

Lateralization of tool use in New Caledonian crows (*Corvus moneduloides*)

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We studied laterality of tool use in 10 captive New Caledonian (NC) crows (*Corvus moneduloides*). All subjects showed near-exclusive individual laterality, but there was no overall bias in either direction (five were left-lateralized and five were right-lateralized). This is consistent with results in non-human primates, which show strong individual lateralization for tool use (but not for other activities), and also with observations of four wild NC crows by Rutledge & Hunt. Jointly, these results contrast with observations that the crows have a population-level bias for manufacturing tools from the left edges of *Pandanus* sp. leaves, and suggest that the manufacture and use of tools in this species may have different neural underpinnings.

Keywords: New Caledonian crows; tool use; laterality; handedness

1. INTRODUCTION

The predominance of right-handedness in humans, especially for tasks involving fine manipulation, has led some researchers to postulate a link between this asymmetry and other uniquely human traits, such as language (reviewed by Corballis (2003) and commentaries therein). Species-level rather than individual laterality is important because our closest relatives, chimpanzees (*Pan troglodytes*), show strong *individual* hand preferences in tool-use tasks, but no species-level laterality in the wild (McGrew & Marchant 1997, 1999; but see Hopkins *et al.* (2003) for evidence of right-handedness in captivity). However, the hypothesis of a link between species-level laterality and human uniqueness is challenged by work showing that many other vertebrates (from fishes to mammals and birds) show behavioural, motor and anatomical asymmetries, possibly reflecting a common evolutionary origin for laterality (e.g. Bradshaw 1991; Rogers 2002).

New Caledonian (NC) crows are notable for their frequent manufacture and use of tools, and appear to have many tool-related behavioural and cognitive adaptations (Hunt 1996; Chappell & Kacelnik 2002, 2004; Weir *et al.* 2002; Hunt & Gray 2003). They therefore represent an important case in which to establish whether tool use is associated with individual and/or species-level laterality. This possibility is supported by observations that throughout New Caledonia, NC crows leave more tool templates on the left than the right sides of pandanus leaves (Hunt 2000; Hunt *et al.* 2001), and that an individual wild crow

made more tools from the left than the right edges of pandanus leaves (Hunt & Gray 2004). However, evidence for lateralized tool *use* as opposed to manufacture is only now becoming available. We are aware of observations of only four wild unsexed individuals have been reported (Rutledge & Hunt 2004). Here, we examine laterality in a larger sample of individuals of known sex under controlled experimental conditions.

2. METHODS

(a) General approach

We presented NC crows with a task similar to some that they face in the wild: retrieving larvae from holes in a tree stump. We provided them with symmetrical artificial tools and recorded the manner in which they held them when probing for food: that is, whether the end of the tool was held against the left or right side of the head.

(b) Subjects

The subjects were 21 NC crows held at the Department of Zoology, University of Oxford. Twenty crows had been trapped in two locations (near Tendéa (ca. 21°38' S, 165°43' E) and near Boulouparis (ca. 21°53' S, 165°59' E)) in July to August 2002, while another, 'Betty', had been trapped at Yaté (ca. 22°11' S, 166°57' E) in March 2000, and has already participated in laboratory experiments (for details of capture and housing see Chappell & Kacelnik (2002) and Kenward *et al.* (2004)). Neither trapping nor transportation caused any injuries to the birds. Capture was carried out with permission of the NC Parks Authority, and all relevant laws for trapping and transport were complied with.

(c) Housing

The birds were housed (free-flying) in two groups of nine and 12 individuals, each with permanent access to an indoor room (3.25 m × 4.10 m × 2.25 m high) and outdoor aviary (3.25 m × 0.86 m × 2.25 m high). Each group consisted of crows from only one area (except for Betty, who was housed with the Tendéa group). Both indoor and outdoor accommodation contained many natural perches of varying widths and heights. Plastic childrens' toys provided environmental enrichment, and tree branches provided sources for tool-making. Drinking and bathing water were permanently available.

The crows are fed *ad libitum* on soaked cat biscuits (Go-Cat), an insect and fruit mix (Orlux Universal and Orlux granules), peanuts, and mealworms. They were encouraged to use tools regularly by making some of their preferred food otherwise inaccessible: mealworms were placed in holes drilled into tree stumps, and occasionally pieces of pig heart were placed in clear Perspex tubes that were left in the aviaries. All individuals have been observed using tools.

(d) Apparatus and procedure

The probing apparatus was a tree stump (ca. 25 cm high × 30 cm diameter), with two holes drilled on its sides (ca. 10 cm deep × 2 cm diameter). The holes were slanted downwards, 20 cm apart and 10 cm from the stump's base, and both were visible from one side of the stump. Prior to the start of each session, the holes were almost filled with mealworms that had been chilled to reduce their activity and thus prevent them from crawling out.

The stump was placed on a table (41 cm × 77 cm × 75 cm high) in front of a dark Perspex observation window (roughly half of the sessions were conducted indoors and half outdoors), with the holes facing the window. A piece of dowelling (0.3 cm in diameter and 15 cm long, i.e. within the size range of natural tools) was placed on the table in front of the stump, equidistant from the two holes and parallel to the edge of the table.

Sessions were performed between February and May 2003, and lasted for 1–2.5 h, depending on the crows' level of activity. *Ad libitum* food was removed 3 h before observations began and replaced after the session finished. The dowelling was replaced whenever a bird removed it from the table and dropped it, and the mealworms were replenished when they became scarce. All sessions were recorded on video for later analysis.

(e) Scoring and analysis

Behaviour was scored by A.A.S.W. from the videos. Lateral tool use was defined as when the non-working tip of the tool projected on one side of the crow's beak or head. Thus, for example, if a crow held a tool with the non-working end against its left cheek, this was scored as 'left lateral' (see movie clip in electronic Appendix A). Note that although this is scored as 'left', the distal tip would be on the other side of the head's axis and hence it is probable that the contralateral (here, the right) eye would be monitoring the working end of

Table 1. Laterality of tool use in NC crows (by hole).

(Bird, the identification of each subject (in terms of ring colour); % left, left lateral tool use as a percentage of total lateralized tool use; % straight, non-lateral tool use as a percentage of total tool use.)

bird	sex	left laterality (bouts)			right laterality (bouts)			total lateral	% left	total	
		hole a	hole b	total	hole a	hole b	total			straight	% straight
BB	F	0	0	0	4	13	17	17	0.0	3	15.0
BK	M	0	0	0	24	15	39	39	0.0	51	56.7
YB	M	0	0	0	20	0	20	20	0.0	1	4.8
YK	F	0	0	0	9	31	40	40	0.0	0	0.0
PY	M	1	0	1	34	5	39	40	2.5	12	23.1
BG	M	29	1	30	6	0	6	36	83.3	49	57.6
GY	M	11	26	37	1	0	1	38	97.4	65	63.1
BP	F	1	39	40	0	0	0	40	100.0	1	2.4
KY	M	0	38	38	0	0	0	38	100.0	0	0.0
YY	M	1	39	40	0	0	0	40	100.0	0	0.0

the tool. Cases where the tip was inside the crow's beak were scored as 'straight'; this category conflates 'truly' non-lateral tool use with weakly lateralized cases where it was impossible to determine the direction of laterality, and for this reason was not formally analysed.

Laterality was scored for each 'bout' of tool use. A new bout was scored either when a bird released a tool and significantly changed its posture (to avoid counting as independent bouts occasions when crows momentarily released and re-grasped tools without moving their heads), or when a bird changed its hold on a tool (e.g. from straight to right, or from right to left). The hole that was probed during each bout was also scored.

Because there was variability in the number of bouts that different birds performed, we ceased scoring individuals after they had reached a total of 40 bouts of lateralized tool use in either direction: a power test showed that with 40 trials we would have a 90% chance of detecting an individual bias of 75% or greater. Individuals that performed fewer than 10 bouts of tool use were not included in the analysis. The experiment was terminated when 10 individuals had completed at least 10 bouts.

Binomial tests were used to determine whether individuals were laterally biased. A one-sample (two-tailed) *t*-test was used to examine whether there was a population bias in laterality over our sample: the proportion of birds that had a majority of left-sided bouts was tested against an expected mean of 0.5 (no bias).

To test whether the particular hole used biased the birds' laterality, we first calculated (for each individual) the proportion of left-lateral tool use in each hole relative to total left-lateral tool use, as in the equations below:

$$p(\text{La}) = \#L_a / (\#L_a + \#R_a),$$

$$p(\text{Lb}) = \#L_b / (\#L_b + \#R_b).$$

The first (capital) letter in each identifier indicates the laterality of tool use and the second (lower case) letter the hole being probed. Thus, $p(\text{La})$ is the proportion of left lateral tool use in hole a (the left hole), $\#L_b$ is the number of bouts of left-lateral tool use in hole b.

To measure differences in laterality between the two holes, we subtracted $p(\text{Lb})$ from $p(\text{La})$ and did a one-sample (two-tailed) *t*-test over all individuals asking if this significantly differed from zero (individuals that used only one hole were excluded). A significant result here would indicate that the hole probed did affect the laterality of tool use.

3. RESULTS

Out of the 10 subjects, five were left- and five right-biased (all with $p < 0.0001$); thus, there was no overall preference (see table 1 and figure 1 for full results). Bilateral tool use was rare: only three birds ever used tools bilaterally, and the most bilateral individual used just 17% on its minority side. Seven out of the 10 subjects also showed at least one bout of straight tool use, ranging from 2.4% to 63% of total tool-use bouts. However, this should

be interpreted with caution because (as noted above) this category might also include cases where laterality could not be determined.

Because only three birds were female, the sample is too small for statistical testing of an effect of sex. Inspection of the data shows that the ratio of right- to left-biased individuals was 2 : 1 in females and 3 : 4 in males, providing no suggestion for a sex difference in laterality.

The mean difference in proportion of left-lateral tool use between holes a and b was -0.0283 , which was not significantly different from zero ($t_7 = -1.21$, $p = 0.267$; two subjects were excluded from this test because they exclusively used one hole), failing to demonstrate a difference in laterality as a function of which hole was probed.

4. DISCUSSION

We observed very strong individual laterality in tool use: only 2.3% (8 out of 348) of all bouts of tool use were on birds' less preferred sides. There was no evidence for a population bias in laterality: the numbers of left- and right-biased subjects were identical. Laterality did not obviously differ between males and females, but the sample size was insufficient for statistical testing. There was large variation in the extent to which individuals appeared to use tools non-laterally.

Our findings are similar to those reported by Rutledge & Hunt (2004), who found strong laterality in four wild crows in similar tasks, also split equally by side. Thus, there appears to be no species-level laterality in tool use, in contrast with the observations of Hunt *et al.* (2001) that 66% of tool templates had been cut from left edges of pandanus leaves. However, assuming that tool use and tool manufacturing are equally biased and pooling our 10 individuals with the four observed by Rutledge & Hunt (2004), a power test ($\alpha \geq 0.95$) shows that with 14 individuals there is only a 31% chance of detecting a population bias of this magnitude or greater, so we cannot confidently exclude a weak species-level bias in tool use.

As mentioned above, Hunt's (2000) and Hunt *et al.*'s (2001) discovery of population laterality in tool manufacture was based upon the templates of tools cut from pandanus leaves, which were consequently not attributable to individuals. However, in a recent paper, Hunt & Gray

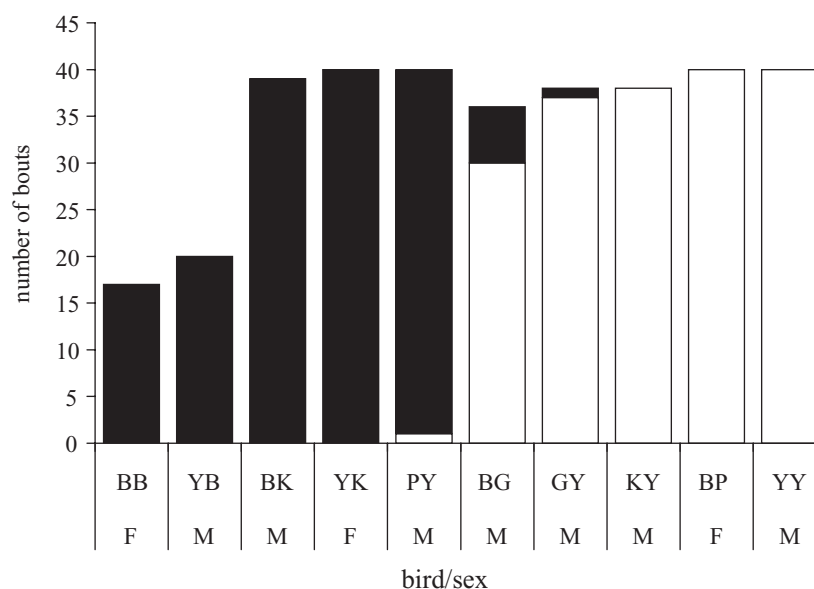


Figure 1. Laterality of tool use in NC crows. Filled bars represent 'right-lateral' tool use, and open bars represent 'left-lateral' tool use. Bird identification and sex are shown on the x-axis, and the number of bouts of lateralized tool use is shown on the y-axis.

(2004) provided the first report of direct observations of a crow making and using pandanus tools. Strikingly, they found that this single individual made tools from both the left and the right edges of pandanus leaves, with a preference (74%, if results from clockwise- and anticlockwise-spiralling trees are combined) for the left edge. This contrasts with the exclusive left-lateralized use of pandanus tools by the same individual, and the observations here of exclusive lateralization in nearly all individuals. If future studies confirm that other wild NC crows make tools from both the left and the right edges of pandanus leaves, this would strongly suggest that tool use and manufacture have different neural bases: the first demonstration (to our knowledge) of such a difference in any organism.

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