of a new foraging technique, based on terms in the short note such as 'first report', 'unusual', 'unknown', 'rare', 'opportunistic', 'adaptable', 'strange', 'not noted before', 'not recorded', 'not mentioned in the literature'. All measures taken up to now indicate that innovation frequency is a valid and reliable operational estimate of feeding flexibility in birds. Correlations between the taxonomic distribution of innovation rates obtained by different readers (usually blind to the hypothesis) on the same sets of journals vary between 0.827 and 0.910 (p < 0.001; Lefebvre *et al.*, 1998; Nicolakakis & Lefebvre, 2000). Intertaxon differences in innovation rate correlate with problem-solving differences found in the literature (Timmermans et al., 2000) and in experimental tests conducted in the field and in captivity (Webster & Lefebvre, 2001). Nine potential biases have been examined: number of species per taxonomic group, avian population size, research effort per taxon, interest by ornithologists, reporting bias, journal source, editorial style, juvenile development mode, phylogeny. Only the first of these variables, species number, needs to be included in multiple regressions to express innovation rate as an unbiased index (Lefebvre *et al.*, 1998, 2001; Nicolakakis & Lefebvre, 2000). The five tool use categories taken from the specialized literature were used with the innovation data base. 61 cases of true or bordeline tool use were found in the data base; seven of these also appeared in the specialized literature and were eliminated. Among the dropping cases, we included breaking of booby eggs on rocks by Geospiza difficilis (Köster & Köster, 1983; Grant, 1986). In this case, the eggs are not dropped from the air, but thrown down by pushing, rolling, bracing and levering with the bill and feet; substrate use is thus the same as in other dropping cases, even if the bird is not in flight when it drops the egg.

Once all tool use cases in the innovation data base had been identified, they were removed from the data set in each geographic zone. For each zone, innovation frequency per taxon was then regressed against its most important confound, species number, obtained from standard ornithology texts (India: Ali & Ripley, 1995; New Zealand: Falla *et al.*, 1979; Australia: Simpson & Day, 1996; North America: Scott, 1987; Europe: Hagemeijer & Blair, 1997; southern Africa: Sinclair & Hockey, 1996) and reclassified according to Sibley & Monroe (1990) if initially given in non-molecular taxonomy. Standardized residuals were then determined for each zone where a taxonomic group was present and a weighted average innovation rate calculated by taking into account the number of innovation cases yielded by each zone, similar to the procedure used by Timmermans *et al.* (2000). Sampling error potentially caused by a small regional data set is minimized when each zone with extensive literature coverage (*e.g.* western Europe: 701 innovations in 24 journals) is likely to yield a more reliable measure than is a smaller zone with fewer journals (*e.g.* New Zealand: 57 innovations in only one journal).

Neuroanatomical data

Data on whole brains were taken from Mlikovsky (1989a, b, c, 1990). These data include cranial volumes (with appropriate corrections to estimate actual brain mass) measured by the author on museum specimens for 615 species (Mlikovsky, 1989a), as well as fresh-weight data on 151 species taken from previously published sources (e.g. Crile & Quiring, 1940; Portmann, 1947; Armstrong & Bergeron, 1985). We first checked all secondary data included in Mlikovsky's tables against the previously published source and averaged sets of species listed as separate by Mlikovsky but now considered monospecific by Sibley & Monroe (1990). We then took standard body weights from the CRC Handbook (Dunning, 1993) and regressed log brain size against log body weight for all species. From the residuals of this regression, we looked for outliers that could potentially indicate an unreliable source; any species whose residual brain size was more than 2 standard deviations away from the mean of its family was eliminated. We reran the regression of log brain size against log body weight for the 737 remaining species and used the residuals of this regression as our final data. Mean residuals were calculated for each parvorder, following the procedure used in previous papers on innovations and neural structure size (Lefebvre et al., 1997, 1998, 2001; Nikolakakis & Lefebvre, 2000; Timmermans et al., 2000). In the analyses below, the species level residual is used whenever a tool using species is included in Mlikovsky's data base (61 of the 125 cases of tool use). When it is not, the mean residual of the closest available taxonomic level (genus: 21 cases; family: 36 cases; parvorder: 1 case; suborder: 6 cases) is used as an estimate. Mean residual at the parvorder/suborder level predicts 73% of the variance at the species level, while means at the genus and family level respectively predict 91% and 82% of the species level variance. Mlikovsky's data base includes the 32 species featured in Boire (1989) and Rehkämper et al. (1991); the correlation between the brain sizes measured in the two data sources is 0.998 (N = 32, p < 0.001), indicating that Mlikovsky's measurements are reliable.

Volumetric data for the four telencephalic areas (Fig. 1) were taken from Boire (1989; 28 species) and Rehkämper et al. (1991; 4 species). Rehkämper et al. (1991) cover 6 species, but two of these, Coturnix coturnix and Phasianus colchicus, are also included in Boire (1989); for these cases, we used the mean of the data reported in the two sources. Of the four telencephalic areas used in the analysis, only the hyperstriatum ventrale is anatomically defined in identical terms in Boire (1989) and Rehkämper et al. (1991). For the other three structures, areas are lumped or split in different ways and must be regrouped at a level where they are identical. The neostriatum of Rehkämper et al. (1991) includes the archistriatum, neostriatum and nucleus basalis prosencephali of Boire (1989). The striatopallidal complex comprises the paleostriatum in Rehkämper et al. (1991) and the basal telencephalon, paleostriatum augmentatum and paleostriatum primitivum in Boire (1989). The wulst is measured as a single structure in Boire (1989), whereas it corresponds to the sum of the hyperstriatum accessorium (incorporating the hyperstriatum intercalatus superior) and hyperstriatum dorsale in Rehkämper et al. (1991). As was done for the whole brain, volume of each of the four structures was regressed (after log transformation) against the body weight of the subjects given in Boire (1989) and Rehkämper et al. (1991); average residual deviations were then calculated for each of the 17 parvorders present in the sample.

Regressions, phylogeny and independent contrasts

All regressions were conducted on Systat (Wilkinson, 1995). Depending on the analysis, the dependent variable was the taxonomic distribution of either true or borderline tool use reports.

The number of reports was log transformed before analysis to normalize its distribution, since the data include very large numbers (true tool use in Corvida represents 40% of the sample) and very small ones (several parvorders with zero cases). Depending on the analysis, the independent variables were (1) mean residual brain size per taxon; (2) mean residual size per taxon of each of the four telencephalic areas; (3) innovation rate (calculated as a weighted average per taxon for the 6 zones of the world, excluding tool use cases); (4) number of species per taxon (log transformed), an obvious confounding variable of the number of tool use reports (a parvorder like Passerida, which has 3556 species according to Sibley & Monroe, 1990, is likely to yield more reports than the parvorder Odontophorida, which has only six species); and (5) juvenile development mode, a known confounding variable of avian brain size (Bennett & Harvey, 1985; nidicolous, altricial birds have larger brains as adults than do nidifugous, precocial ones).

Three estimates of tool use were used in the multiple regressions. The first one used all cases found (39 true tools, 86 borderline), tabulated them at the level of the parvorder and entered them in the regressions as independent cases. The second estimate eliminated potential pseudoreplication and phyletic confounds caused by genera with many tool use reports. Some genera include several species that use one or more techniques. For example, there are 10 cases of borderline tool use in Larus (dropping and baiting), five in Pitta (all battering) and 11 in Corvus (dropping and battering). These multiple entries could bias the results by artificially creating many data points with similar relative brain size values. We eliminated the 48 cases where more than one species and/or more than one technique are reported in a genus and redid the regressions on these genus-level data. The third estimate was based on independent contrasts, not frequencies per taxon. If Passerida and Corvida both have large brains and a high number of tool use reports, the association between these traits could be caused by the relatively recent divergence of the two parvorders; a similar phyletic confound is less likely to be the case for Corvida and Psittaciformes, which are very distantly related (see phyletic trees in Figs. 3 to 6). We used the CAIC computer program written by Purvis & Rambaut (1995), a technique that factors out common ancestry by estimating trait values at ancestral nodes, averaging empirical values for related extant taxa weighted by phyletic distance. The phyletic branch lengths entered in the CAIC regressions are taken from Sibley & Ahlquist (1990) and are based on DNA hybridization distances. Multiple regressions (forced through the origin) are then conducted on the contrasts, not the actual parvorders used in our first two estimates.

Results

Tool use distribution

A total of 125 cases were found in the two data sources, after removal of the 7 overlapping reports. Despite the low degree of overlap, the two data sources provide similar taxonomic distributions of total tool use reports: the correlation between the two sources is 0.806 (p < 0.001, N = 35 taxonomic groups). The 125 cases are listed in Table 1 by tool use category and taxonomic group. Several trends are immediately obvious in

this table. The cases are widely distributed amongst 104 species in 15 parvorders. Nineteen species use more than one technique, seven of them in the genus Corvus. The common crow Corvus brachyrhynchos is the species showing the most techniques; it uses stone hammers to open acorns, sharpens a piece of wood to probe a hole, drops palm fruits and nuts on asphalt roads (but may not systematically use cars to break the food open, Cristol et al., 1997, contra Maple, 1974 and Grobecker & Pietsch, 1978; see however Caffrey, 2001), batters fish on hard sand (also scaling it on the sand by scraping), and, in captivity, uses a scoop to carry water to dry food. Several tool use categories are concentrated in particular taxa. Twenty-eight of the 39 cases of true tool use occur in two Passeriforme parvorders, Passerida and Corvida (suborder Passeri). All four cases of tool use in Psittaciformes involve captive birds. Holding food with a wedge or a skewer is reported in Corvida and Piciformes. Dropping food to break it open on a hard surface is equally distributed among three parvorders, Charadriida, Accipitrida and Corvida. There are no tool use reports in large, well-studied taxa like Phasianida, Anseriformes, Columbiformes, Falconida, Apodiformes and Podicipedida, nor in smaller, poorly-studied groups like Coliiformes, Galbuliformes, Trogoniformes, Phaethontida and Pteroclides (see phyletic trees in Figs. 4 and 6).

The relationship between brain size and each of the tool use categories is illustrated in Fig. 2. Brain sizes are directly available for the species involved in 61 cases. In the 64 others, the species are assigned the mean residual brain size of its genus (N = 21), family (N = 36), parvorder (N = 1) or suborder (N = 6, all Tyranni). As can be seen in Fig. 2, dropping, baiting and battering on an anvil are used by birds with a wide range of brain sizes. Several of these (*e.g.* gulls, herons, anhingas, roadrunners) have negative brain size residuals. In contrast, true tool use is overwhelmingly shown by birds with positive residuals. The two notable outliers are a captive oystercatcher that uses sticks to dislodge invertebrates in a zoo (residual brain size -0.598; Olney, in Boswall, 1978) and the bristle-thighed curlew, who throws coral stones at albatross eggs on Pacific islands (Marks & Hall, 1992). It is noteworthy that this species, *Numenius tahitiensis*, is the one with the largest brain in its parvorder, Scolopacida (residual = -0.236; parvorder mean = -0.757, N = 20).

On average, true tool users have a larger residual brain size than do borderline tool users; the mean for the first category (1.060, SEM = 0.130,

TABLE 1. Bord	erline and true tool technique	es used by different species,	classified by taxon. Brain size	e given as
	residual deviation f	rom log-log regression agains	st body weight	
Taxon	Species	Technique	Reference	Brain size
		Bait fish		
Coraciiformes	Ceryle rudis	Bait with bread	Root, in Boswall 1983a	0.161
Grui	Eurypya helias	Bait with maggots	Alders, in Boswall 1977	-0.066
Charadriida	Larus fuscus	Bait with bread; captive	Sinclair 1984	0.155
Accipitrida	Milvus migrans	Bait with bread	Roberts 1982	0.325
Ciconiida	Ardeola ralloides	Bait with insects	Crous 1994	-0.761
	Butorides striatus	Bait with bread,	Higuchi 1986; Keenan 1981;	-0.308
		insects, twigs, feathers	Foxall & Drury 1987;	
			Wood 1986; English 1987;	
		Batter on anvil		
Coraciiformes	Ceryle rudis	Batter crab on rocks	Cooper 1981	0.161
	Dacelo novaeguineae	Batter rat and bone	Roberts 1961	0.790
	Halcyon smyrnensis	Batter frog on branch	Tehsin 1989	0.193
Cuculiformes	Geococcyx californianus	Batter reptiles on rocks	Meinzer 1993	-0.246
Caprimulgi	Podargus strigoides	Batter feathers off	Wheeler 1943	0.716
		prey against dead bough		
Ralli	Eulabeornis castaneoventris	Batter shells on anvils	Woinarski et al. 1998	-0.577^{*}
Scolopacida	Numenius tahitiensis	Batter crabs on rocks	Marks & Hall 1992	0.236
Accipitrida	Buteo jamaicensis	Slam snake on rock in flight	Ellis & Brunson 1993	0.843
	Gypaetus barbatus	Batter bones on rocks	Fleming 1955	0.860
Sulida	Anhinga anhinga	Batter fish on branch	Wellenstein & Wiegmann 1986	-1.342
Ciconiida	Threskiornis molucca	Batter mussels on anvils	Vestjens 1973	-0.021
Tyranni	Xenicus gilviventris	Batter grasshopper	Sibson 1974	0.771^{*}
		on corrugated iron		
	Pitta erythrogaster	Batter hard-shelled prey	McDonald 1974	0.771^{*}

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Taxon	Species	Technique	Reference	Brain size
	Pitta guajana	Batter hard-shelled prey	Chasen 1939	0.771^*
	Pitta moluccensis	Batter hard-shelled prey	Robinson 1927	0.771^{*}
	Pitta sordida	Batter hard-shelled prey	Robinson 1927	0.771^{*}
	Pitta versicolor	Batter hard-shelled prey	Hindwood 1966	0.771^{*}
Corvida	Lanius collaris	Batter grasshopper on	Gore 1981	0.318
		post then skewer on thorn		
	Corvus brachyrhynchos	Batter fish on sand,	Phillips 1978	2.121
		wipe on sand (to scale?)		
	Colluricincla harmonica	Batter mouse on stump,	Tilt 1962; Reilly 1966	1.554^*
		wren and robin on rock		
	Corcorax melanorhamphos	Batter mussels	Hobbs 1971	1.554^*
	Ailuroedus dentirostris	Batter snails on stones	Marshall 1954	1.313^{*}
	Daphoenositta chrysoptera	Bash insects on branch	Noske 1985	1.554^*
	Falcunculus frontatus	Bash insects on branch	Noske 1985	1.554^*
Passerida	Ficedula hypoleuca	Batter snails	Page 1978	-0.045^{*}
	Myiophonus caeruleus	Batter shells on rocks	Smythies, in Boswall 1978	-0.045^{*}
	Oenanthe leucura	Batter lizard on stone	Heselden et al. 1996	-0.045^{*}
	Oenanthe oenanthe	Batter caterpillars	King 1978	-0.045^{*}
	Saxicola rubetra	Batter caterpillars	King 1978	-0.234
	Saxicola torquata	Batter snails	Fisher 1979	-0.234^{*}
	Saxicoloides fulicata	Batter frog and gecko	Sivasubramanian 1991	-0.045^{*}
	Turdus iliacus	Batter snails	Richards 1977	0.364
	Turdus pelios	Batter snails on rocks	Walsh & Walsh, in Boswall 1983b	0.379
	Turdus philomelos	Batter snails on rocks	Boswall 1977	0.088
	Anthus petrosus	Batter snails	Tutt 1990	-0.846^{*}
	Passer domesticus	Batter wings	Hammond 1997	0.402
		off damselflies		

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		[ABLE 1. (Continued)		
Taxon	Species	Technique	Reference	Brain size
	Ploceus philippinus	Batter frogs	George 1973	-0.347^{*}
		on electrical wire		
	Pycnonotus cafer	Batter gecko on wall	Bharos 1999	0.455^*
	Acridotheres fuscus	Batter mouse	Johnsingh 1979	0.496^{*}
		Drop on substrate		
Grui	Cariama cristata	Drop eggs on stones	Kooij & van Zon 1964	-0.013^{*}
Scolopacida	Numenius tahitiensis	Drop eggs	Marks & Hall 1992	0.236
Charadrida	Catharacta skua	Drop penguin eggs	Sladen, in Boswall 1977	-0.198^{*}
	Larus argentatus	Drop rabbits on rocks	Young 1987	-1.179
	Larus canus	Drop molluscs	Cristol & Switzer 1999	0.142
	Larus delawarensis	Drop molluscs	Cristol & Switzer 1999	-0.198^{*}
	Larus dominicanus	Drop egg on water	Moon 1992	-0.098
	Larus glaucescens	Drop molluscs	Cristol & Switzer 1999	-0.198^{*}
	Larus marinus	Drop crabs on hard sand;	Cramp & Simmons 1983	-0.287
		drop rat	Harber & Johns 1947	
	Larus melanocephalus	Drop molluscs	Cristol & Switzer 1999	-0.198^{*}
	Larus occidentalis	Drop molluscs	Cristol & Switzer 1999	-0.198^{*}
	Larus pacificus	Drop mussels on road	Wheeler 1946	-0.198^{*}
Accipitrida	Aquila chrysaetos	Drop tortoises	Leshem 1985	0.164
	Gypaetus barbatus	Drop bones and tortoise	Boswall 1977	0.860
	Haliaeetus leucocephalus	Drop tortoises	Bindner 1968	0.403
	Neophron percnopterus	Drop tortoise and lizards	Leshem 1985	0.264
	Pandion haliaetus	Drop conches on	Leshem 1985	0.810
		concrete-filled drums		
Corvida	Corvus albicollis	Drop tortoises	Uys 1966	1.780

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Taxon	Species	Technique	Reference	Brain size
	Corvus brachyrhynchos	Drop nuts on freeway	Grobecker & Pietsch 1978;	2.121
			Maple 1974; Cristol et al. 1997	
	Corvus caurinus	Drop shells	Zach 1978, 1979	1.694^*
	Corvus corax	Drop bones	Lorenz, in van Lawick	1.973
			Goodall 19/0	
	Corvus corone	Drop shells on roads,	Conder & Everett 1979	1.530
		place nuts at traffic lights	Nihei 1995	
	Corvus frugilegus	Drop mussels	Priestley 1947	1.554
	Corvus monedula	Drop horse chestnuts	Gibson 1992	1.278
	Corvus moneduloides	Drop nuts	Hunt 1996	1.694^*
	Corvus rhipidurus	Drop 'egg' on soil	Andersson 1989	1.694^*
	Corvus splendens	Drop gerbil	Fitzwater 1967	1.694^*
Passerida	Geospiza difficilis	Push, lever, bill brace	Köster & Köster 1983;	0.230^{*}
		eggs down on rocks	Grant 1986	
		Hold with wedge or skewer		
Piciformes	Dendrocopos major	Wedge in enlarged hole	Sielmann, in Boswall 1977	1.435
	Dendrocopos syriacus	Crack in wall as	Gorman 1998	1.352^{*}
		wedge and anvil		
	Melanerpes lewis	Wedge in enlarged hole	Law 1929	1.189^*
	Melanerpes carolinensis	Wedge seed in crevice	Erlwein 1996	1.189^*
	Picoides villosus	Wedge seed in crevice	Erlwein 1996	2.215^{*}
	Picoides pubescens	Knothole as vice	Davis 1995	2.215^{*}
	Sphyrapicus varius	Wedge seeds in bark	Labedz 1980	1.427^{*}
Corvida	Cracticus spp	Thorns to impale prey	Boswall 1977	1.554^*
	Cracticus torquatus	Wedge in forks and	Sedgwick 1947	1.554^*
		crevices; skewer on branch		

TOOLS AND BRAINS IN BIRDS

Taxon	Species	Technique	Reference	Brain size
	Pica pica	Wedge nuts in crevice	Rolando & Zunino 1992	1.916
	Lanius spp	Thorns to impale prey	Boswall 1977	0.381
Passerida	Thryothorus ludovicianus	Wedge sunflower seeds	Haney 1982	0.187^{*}
		between bricks		
	Sitta carolinensis	Knotholes as vice	Davis 1995	0.929^*
		True tools		
Piciformes	Melanerpes uropygialis	Gouges bark chips to	Antevs 1948	1.189^*
		bring honey to young		
Psittaciformes	Amazona ochrocephala	Bell to scoop seed, captive	Murphy, in Boswall 1983a	1.900
	Cacatua galerita	Bottle top to scoop	Longthorp, in Boswall 1983a	1.310
		water, captive		
	Psittacus erithacus	Pipe to bail water, captive	Smith 1971	1.606^*
	Anodorhynchus hyacinthinus	Leaf to steady nutcracking;	Bertagnolio 1994	2.913
		captive		
Scolopacida	Numenius tahitiensis	Throw stones at eggs	Marks & Hall 1992	0.236
Charadriida	Haematopus ostralegus	Stick to dislodge	Olney, in Boswall 1978	-0.598
		invertebrates; captive		
Accipitrida	Neophron percnopterus	Stones to hammer	van Lawick Goodall 1970	0.264
		ostrich eggs, smash lizard	Iankov 1983	
	Hamirostra melanosternon	Throw stones at eggs;	Debus 1991; Pepper-	0.543^{*}
		captive	Edwards & Nottley 1991	
Ciconiida	Ciconia ciconia	Wring moss in beak to	Rekasi 1980	0.287
		give chicks water		
	Leptoptilos crumeniferus	Stick to get prey in hole	Marshall 1982	1.393
Corvida	Colluricincla harmonica	Twigs for probing	Mitchell, in Boswall 1977	1.554^*

Taxon	Species	Technique	Reference	Brain size
	Corcorax melanorhamphos	Empty shells to hammer	Hobbs 1971	1.554^{*}
		open closed mussels		
	Corvus brachyrhynchos	Stone to smash acorn	Duvall, in Boswall 1978	2.121
	Corvus brachyrhynchos	Cup to carry water to	Beck 1980	2.121
		dry mash, captive		
	Corvus brachyrhynchos	Sharpen wood to probe	Caffrey 2000	2.121
	Corvus caurinus	Stick to pry peanut	Jewett, in Boswall 1983a	1.694^*
		from bamboo, captive		
	Corvus corax	Pull fishing lines to	Holmberg, in Boswall 1977;	1.973
		get fish under ice	Scott 1974	
	Corvus corone	Pull fishing lines to	Holmberg, in Boswall 1977;	1.530
		get fish under ice	Scott 1974	
	Corvus moneduloides	Twigs, leaves as	Orenstein 1972; Hunt 1996	1.694^*
		probes, hooks		
	Corvus rhipidurus	Hammer 'egg' with rock	Andersson 1989	1.694^*
	Corvus splendens	Leaf to get ants from hole	Rajan & Balasubramanian 1989	1.694^*
	Cyanocitta cristata	Tear paper, use as	Jones & Kamil 1973	1.621
		rake and sponge, captive		
	Cyanocorax yncas	Twig under bark	Gayou 1982	1.181
	Daphoenositta chrysoptera	Use and carry twigs to	Green 1972	1.554^{*}
		open wood-borer grub		
	Falcunculus frontatus	Twigs for probing	Richards, in Boswall 1977	1.554^{*}
Passerida	Camarhynchus heliobates	Twigs for probing	Curio & Kramer 1964	0.230^{*}
	Camarhynchus pallidus	Wood chips scrapers	Greenhood & Norton 1999	0.230^{*}
	Camarhynchus pallidus	Twig probes and levers	Millikan & Bowman 1967	0.230^{*}
	Certhidea olivacea	Twig probes	Hundley 1963	0.230^{*}

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Taxon	Species	Technique	Reference	Brain size
	Euphagus cyanocephalus	Dunked prey as sponge	Koenig 1985	0.230^{*}
		to bring nestlings water		
	Bradornis microrhynchus	Grass stem in hole	McNaughton, in Boswall 1983b	-0.045^{*}
		to fish for termites		
	Turdus merula	Twig broom to search	Priddey 1977	-0.110
		for food in snow		
	Parus caeruleus	Twig to push nuts	Coombes, in Boswall 1977	0.510
	Parus gambeli	Splinter in crack	Gaddis, in Boswall 1983b	0.680^{*}
	Parus major	Pine needles in crevices	Duyck & Duyck 1984	0.626
	Parus palustris	Sponge up food powder,	Clayton & Jollife 1996	0.430
		wrap to store; captive		
	Sitta pusilla	Bark scale levers	Morse 1968; Pranty 1995	0.929^*
	Sitta carolinensis	Bark lever	Mitchell 1993	0.929^*
* Data unav:	ailable for this species; value is mean	residual for the genus, family or sub	oorder.	



Fig. 2. Residual brain size for the species using true tools and the four sub-categories of borderline tools. The dotted line represents the mean residual for all birds.

N = 39) is significantly different from the mean for the second category (0.581, *SEM* = 0.090, N = 86; $F_{1,123} = 8.99$, p = 0.003). The difference in residual brain size between true and borderline tool users is robust; it remains significant when we restrict the analysis to one case per genus, eliminating 49 reports (p = 0.017), and when we exclude the 11 cases from captivity (p = 0.035), the two line pulling reports (p = 0.005), or the 64 cases where a species' brain size was estimated from the mean of its genus, family, parvorder or suborder (p = 0.009).

True tools and telencephalic areas

The difference between true and borderline tool use is also evident in the taxonomic distribution of reports. Overall, the distribution of borderline tool reports is most consistently correlated with innovation rate, while neural structure size is the best correlate of true tool use reports (Tables 2 and 3). Species number per taxon (an obvious confounding variable of the number of tool use reports) also remains in most of the final multiple regression models. Tables 2 and 3 first present the individual correlation (r, then p) of each independant variable with true or borderline tool use, then the p value for

that variable at the end of the multiple regressions. As predicted, size of the neostriatum and hyperstriatum ventrale is more strongly correlated with true tool use than is size of the striatopallidal complex and wulst (Table 2). In the multiple regressions, the neostriatum is the only structure that remains along with species number. The four telencephalic areas are highly correlated with each other (r of residual neostriatum size with that of hyperstriatum ventrale: 0.989; with wulst: 0.798; with striatopallidal complex: 0.962; all p < 0.001, N = 17). The one with the highest correlation with true tool use. the neostriatum, thus accounts for the common variance of the four areas in the multiple regression, causing all others to drop out. Innovation rate also drops out of the final model despite a strong individual correlation with true tool use before the multiple regression. This is because innovation rate is correlated with size of the telencephalic areas; its share of the variance in true tool use reports is accounted for by the stronger effect of neostriatum size. Note that innovation rate is even more highly correlated with size of the hyperstriatum ventrale (individual correlation = 0.653; p after multiple regression = 0.006) than it is with size of the neostriatum (individual correlation = 0.611; p after multiple regression = ns); if we omit tool use from the multiple regression and put innovation rate as the dependent variable, then the hyperstriatum ventrale is the only structure that remains in the final model ($r^2 = 0.385$, $F_{1,14} = 10.39$, p = 0.006).

Identical conclusions apply whether we include all reports or keep only one per genus (Table 2). Independent contrasts also yield similar results to regressions on phyletically-uncorrected taxa (Table 2), despite an obvious concentration of cases in Corvida and Passerida (Fig. 3). Juvenile development mode is non-significant in all analyses here and below, both in the individual correlations and multiple regression models. Figure 3 illustrates the taxonomic distribution of true tool use residuals (regressed against species number), as well as residual size of the neostriatum (regressed against body weight) for the 17 parvorders (phyletic tree proportional to DNA hybridizations distances in Sibley & Ahlquist, 1990).

True tools and whole brains

The results on telencephalic areas are confirmed at the level of the whole brain for three of the four estimates of true tool use distribution. Relative brain size is (with species number) the only variable that remains in the

		True to	pols		Borderli	ine tools
	individual correlations	р	<i>p</i> in multiple regression	individual correlations	р 5	<i>p</i> in multiple regression
Total freque	ncy/taxon					
Neostriatum	0.803	< 0.001	0.001	0.598	0.014	ns
HV	0.790	< 0.001	ns	0.581	0.018	ns
Pallidal	0.756	0.001	ns	0.536	0.032	ns
Wulst	0.658	0.006	ns	0.455	0.076	ns
Species	0.694	0.003	0.020	0.589	0.016	ns
Innovation	0.728	0.001	ns	0.656	0.006	0.006
	$r^2 = 0.739$	$F_{2,14} =$	23.70, $p < 0.001$	$r^2 = 0.389$, <i>F</i> _{1,14} =	= 10.55, p = 0.00
Without mul	tiple entries/	'genus				
Neostriatum	0.815	< 0.001	0.001	0.614	0.011	ns
HV	0.811	< 0.001	ns	0.596	0.015	ns
Pallidal	0.794	< 0.001	ns	0.522	0.038	ns
Wulst	0.634	0.008	ns	0.585	0.017	ns
Species	0.690	0.003	0.013	0.622	0.010	ns

TABLE 2. Association between true and borderline tool use frequency and relative size of the four telencenhalic areas species number par taxon and

 $r^2 = 0.751, F_{2,14} = 25.11, p < 0.001$ $r^2 = 0.346, F_{1,14} = 8.94, p = 0.010$

Independent	contrasts					
Neostriatum	0.745	0.001	0.002	0.493	0.062	ns
HV	0.729	0.002	ns	0.457	0.087	ns
Pallidal	0.708	0.003	ns	0.418	0.121	ns
Wulst	0.544	0.036	ns	0.324	0.239	ns
Species	0.576	0.025	0.031	0.444	0.097	ns
Innovation	0.526	0.044	ns	0.567	0.027	0.022
	$r^2 = 0.670$	$F_{2,13} = 1$	4.72, $p < 0.00$	$r^2 = 0.32$	2, $F_{1,14}$	= 6.64, p = 0.022

final multiple regression model for phyletically-uncorrected frequencies, for the data set that eliminates multiple entries per genus and for one of the two regressions on independent contrasts. Two versions of the independent contrasts are needed here, because the contrast produced by CAIC at the node where suborders Tyranni and Passeri meet is an outlier that skews the distribution of true tool use cases, causing it to significantly differ from normality (p < 0.05). The problem is caused by the very large difference

		True to	ools		Borderlir	ne tools
	individual correlations	р	<i>p</i> in multiple regression	individual correlations	р	<i>p</i> in multiple regression
Total frequ	uency/taxon					
Brain size	0.493	0.004	0.034	0.456	0.008	ns
Species	0.597	< 0.001	0.002	0.653	< 0.001	0.001
Innovation	0.467	0.006	ns	0.510	0.002	0.037
	$r^2 = 0.413$	$, F_{2,32} =$	12.94, $p < 0.001$	$r^2 = 0.472$	$F_{2,30} =$	15.30, $p < 0.001$
Without m	ultiple entrie	s/genus				
Brain size	0.516	0.002	0.021	0.454	0.008	ns
Species	0.602	< 0.001	0.002	0.650	< 0.001	0.001
Innovation	0.466	0.006	ns	0.533	0.001	0.022
	$r^2 = 0.434$	$F_{2,32} =$	14.04, $p < 0.001$	$r^2 = 0.483$	$F_{2,30} =$	15.97, $p < 0.001$
Independe	nt contrasts					
Brain size	0.389	0.028	ns	0.373	0.035	ns
Species	0.415	0.018	ns	0.575	0.001	< 0.001
Innovation	0.422	0.016	0.014	0.433	0.013	ns
	$r^2 = 0.178$	8, $F_{1,31} =$	6.73, $p = 0.014$	$r^2 = 0.331$	$F_{1,31} =$	15.31, $p < 0.001$

 TABLE 3. Association between true and borderline tool use frequency and mean residual brain size, species number per taxon and innovation rate (see text for details)

in true tool use cases between Passeri (Passerida plus Corvida, 28 cases) and Tyranni (no reported cases), given the small genetic distance between the suborders (Fig. 4). We therefore ran mutiple regressions with the outlier and without it. When the Tyranni-Passeri node is omitted, brain size is the only variable (with species number) that remains in the final model; note that exclusion of this node does not eliminate the 28 Passeri cases, but simply contrasts them with other taxa at higher nodes in the phyletic tree. When the outlier is included, brain size is significantly correlated with true tool use distribution in individual correlations, but drops out of the multiple regression because of the higher contribution of innovation rate. Innovation rate is correlated with relative brain size (r = 0.499, p = 0.003, N = 32), which is why it accounts for the common variance with true tool use distribution in the final step of the regression. Figure 4 illustrates residual true tool use per taxon (regressed against species number) and residual size



Fig. 3. (A) Phyletic tree of the 17 taxa for which telencephalic areas are available; branch lengths are proportional to DNA hybridisation distances given in Sibley & Ahlquist (1990). (B) Residual true tool use reports per taxon. (C) Residual size of the neostriatum.

of the whole brain (regressed against body weight) for the 35 parvorders (phyletic tree proportional to DNA hybridizations distances in Sibley & Ahlquist, 1990).

Borderline tools

In five of the six analyses conducted on borderline tools (Tables 2 and 3), frequency per taxon is more strongly associated with innovation rate than it is with size of the whole brain or of specific telencephalic areas. At the level of the whole brain, innovation rate is the only variable remaining (with species number) in the final multiple regression model on phyletically-uncorrected frequencies and on data that eliminate multiple entries per genus. In the independent contrasts, the effect of innovation rate falls just short (0.087) of the 0.05 level of significance. Contrary to the case seen above for true tools, the contrast between Tyranni and Passeri does not yield an extreme value in this analysis (Fig. 5). At the level of the four telencephalic areas, relative size of the neostriatum and hyperstriatum ventrale is significantly correlated with borderline tool use per taxon in the individual correlations, but drops out for two of the three mutiple regressions due to a stronger effect of innovation rate (illustrated in Fig. 6). Relative size of the neostriatum remains in the final model only for independent contrasts (Table 2).



Fig. 4. (A) Phyletic tree of the 35 taxa for which whole brain data are available; branch lengths are proportional to DNA hybridisation given in Sibley & Ahlquist (1990). (B) Residual true tool use reports per taxon. (C) Residual brain size.

Discussion

Two conclusions can be drawn from our results. First, tool use in birds is much more common than is often thought. Contrary to Thomson's (1964) statement, we found over 120 cases in 104 species, with 39 cases in the true tool category. A search through the innovation data base, an often disregarded, low impact factor section of the literature, allowed us to double the data set obtained from specialized reviews, yielding taxonomic trends that were highly correlated with those of the specialised literature. Secondly, three lines of evidence show that true tool users differ from borderline tool users in the size of key neural structures: true tool users show a larger average brain size, as well as a positive relationship between frequency of cases per taxon and both size of the whole brain and size of the neostriatum. In contrast, innovation rate is the best predictor of borderline tool use per taxon in most of our regressions.



Fig. 5. (A) Phyletic tree of the 35 taxa for which whole brain data are available; branch lengths are proportional to DNA hybridisation given in Sibley & Ahlquist (1990). (B) Residual borderline tool use reports per taxon. (C) Weighted innovation rate.

Our data confirm the distinction between true and borderline tool use emphasized by van Lawick Goodall (1970), Parker & Gibson (1977), Beck (1980), Boswall (1977, 1978, 1983a, b) and McFarland (1982). Compared to borderline cases, true tool use probably involves a more sophisticated integration of the potential uses of an object (Hansell, 1987), as well as the intricate movements needed for its manipulation. This integration should be favoured by larger brain areas involved in tool use control. Our results support Parker & Gibson's (1977) and Vauclair's (1997) suggestions that borderline and true tool use categories represent different degrees of cognitive ability, perhaps associated with differences in Piagetian sensorimotor stages (see Parker & Gibson, 1977). Whether a species is capable of using a given degree may depend on the relative size of its neostriatum, but even species capable of true tool use may first try simpler techniques. This is illustrated by Andersson's (1989) description of 'egg'-breaking attempts by a fan-tailed crow in Kenya. Because the 'egg' (a ping-pong ball mistakenly treated as an egg) could not be broken, the crow used a sequence of increasingly com-



Fig. 6. (A) Phyletic tree of the 17 taxa for which telencephalic areas are available; branch lengths are proportional to DNA hybridisation distances given in Sibley & Ahlquist (1990). (B) Residual borderline tool use reports per taxon. (C) Weighted innovation rate.

plex techniques: it first simply pecked at the shell with its beak, then flew up with the 'egg' and dropped it, then attempted to hammer the shell with an oversize stone, switching at last to a stone of manageable size to increase hammering efficiency. In a similar vein, some individuals and populations in a normally tool-using species may not utilise tools as a result of local ecological conditions or lack of learning. Tebbich *et al.* (2001) report that woodpecker finches do not use tools in habitats and seasons where gleaning for insects yields higher payoffs. Tebbich *et al.* also show that some wildcaught individuals never use twig tools despite extensive exposure to social and trial-and-error learning possibilities.

In the fan-tailed crow example, and in several others, the co-existence of true and borderline techniques in the same species suggests that true tool use may have evolved from simpler borderline tools, but the data offer only ambiguous support for this idea. On the positive side, 16 of the 39 true tool use cases occur in taxa where borderline cases are reported in the same species or genus. This is particularly evident in the seven *Corvus* species that use both true tools and dropping, as well as in the genus *Turdus* (use of a broom in *T. merula*, battering on anvils in three other *Turdus* spp) and *Melanerpes* (use of a sponge in *M. uropygialis*, holding in a wedge in *M. lewis* and *M. carolinensis*). In six species (*Numenius*)

tahitiensis, *Neophron percnopterus*, *Corcorax melanorhamphos*, *Corvus brachyrhynchos*, *C. moneduloides*, *C. rhipidurus*), similar prey are handled with a proto tool (batter or drop on an anvil) and a true tool (hammer, probe). On the negative side, true tool use shows no borderline equivalents in Paridae, Psittaciformes, Charadriidae or Ciconiidae; gulls also have no true tool alternative to their frequent use of dropping. Overall, the data thus provide poor evidence that proto tool users are preadapted for the use of true tools.

As predicted, the two telencephalic areas thought to be avian equivalents of the mammalian neocortex come out as the strongest predictors of the taxonomic distribution in tool use reports (Table 2). This does not mean that the wulst and striatopallidal complex play no role in tool use, but that the high correlation between the four telencephalic areas leads to the elimination of those that contribute less in the multiple regression. Contrary to feeding innovations (Timmermans et al., 2000; this study), the neostriatum comes out slightly ahead of the hyperstriatum ventrale and is thus the only remaining telencephalic predictor in the final multiple regression models. This result is not due to the fact that we measured innovation rate on a larger sample here (6 geographical areas, 1796 innovation reports) than did Timmermans et al. (1030 reports; only 5 of the 6 geographical areas covered, to the exclusion of southern Africa). In our sample, the hyperstriatum ventrale is still the best telencephalic predictor of innovation rate both with and without phyletic corrections. Caution should be exercised because the data set for tools is much smaller than the one for innovations. If, however, the difference between tool use and innovation rate is not due to sample size, this may mean that the intricate control of movement present in tool use but not in most feeding innovations (often simply the ingestion of a new food) could be most strongly associated with a different telencephalic structure (Fig. 1). The hyperstriatum ventrale consists of higher order, multimodal processing areas. The neostriatum features tertiary areas of this type, but also includes primary projection fields from both somatosensory (nucleus basalis) and visual (ectostriatum) pathways, as well as secondary areas that receive input from these primary termination fields (Rehkamper et al., 1985). The neostriatum thus has the necessary features for both the cognitive and sensory-motor aspects of tool use. True tool use in particular requires a subtle coordination of visual and somatosensory information. Probes, for instance, are held in the beak and must be moved in very precise ways inside crevices to force out insects, using both tactile and visual feedback. Ascending visual pathways to the forebrain terminate in the ectostriatum, located in the core of the neostriatum, and in the wulst. Sensory representation for the bill is located in the nucleus basalis prosencephali, included here in the neostriatum. The nucleus basalis is particularly large in tactile feeders like the Scolopacida (Boire, 1989). It is striking that a species from this small-brained, non-innovative parvorder, the bristle-thighed curlew, has evolved three types of tool use, stone throwing, egg dropping and food slamming on rocks (Marks & Hall, 1992). *N. tahitiensis* has the largest brain in its parvorder. As pointed out by Marks & Hall (1992), the specialised somatosensory receptors on its bill may, in an island context where birds are often more opportunistic than on continents, favour flexibility in the use of this food handling organ.

In Fig. 2, one borderline category, holding food with a wedge or skewer, is associated with the same range of brain sizes as is true tool use. Wedging is seen in large-brained woodpeckers (Piciformes), while skewering is a specialized technique used by two types of Corvida, shrikes (genus Lanius) and butcherbirds (genus Cracticus). Such concentrations of particular techniques in particular genera are seen for other types of tools. The genus Pitta, for example, includes several species that batter prey on anvils, as does the genus Turdus. Dropping prey on a hard surface is seen in several Larus and Corvus species (see Cristol & Switzer, 1999 for a detailed discussion of dropping). Several species of Galapagos finches use twig probes for removing insects from crevices. Common ancestry is an obvious explanation for the concentration of particular techniques in particular genera. This concentration could be caused by independent selection for each technique in each genus or by a general set of cognitive processes present in all tool-using taxa, which only takes a particular form when exploitation of a particular food type is required. In the latter view, the cognitive basis for hammering with a stone and poking with a twig is similar, *i.e.* changing the function of an object and manipulating it to reach hidden food. Differences between the techniques would be driven instead by the particular defence mechanisms of the prey (hiding in a shell vs hiding in acrevice). The two possibilities, independent selection for each technique vs common cognitive basis shaped by particular food handling constraints, cannot be distinguished for the moment, but are in any case not mutually exclusive.

Despite the fact that some techniques are prevalent in particular taxa, most of our evidence suggests that phyletic confounds are not responsible for the overall trends in the data. In all cases, eliminating multiple entries per genus yielded identical results to the analyses conducted on the full data set. For telencephalic areas, the regressions on independent contrasts and phyletically uncorrected taxa both point to the neostriatum as the best predictor of true tool use reports. It is only at the level of the whole brain that common ancestry poses a statistical problem at the node that joins suborders Passeri and Tyranni (Fig. 4). The contrast produced by CAIC at the Passeriforme node is so large that it leads to a violation of the normality assumption of linear regressions. Eliminating the outlier solves the statistical problem, but obscures the fact that the two Passeriforme suborders differ sharply in the number of true tool use cases. Conversely, keeping the outlier accounts for the Passeri-Tyranni difference, but may cause the results of the regression to be statistically meaningless. Since both solutions pose problems, we have included the two versions in our results.

In agreement with Boswall (1977, 1978, 1983a, b), our study suggests that tool use in birds is more common than is often assumed. Over 120 cases were found in birds, but this is still much smaller than the 607 cases collected by Reader & Laland (2002; Reader, 1999) in the order Primates. The current avian total may underestimate actual frequencies because biologists do not expect as many cases in birds as they do in primates. Primates (apes in particular) could still be more frequent tool users than are birds, however, be it for reasons of cognition, dexterity or dietary specialisation on embedded foods (Gibson, 1986; Parker, 1996). The important point is that the association between larger telencephalic structures and tool use in several groups of birds provides independent support for the joint evolution of these traits in widely divergent taxa. Comparing primates to humans is instructive, but raises the possibility of a phyletic confound, since the highest number of tool use reports occurs in Pan, the genus most closely related to Homo (Reader & Laland, 2002; van Lawick Goodall, 1970; Whiten et al., 1999; McGrew, 1992). In their study, Reader & Laland (2002) were careful to exclude common ancestry through the use of independent contrasts, but our results on birds further strengthen the case for independent evolution in two ways: not only are birds as a whole very distantly related to primates, but in addition, most large-brained, tool using groups of birds are distantly related to each other. As is evident in Figs. 4 and 6, Passeri, Accipitrida, Charadriida, Psittaciformes, Coraciiformes and Piciformes, six groups that

show positive residuals, come from widely-divergent branches of the avian phyletic tree.

Caution must be exercised in interpreting anecdotal observations (see the open peer commentary that follows Whiten & Byrne, 1988). In some cases, detailed work (Hunt, 1996) has confirmed a single chance observation (Orenstein, 1972). In other cases, however, initial claims have not been supported. The dropping of nuts (Maple, 1974) and palm fruit (Grobecker & Pietsch, 1978) on roads by C. brachyrhynchos, for example, has been validated by experimental work (Cristol & Switzer, 1999), but the suggestion that vehicles are used as nut-crackers in these cases has not (Cristol et al., 1997; Shettleworth, 1998; see however Caffrey, 2001 and similar work by Nihei, 1995 on C. corone). Captivity can also introduce some biases (e.g. training effects; Powell & Kelly, 1977), althought close proximity between humans and captive animals may make detection of tool using ability easier than it is in the field. Beyond these cautionary remarks, however, it is still reasonable to assume that complex cognitive processes are often operating when a vertebrate uses a tool. Parallel findings on primates (Reader & Laland, 2002) and widely-divergent groups of birds (this study) suggest that these cognitive processes may have independently co-evolved with large brains a number of times, allowing several species to profit from otherwise inaccessible food (Parker & Gibson, 1977; Gibson, 1986).

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