



Modulation of behavioural laterality in wild New Caledonian crows (*Corvus moneduloides*): Vocalization, age and function

Cyrielle Mack & Natalie Uomini

To cite this article: Cyrielle Mack & Natalie Uomini (2022): Modulation of behavioural laterality in wild New Caledonian crows (*Corvus moneduloides*): Vocalization, age and function, *Laterality*, DOI: [10.1080/1357650X.2022.2098969](https://doi.org/10.1080/1357650X.2022.2098969)

To link to this article: <https://doi.org/10.1080/1357650X.2022.2098969>



© 2022 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group



[View supplementary material](#)



Published online: 14 Jul 2022.



[Submit your article to this journal](#)



Article views: 69





[View related articles](#)



[View Crossmark data](#)

Modulation of behavioural laterality in wild New Caledonian crows (*Corvus moneduloides*): Vocalization, age and function

Cyrielle Mack  and Natalie Uomini 

Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

ABSTRACT


The New Caledonian crow (*Corvus moneduloides*) is known for displaying a unique set of tool-related behaviours, with the bird's bill acting as an individually consistently lateralized effector. However, we still fail to understand how such laterality develops, is modulated or even if its expression is consistent across other behavioural categories. Creating the first ethogram for this species allowed us to examine laterality and vocalisations in a population of wild, free-flying New Caledonian crows using detailed analyses of close-up video footage. We revealed the existence of an overall strong left-sided bias during object manipulation only and which was driven by the adult crows of our focal population, the stabilization of individual preferences occurring during the birds' juvenile years. Individually, at least one crow showed consistent side biases to the right and left within different behavioural categories. Our findings highlight previously unknown variability in behavioural laterality in this species, thus advocating for further investigation. Specifically, we argue that a better understanding of the New Caledonian crow's biology and ecology is required if one wishes to pursue the promising comparative road that laterality could be connected to the evolution of tool-making.


ARTICLE HISTORY Received 4 March 2022; Accepted 29 June 2022

KEYWORDS Corvids; object manipulation; tool behaviour; laterality; limb preferences

Introduction

A species' comparatively enhanced sensory and/or motor abilities have often been linked back to asymmetrical hemispheric lateralization (see Rogers, 2021), a trait long seen as uniquely human (Corballis, 2002) and which

CONTACT Natalie Uomini  natalie_uomini@eva.mpg.de  Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany

 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/1357650X.2022.2098969>.

© 2022 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way.

these faculties reflect (Brown & Magat, 2011b; Hellige, 1993). Contrary to the idea of human uniqueness, however, reports of differential cerebral information processing, namely because of regional structural discrepancies (Bisazza, Rogers, & Vallortigara, 1998), have flourished in the last few decades across all kinds of taxa, both vertebrates (see Rogers & Andrew, 2002; Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Versace, 2017) and invertebrates (see Frasnelli, 2013; Frasnelli, Vallortigara, & Rogers, 2012). Nonetheless, a certain form of “chimpancentrism”, as identified by Beck (1982), still prevails, as the subject of laterality has most notably been discussed in relation to language and handedness in object manipulation, i.e., research topics heavily focused on primate observation and experimentation (see Fitch & Braccini, 2013; Marchant, 2018). However, whether one is interested in vertebrate laterality for the purpose of studying the evolution of human laterality, or to understand the evolution of laterality more broadly, it is beneficial to broaden the approach by considering taxa beyond the primates (Fairlie & Uomini, 2022). Here we focus on laterality in a species of corvid bird.

Behavioural laterality is defined as a side bias that can be manifested in any aspect of animal behaviour. Examples include the direction of turning in a school of fish (Miletto Petrazzini, Sovrano, Vallortigara, & Messina, 2020), the choice of which cheek to kiss first in a French greeting (Chapelain et al., 2015), or the side of lunge rolling of a baleen whale while foraging which results in greater wear on one side of baleen plates (MacNeilage, 2013). We focus here on the sub-category of motor laterality, which refers to general organ-use preferences, whether those are sagittally paired or not (McGrew & Marchant, 1997), with pawedness (e.g., Bisazza, Cantalupo, Robins, Rogers, & Vallortigara, 1996), footedness (e.g., Izawa, Kusayama, & Watanabe, 2005), eyedness (e.g., Ventolini et al., 2005) or even tail (e.g., Quaranta, Siniscalchi, & Vallortigara, 2007) and tongue movements (e.g., Ying, 2019) being discussed in the literature. Of particular interest are organ-use preferences outside of handedness (i.e., in species who do not have hands) because they represent convergent evolution (Osvath, Kabadayi, & Jacobs, 2014) of the traits which are of interest. In this respect, the New Caledonian crow (*Corvus moneduloides*) makes for a highly interesting model for two reasons. Firstly, it would provide further input into our understanding of avian cognition, which was deemed one of “the best examples of brain asymmetry in a non-human species” (Rogers, 1980). Secondly, this corvid species also possesses both a larger relative brain size (Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008) and a unique tool-related repertoire (Hunt & Gray, 2004a; McGrew, 2013) when compared to other passerines. Patterns of asymmetry are exponentially complexified following an increase in brain size (Herculano-Houzel, 2009; Kaplan & Rogers, 2021; Uomini & Ruck, 2018). Therefore, the New Caledonian crow, with its relatively large brain size compared to other passerines, becomes a

model of interest, especially when looking for laterality patterns outside of the more classically explored and lateralized tool repertoire. Extensive descriptions of tool manufacture (Hunt, 1996; Hunt & Gray, 2004b, 2006) and tool use (Hunt, 1996; Hunt & Gray, 2004b; Rutz & St Clair, 2012) have been made, highlighting how the bird's bill can act as an individually consistently lateralized effector (Hunt, 2000a; Rutledge & Hunt, 2004).

Given trends, however, do emerge within every field of research, and that of avian behavioural laterality is no stranger to it. Previous studies only focused on, and thus collected data for a few behaviours per study, all comprised within the same behavioural category, and no comprehensive ethogram exists (e.g., Baciadonna, Zucca, & Samour, 2021; Holzhaider, Hunt, & Gray, 2010a; Hunt & Gray, 2004b; Kenward, Rutz, Weir, & Kacelnik, 2006). Thus, with this study, we aimed to redress the imbalance in knowledge. Concretely, the New Caledonian crow's tool behaviour is being deeply explored whereas the biology and ecology of this species remain relatively unknown (Hunt, Holzhaider, & Gray, 2012; Kenward, Rutz, Weir, Chappell, & Kacelnik, 2004; McGrew, 2013; Rutz & St Clair, 2012) and even qualitative studies aiming to identify the factors driving tool-related behavioural laterality are scarce (see Table 1 for a summary of all data published to date on laterality in New Caledonian crows).

More specifically, we still fail to understand how the New Caledonian crow's laterality develops, is modulated and if its expression is consistent across other behavioural categories. Therefore, in the present study, we aimed to address these three questions by studying a population of wild, free-flying New Caledonian crows. These questions were motivated by the striking parallels recently found with human ancestor *Homo erectus* (Hunt & Uomini, 2016) which have already been addressed within other prone-to-comparison taxa, such as primates. For instance, tool use in immature chimpanzees (*Pan troglodytes*) is not as strongly lateralized as it is in adult individuals (Humle & Matsuzawa, 2009). Thus, our first prediction was that New Caledonian crow juveniles, who go through a similarly extended immature period offering opportunities to both observe and practice tool behaviour (Pereira & Fairbanks, 1993; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Uomini, Fairlie, Gray, & Griesser, 2020), will display an analogous instability in lateralization – at least in the tool domain. Secondly, many primates and birds show individually consistent hand / foot preferences for particular action types (Allen et al., 2018; Prieur, Pika, Barbu, & Blois-Heulin, 2018; Prieur, Lemasson, Barbu, & Blois-Heulin, 2019; Regaiolli et al., 2021a; Rodgers & Cain, 2019), leading to our second prediction that adult crows will maintain, given a certain behavioural category, an individual side bias as well. Thirdly, in order to explore the hypothesis about one possible evolutionary pathway to language that has been proposed specifically for the human lineage, namely that behavioural motor lateralization in the tool-making activities of early hominins led to increased motor skill laterality,

Table 1. Previous studies reporting laterality data on New Caledonian crows (*Corvus moneduloides*). Studies are listed in chronological order with the behaviours studied, age and number of participants, and laterality results found. “Tool use” here is always for extracting food.

Authors (Date)	Behaviour	Participants	Laterality
Hunt (2000b)	Pandanus tool manufacture	Unknown crows – most likely adults; at least 2 different crow populations; 1532 different tool-making events	65–89% of tools made on the left edge of pandanus leaves
Hunt et al. (2001)	Pandanus tool manufacture	Unknown crows – at least 2 different crow populations; 3727 tools from 19 locations across New Caledonia	2463 tools (68%) made on the left edge of pandanus leaves, 1264 made on the right edge, with a significant effect of leaf-spiral direction
Hunt and Gray (2004b)	Pandanus tool manufacture and use	1 free-living crow, probably adult; 121 tool-use events; 52 different tools used; 46 tool-manufacture events	88 of 121 (72.7%) of tool-use events on the left-side cheek, the remainder with the tool held centrally; 67–81% bias to make tools on the left edge of pandanus leaves
Rutledge and Hunt (2004)	Use of own manufactured stick tools	4 free-living crows, at least one likely adult; 216 different tools used, of which 173 lateralized, 7 bilaterally used	96.1% of unilateral tool use, with all birds having a significant bias to hold tools on the left or right cheek (2 individuals right-sided, 2 left-sided)
Weir et al. (2004)	Use of provided wooden tools	10 permanently captive crows trapped in 2 different locations (21 tested but only 10 analysed); 7 males, 3 females; 530 tool-using bouts (20–1030 per bird). Individuals not named	65.7% of unilateral tool use, with equally divided strong individual bias to hold tools on left or right cheek but no overall trend (5 birds right-sided, 4 birds left-sided, 1 bird 83% left-sided)
Hunt et al. (2006)	Pandanus tool manufacture	Unknown crows; 5851 tool counterparts at 23 locations across New Caledonia	Differed by site; overall bias to make tools on the left edge of pandanus leaves for stepped tools and on the right edge for narrow tools
Hunt et al. (2007)	Use of own manufactured stick tools	2 adult males: 1 free-living male (46 tool-making events, 298 tool-use events, and 203 events trapping the tool under the foot); 1 temporarily captive male (54 tool-use events)	Free-living male: 100% tools used on the left cheek, right-foot bias (141 left foot, 62 right foot); temporarily captive male: 100% tools used on the right cheek
Troscianko et al. (2012)	Use of provided wooden tools	3 permanently captive adult crows from same group as Weir et al. (2004); 747 tool-gripping events. Individuals not named	All crows had a strong bias to hold the tool on left or right cheek; 2 birds right-sided, 1 bird left-sided

(Continued)

Table 1. Continued.

Authors (Date)	Behaviour	Participants	Laterality
St Clair and Rutz (2013)	Use of human- manufactured, naturalistic stick tools	8 temporarily captive crows (2 adult males, 1 adult female, 5 juvenile females); 9 tool-use events per bird	7 crows had an exclusive bias: 3 birds left-sided, 4 birds right-sided; 1 bird preferred the right side
Martinho et al. (2014)	Use of provided wooden tools; looking at prey inside a tube	13 permanently captive crows from same group as Weir et al. (2004) (7 females, 6 males); 10 tool- use bouts per bird; first looking eye per bird. Individuals named	Eye dominance: 4 birds right eye, 5 birds left eye; tool use: 3 birds 90–100% right- sided, 6 birds 50–100% left-sided; 8 birds' looking eye matched their dominant tool side preference

and then brain laterality in these species (Prieur et al., 2019; Ruck & Uomini, 2021), which in turn would have facilitated the emergence of language (Meguerditchian, Cochet, & Vauclair, 2011; Mosquera, Geribàs, Bargalló, Llorente, & Riba, 2012; Uomini & Meyer, 2013), we explored the potential co-occurrence of vocalisation and action in New Caledonian crows. Just as chimpanzees' right-hand lateralization is enhanced during such instances (Hopkins & Cantero, 2003), we predicted that, for a given behaviour, its combination with a vocal event would lead to a more pronounced lateralization than the same behaviour expressed alone.

Although previous studies of laterality in New Caledonian crows point to an overall trend towards a left-sided bias at the populational level and the existence of an often consistent lateralization in identified birds (see Table 1), these data alone are not sufficient. Indeed, they only cover quite limited populations throughout the archipelago. While large datasets on laterality in free-living crows behaving in their natural environment are mostly from unknown individuals, with only very few data from identified individuals in the wild, controlled experiments stem from a handful of well-known now permanently captive crows who were brought from New Caledonia to Oxford, UK between 2000 and 2010 and later moved to their current home in Seewiesen, Germany (Jacobs, von Bayern, & Osvath, 2021). In total, results on only 15 identified free-living crows and 13–26 permanently captive crows have been published (see Table 1).

In other words, these studies, although being challenged by a variety of contexts, situations, and motivations, have all demonstrated sizeable limitations, hereby illustrating the complex expression of laterality in this species. For instance, every captive study solely offered human-made tools to the crows, whereas the more naturalistic studies allowed the free-living birds to make their own. This difference might affect the results due to a potential effect of manipulating a familiar vs. unfamiliar object, e.g., laterality could be expressed either more or less strongly (Baragli, Scopa, Felici, &

Reddon, 2021; Blazeovich & Gill, 2006) depending on whether the crows use their own manufactured vs. a provided tool.

In summary, our study fills three important gaps in the existing data on New Caledonian crow laterality by examining: (i) a new population of wild free-living crows who are partly identified and (ii) performing a full range of spontaneous actions of their natural daily repertoire (iii) with the objects of their choice.

Methods

Species ecology

In 2019, a fieldwork trip totalling 61 days was led between October and December in a 50-acre private land consisting of lowland dry forest in La Foa, on the main island of Grande Terre, New Caledonia (north-western point: 21°43'51.3"S 165°52'35.2"E; south-eastern point: 21°43'56.0"S 165°52'52.1"E) on which the New Caledonian crow is endemic (Kacelnik, Chappell, Weir, & Kenward, 2006). This Corvid species typically builds up small mixed-aged family units in which offspring can stay up to two years post-fledging, i.e., until about 30 months of age (Holzhaider et al., 2011; Kenward et al., 2004). However, these family groups of three-to-four individuals are also part of larger groups of up to 50 individuals (as registered in Rutz, Ryder, & Fleischer, 2012a) that only temporarily encounter each other (Kenward et al., 2004) but make up genetically differentiated subpopulations (Abdelkrim, Hunt, Gray, & Gemmell, 2012; Rutz et al., 2012a). In our study, based on the largest number of individuals observed simultaneously during gatherings in which they made grouping calls, i.e., the emission at once of single and multiple calls by different individuals usually spanning several minutes (Kenward et al., 2004), we estimate the La Foa group to consist of 12 individuals. Reports by the local landowners independently confirmed that this crow population has remained stable at about a dozen individuals for the last 30 years. Although subjects were untagged, some of them could be individually identified *via* their physical peculiarities (injuries, damaged plumage, spiderweb stuck to head and/or body after foraging under log piles, body size), as New Caledonian crows present a slight sexual dimorphism in weight, but not in shape (Kenward et al., 2004). Juveniles were identified by pink mouth or throat coloration (Heinrich & Marzluff, 1992; Hunt, 2016), begging behaviours, and being fed by another bird (Holzhaider et al., 2011). Adults, on the other hand, present an all-black mouth coloration (Heinrich & Marzluff, 1992; Hunt, 2016) and/or were identified as such when seen feeding another bird (Holzhaider et al., 2011). We estimated age by the range of months in which breeding attempts were observed in New Caledonian crows (September to March) in an island-wide landbird survey from 1998 to 2011 (Barré et al., 2013). Thus, we estimated that the juveniles in our videos were between 7 and 23 months old.

Data collection

Video footage was obtained in the field using a set of automated and human-operated cameras (see below for details). Filming took place *ad libitum*, each time a crow approached an experimental setup made of three baited logs similar to those used in Holzhaider et al. (2010a, 2010b, 2011). The apparatus consisted of naturally fallen tree logs from the same forest, attached to wooden legs which held the logs horizontally at a height of 30–50 cm above the surface – either the ground or a wood pile. They were drilled with one or more 10-centimetre deep and 1–2-centimetre diameter vertical holes, following previous protocols (Hunt & Gray, 2004a; Hunt et al., 2007; Hunt, Corballis, & Gray, 2006; Rutz & St Clair, 2012). A pea-sized amount of prey-like food item (either ground beef or a piece of beef heart) or one actual prey item, here a live longhorn beetle larva (*Agrianome fairmairei*) obtained locally so as to retain the same prey that the crows forage for themselves at this location, was placed at the bottom of each hole (Bluff, Troschianko, Weir, Kacelnik, & Rutz, 2010b; Rutz et al., 2010; Sugawawa, Klump, St Clair, & Rutz, 2017). The crows could only access this food by manipulating elongated tools, here twigs or leaf-stems from four tree species which are locally abundant in this forest (*Albizia saman*, *Aleurites moluccana*, *Diospyros fasciculosa*, and *Syzygium cuminii*; Figure 1). The crows used these twigs or leaf-stems either unmodified, or modified (using its bill, a crow snaps the leaves off, bites off a length of the tool, and/or bends the tool (Hunt & Gray, 2004a)). These tools were sourced from the ground near the feeding logs, plucked fresh from a nearby tree, or crows arrived already transporting a tool.

The baited logs were placed at a location crows were known to regularly visit, and which was visible from a secluded single point where two



Figure 1. Example of right-sided tool-use. A juvenile uses a candlenut (*Aleurites moluccana*) leaf-stem tool to retrieve food from our baited log.

researchers sat in chairs. At times when crows were absent from the feeding area, one of the experimenters would walk around the forest to locate the birds and film them *ad libitum* while foraging freely. Filming was done using a Panasonic HC-VX989 4 K camcorder, a Sony XDCAM PXW-Z150 camcorder, a Sony α 7s II mirrorless digital camera, and a GoPro Hero4 action camera. In addition, video footage was obtained from automatic trail cameras (12 MP WildBlick 3.0c RL, p. 2019 Browning Strike Force Pro X, 2020 Browning Patriot, Bushnell Aggressor HD Red Glow, Bushnell Core Dual Sensor No Glow, Spypoint Force 11 MP D) at nine different locations around the forest where crows repeatedly foraged. Most of these devices also provided a measure of time, date and temperature for each clip taken; when it was not the case, these metadata were manually collected.

From our total library of video clips, we selected those which were filmed close enough for the crows' limb and body movements to be visible. We thus retained 02:13:75 h of video footage for this study, during 01:45:51 h of which wild, free-flying New Caledonian crows individually effectively appear.

Coding for laterality

Identifying behaviours of interest for the present study was a several step process. Indeed, due to the ongoing tendency of avian behavioural laterality research to collect data on only a few behaviours per study, and not to use a comprehensive ethogram (e.g., Baciadonna et al., 2021; Holzhaider et al., 2010a; Hunt & Gray, 2004b; Kenward et al., 2006), no exhaustive New Caledonian crow ethogram has been published as of the start of this study (January 2021). Therefore, we first established an ethogram from a literature review of works existing and in preparation on mammalian, reptilian, avian and Corvid behaviours (Simmons, 1964; Goodwin & Gillmor, 1986; Brown & Veltman, 1987; Ruby & Niblick, 1994; Taylor et al., 2010; Auersperg et al., 2011; Alfredsson, 2012; Miller, Schiestl, Whiten, Schwab, & Bugnyar, 2014; Klump, van der Wal, St Clair, & Rutz, 2015), refined with the help of field researchers' personal observations and videos. More specifically, only behaviours effectively observed by researchers in the wild and potentially being lateralized, i.e., that may display differential limb or side preference during their execution, were considered (Nettle, 2003). Vocalisations, albeit not thoroughly understood as of yet (Bluff, Kacelnik, & Rutz, 2010a), were here identified and named on a descriptive basis (Uomini, unpublished). Our working ethogram consisted finally of 47 behavioural items, 15 of which were vocalisations, which we grouped into 5 behavioural categories (see Supplement A). The grouping was inspired by literature (e.g., Greenberg, 1977; Schleidt, Yakalis, Donnelly, & McGarry, 1984; Stanton, Sullivan, & Fazio, 2015) and, following Miller (1988), was designed to remain uninterpretive in terms of motivation and, thus, easily adaptable to and/or comparable with other species. The

categorization process was functional in the sense that it was based on the observed outcome of the actions, while avoiding interpretations about the reason for the action unless these reasons or motivations are clearly known (for example, allopreening in birds is a documented affiliative behaviour (Radford & Du Plessis, 2006)).

Using video analysis software BORIS, version 7.9.24 (Friard & Gamba, 2016), laterality was coded according to the body side starting a behavioural bout, and from the bird's egocentric perspective (see Supplement A for details). A bout is understood as a behavioural sequence of identical actions, i.e., a succession of behavioural items whose lateralization could not be modified by the focal individual without interrupting the sequence – therefore, bouts mainly concern object manipulation and locomotion (Chapelain & Hogervorst, 2009; Martinho, Burns, von Bayern, & Kacelnik, 2014). Consequently, each data point encoded for our analysis represented the first event comprised within a behavioural bout. This unit was chosen over raw events as bouts ensure data point independence (McGrew & Marchant, 1997) and are most commonly used, thus facilitating interstudy comparisons (Harrison & Nystrom, 2008).

All statistical analyses were performed using R, version 4.0.4 (R Core Team, 2021).

Robustness and reliability in data collection

The descriptive robustness of the aforementioned ethogram, i.e., whether it allowed for both a consistent and cohesive identification of behaviours, was evaluated by calculating Cohen's (1960) kappa as part of an inter-rater reliability assessment performed on a randomly chosen set of 17 video clips independently coded by two scientists (Hallgren, 2012). Following the same procedure, using the package *irr*, version 0.84.1 (Gamer, Lemon, & Puspendra Singh, 2019) supported by the package *lpSolve*, version 5.6.15 (Berkeelaar, 2020), the coder's own reliability was assessed using 10% of the 66 video clips included in the present study that were independently coded a month apart (Hallgren, 2012). Each time, the obtained values were well over the 0.67 threshold of substantial to near perfect agreement between coders (Krippendorff, 1980; Landis & Koch, 1977). Moreover, we verified that the coding session (main vs. reliability coding session) did not significantly influence the quantity of behavioural bouts collected (mean duration of registered state events), *via* Fisher's permutation test for paired data with a stratification for individual identity as included in the package *coin*, version 1.4-1 (Hothorn, Hornik, van de Wiel, & Zeileis, 2006, 2008). Together, these results testify for a substantial consistency between both coders and coding sessions, thus vouching for the quality of the data exploitation (Landis & Koch, 1977).

Statistical modelling

Events in which laterality was not displayed (i.e., symmetrical behaviours) were excluded from further analysis. Therefore, if such an event occurred as part of a behavioural bout, it ended that bout. Associations between age class, behavioural type and the co-occurrence of a vocal event during the remaining bouts ($N=1127$; see Supplement A for a detailed account) were tested at both the populational and individual level using generalized linear mixed-effects models for binomial data (GLMMs) implemented by the *glmer* function of the *lme4* package, version 1.1-26 (Bates, Maechler, Bolker, & Walker, 2015). We ruled out any dependencies the dataset might have included by entering individual identity and video clip as nested random factors. They respectively accounted for repeated measurements and the same origin of some crows, as some individuals did appear across different clips characterized by varying surrounding environments, i.e., arboreal vs. terrestrial, clearing vs. dense foliage, alone vs. in presence of inter- and/or intraspecific individual(s). P -values for GLMMs were obtained using a linear regression model as defined by the *Anova* function of the *car* package, version 3.0-10 (Fox & Weisberg, 2019). Before beginning the analyses, all models had been submitted for diagnosis, with the coder checking that sample size was both large enough and not too imbalanced, as well as verifying the absence of multicollinearities by calculating variance inflation factors using the package *MuMIn*, version 1.43.17 (Barton, 2020). The latter values were always below the 2.5 threshold of notability (Faraway, 2006). The *MuMIn* package also provided the *r.squaredGLMM* function which allowed us to characterize covariate effects, and more specifically the proportion of explained variation by the fixed effects, by calculating a marginal *pseudoR*² (Nakagawa, Johnson, & Schielzeth, 2017). Additionally, the presence of intragroup differences was established *via* a two-tailed Z test ($\alpha=0.05$) performed by the *prop.test* function of the *stats* package (R Core Team, 2021).

Results

Populational level

Behavioural lateralization was significantly influenced by the type of behaviour expressed by the focal individuals (GLMM: *pseudoR*² = 0.479, $\chi^2_{27} = 51.289$, $P=0.003$). More specifically, when manipulating objects, including during tool use, New Caledonian crows presented a left-sided bias (two-tailed Z test: $\chi^2_1 = 53.318$, $P < 0.001$; Figure 2). On the other hand, the lateralization of behavioural bouts belonging to the (a) “activity & exploration”, (b) “locomotion” or (c) “maintenance” categories did not significantly differ from chance (two-tailed Z test: (a): $\chi^2_1 = 0.299$, $P = 0.585$; (b): $\chi^2_1 = 1.542$, $P = 0.214$; (c): $\chi^2_1 = 0.208$, $P = 0.649$).

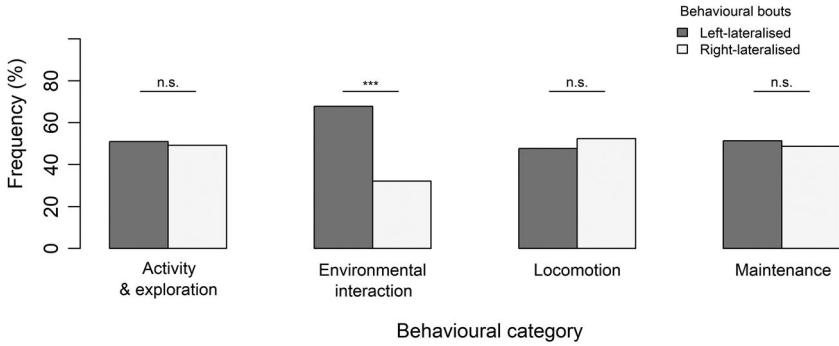


Figure 2. Percentage of side use by focal individuals according to the behavioural category of the bout expressed, i.e., “activity & exploration” ($N_{left} = 218$; $N_{right} = 210$), “environmental interaction” ($N_{left} = 143$; $N_{right} = 68$), “locomotion” ($N_{left} = 158$; $N_{right} = 174$), and “maintenance” ($N_{left} = 79$; $N_{right} = 75$). Asterisks indicate the significance level (***: $P < 0.001$) and *n.s.* that no significant differences have been found.

No significant effect of age class (i.e., juvenile or adult; GLMM: $\chi^2_2 = 0.349$, $P = 0.840$) was found despite significant intra-group differences emerging (Figure 3). Indeed, within the population, adult individuals appeared to express significantly more left- than right-lateralized behavioural bouts (two-tailed Z test: $\chi^2_1 = 8.113$, $P = 0.004$). Nonetheless, (a) juveniles as well as (b) crows whose age could not be identified expressed as many right- as left-lateralized bouts (two-tailed Z test: (a): $\chi^2_1 = 0.009$, $P = 0.923$; (b): $\chi^2_1 = 1.541$, $P = 0.214$).

The co-occurrence of vocalisation did not lead to any side bias (GLMM: $\chi^2_1 = 0.060$, $P = 0.807$) and no association between (a) age class and behaviour type or

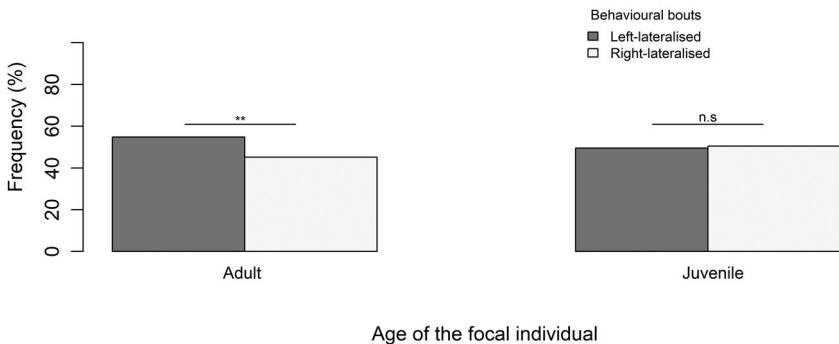


Figure 3. Percentage of side use by focal individuals according to their age class, i.e., adults ($N_{left} = 308$; $N_{right} = 260$), juveniles ($N_{left} = 107$; $N_{right} = 108$). Unidentifiable-aged crows displayed $N_{left} = 196$ left-lateralized bouts and $N_{right} = 179$ right-lateralized ones. Inter-groups comparisons did not reveal any significant differences. Asterisks indicate the significance level (**: $P < 0.01$) and *n.s.* that no significant differences have been found.

(b) behaviour type and the co-occurrence of vocalisation was revealed to significantly influence behavioural lateralization (GLMM: (a): $\chi^2_{33} = 22.640$, $P = 0.912$; (b): $\chi^2_9 = 4.658$, $P = 0.863$). The absence of a vocal effect of the interaction between the co-occurrence of a vocal event and age groups allowed us to pool the latter together (GLMM: $\chi^2_2 = 1.930$, $P = 0.381$). Further analyses at the populational level revealed that, if a significant left-sided behavioural bias was expressed, it was only in absence of a co-occurring vocalisation (two-tailed Z test: $\chi^2_1 = 5.496$, $P = 0.019$; vs. in presence: $\chi^2_1 = 1.655$, $P = 0.193$).

Individual level

Additional analyses were led on two recognizable individuals, i.e., an adult female hereafter named Tracy and her adult male partner referred to as Spike. These analyses highlighted that neither (a) the type of behavioural bout expressed, nor (b) the co-occurrence of vocalisation had any significant influence on their behavioural lateralization (GLMM: (a): $\chi^2_{19} = 24.534$, $P = 0.177$; (b): $\chi^2_2 = 0.760$, $P = 0.383$). Moreover, neither bird expressed a significant side bias (two-tailed Z test: Tracy: $\chi^2_1 = 0.182$, $P = 0.670$; Spike: $\chi^2_1 = 3.682$, $P = 0.055$). However, Spike's behavioural lateralization significantly differed from chance within two behavioural categories (Figure 4). Indeed, his (a) active and explorative behavioural bouts were characterized by a right-sided bias whereas during (b) object manipulation, including tool use, a left-sided bias emerged (two-tailed Z test: (a): $\chi^2_1 = 4.939$, $P = 0.026$; (b): $\chi^2_1 = 44.885$, $P < 0.001$). Both (c) locomotor and (d) maintenance-directed bouts did not display any significant side bias (two-tailed Z test: $\chi^2_1 = 0.621$, $P = 0.431$; $\chi^2_1 = 2.667$, $P = 0.103$). In contrast, Tracy's overall tendency not to express any

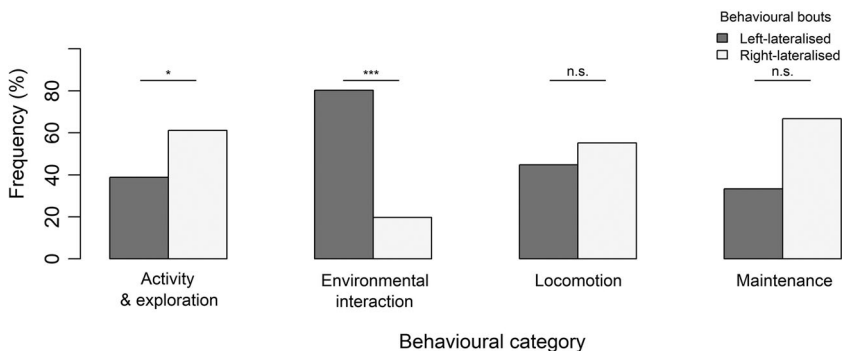


Figure 4. Percentage of side use by the adult New Caledonian crow male Spike according to the behavioural category of the bout expressed, i.e., “activity & exploration” ($N_{left} = 19$; $N_{right} = 30$), “environmental interaction” ($N_{left} = 49$; $N_{right} = 12$), “locomotion” ($N_{left} = 13$; $N_{right} = 16$), and “maintenance” ($N_{left} = 4$; $N_{right} = 8$). Asterisks indicate the significance level (***: $P < 0.001$; *: $P < 0.05$) and *n.s.* that no significant differences have been found.

significant side bias was found again in a more detailed categorical breakdown of her behavioural bouts (two-tailed Z test: (a): $\chi^2_1 = 0.286$, $P = 0.593$; (b): $\chi^2_1 = 0.500$, $P = 0.480$; (c): $\chi^2_1 = 0.857$, $P = 0.355$; (d): $\chi^2_1 = 0.286$, $P = 0.593$).

Discussion

The New Caledonian crow population of our site in La Foa is composed of a dozen individuals. The crows we filmed showed actions that were strongly lateralized when it came to tool behaviour and associated object manipulation, similarly to those of other studied groups of the same species (Table 1). More specifically, this left-sided bias was only found within this behavioural category, which has been described in non-human primates as the most strongly lateralized (see Uomini, 2009). In our case, this bias appeared to be driven by adults alone. Indeed, in contrast to adults, juveniles in our study seemed to fail to express any stable overall side preference. If confirmed, this finding would support our first hypothesis: laterality does develop during the New Caledonian crow's extended childhood – at least in regard to tool behaviour. This effect can be explained by young crows spending the first few years of their life in what can be seen as a “safe haven”, with adults even outside their family unit tolerating their proactive presence (Holzhaider, Hunt, & Gray, 2010b; Uomini et al., 2020). Fledglings are then not only able to observe experienced individuals make and use tools, but also pick up discarded twigs and sticks, try using them to obtain food, and, ultimately, resort to begging if they cannot meet their nutritional needs (Uomini et al., 2020). Adult proficiency is, on average, only reached around 10–12 months of age in this species (Holzhaider et al., 2010b; Hunt et al., 2012). This intergenerational interaction is likely crucial for New Caledonian crows to learn tool skills: captive juveniles who never observed tool-use demonstrations, albeit able to both craft and handle simple tools, ended up less skilled than their wild counterparts (Kenward et al., 2006).

Regarding our second hypothesis, i.e., the existence of a consistent side bias, given a certain behavioural category, in adult crows, we can neither support nor refute it. We did not find a consistent laterality in our adult population for any behavioural categories other than object manipulation, except in the unique case of crow male Spike who also showed a significant right-side bias in his “activity and exploration” behaviours. According to Ströckens, Güntürkün, and Ocklenburg (2013), non-human vertebrates show more variation than humans both across tasks and across individuals in terms of limb preferences. As Table 1 shows, there appears to be an overall left-side bias in New Caledonian crows as a species for object manipulation, which is reflected in our data. Regarding individual patterns, lateralization to the right or left is also consistent with previous findings in New Caledonian crows (Table 1). Likewise, it is consistent with the results on object manipulation with the feet in other birds

such as parrots (Godinho, Marinho, & Bezerra, 2020). This result would support the theory that skilled motor actions are key to the expression of laterality, as proposed by Corballis (1998, p. 1148). If the development of a motor skill serves to strengthen pre-existing lateral biases, then less-skilled actions (such as head turning or stepping) would not be expected to reveal laterality. To our knowledge, ours is the first study to consider laterality for a wide range of behaviours in New Caledonian crows. As stated by Baciadonna et al. (2021), it is crucial to distinguish behavioural contexts of laterality, as they found that laterality varied per task in Gyrfalcons (*Falco rusticolus*). Thus, it would be judicious to repeat this analysis on a wider range of individuals and behaviours, as our current data do not yet allow to establish whether adult crows maintain individual side biases within a given behavioural category.

Our third hypothesis, which aimed to explore a potential evolutionary link between behavioural lateralization in tool-making, brain laterality and the emergence of language, was not supported by our data. The co-occurrence of a vocal event appeared to play no role in the strength of a behaviour's lateralization. *A contrario*, the previously observed left-sided bias seemed to resurface only in *absence* of any vocalisation. We can attribute these results either to the preponderant number of adults building up our list of subjects, as juvenile birds of some species vocalize significantly more than adults (Favaro, Ozella, & Pessani, 2014), or to the overall scarcity of vocalisations co-occurring with what appears as a very limited set of lateralized actions (only 14.02% of lateralized bouts, 73.42% of which were *Scanning*). Either way, it is very much possible that our dataset is, in itself, biased and we would advise to replicate the experiment with both a more balanced division of participants and a matching number of co-occurring vocal events if we wish to come to any conclusive statements about the potential link between actions, vocalisation, and laterality in this species, as it has been suggested in others (Uomini, 2009).

Another key aspect of our results needs to be highlighted: they described an overall bias in a given direction, i.e., biases were found at the populational level, whereas previous studies of laterality in New Caledonian crow behaviours had exclusively testified for individual preferences (Rutledge & Hunt, 2004; Weir, Kenward, Chappell, & Kacelnik, 2004). Our results thus directly confirm previous findings of population-level lateralization on pandanus tool counterparts (Hunt, 2000b; Hunt, Corballis, & Gray, 2001, 2006). These studies reported that task complexity affected the direction and strength of laterality in pandanus counterparts (Hunt et al., 2006). When examining their video footage, Hunt et al. (2006) found that crows preferentially use head movements to the right to begin tool-making, thus reaffirming the key role of birds' left cerebral hemisphere in object manipulation (Vallortigara & Rogers, 2005). Our study, however, highlighted the existence of a *left-sided* bias within our population.

One explanation for this left-side bias could be related to postural control, where the foot supporting posture determines which foot is free for manipulation (Tommasi & Vallortigara, 1999). While New Caledonian crows never manipulate objects with their feet, they could still have postural biases, but our data did not reveal any such biases in their locomotor movements. Another explanation could be related to eye-use preference, as in Australian parrots, where preference has been linked to foot-use laterality (Brown & Magat, 2011a). The study of Martinho et al. (2014) hinted towards this idea, as 8 of the 13 crows had the same side eye preference as their tool-use side. However, New Caledonian crows appear to heavily use their binocular vision when using a tool (Troscianko, Von Bayern, Chapell, Rutz, & Martin, 2012)

Alternatively, the left-side bias could be related to right-hemisphere functions. The manufacture of twig tools, as was observed here, operates within a three-dimensional space whereas that of pandanus tools is fulfilled through a series of complex, and of importance here, two-dimensional cuts and rips (Hunt, 1996; Hunt & Gray, 2004a; Rutz & St Clair, 2012). Indeed, the plant material, if not left raw after selection to be used as a “straight stick probe” (Rutz et al., 2012a, 2012b), could then be snapped and eventually sculpted into a hook by crows (Hunt & Gray 2004a) or made into a curved shape as was specifically done by the La Foa crows (personal observations). In other words, the difference at stake may not be of task difficulty, but related to spatial cognition and recognition, a functional realm typically supported by the right hemisphere in the avian brain (Karenina & Giljov 2022; Vallortigara & Rogers 2005). The limits of such explanation are however reached when accounting for the indiscriminate categorization of both (potential) tools and food items as “objects” in the present study, thus rendering any power assessment impossible.

Similarly, we are currently unable to evaluate individual contributions to this directional tendency, thus not knowing whether the majority of our La Foa subjects actually presented such bias. Indeed, the number of observed crows in our study has artificially been raised to 81 due to an absence of individual identification: the crows in our study were untagged and most of them lacked any physical peculiarities that made them stand out, as this species tends to be phenotypically homogeneous (Kenward et al. 2004). However, two adult birds were both easily recognisable and regularly appeared on camera: Tracy, a female who bared an injured chest, and Spike, her partner, whose right-sided plumage was characterized by an upward bent feather shaft (see Supplementary Video).

Individual analyses for Tracy and Spike departed from overall trends in several ways: the type of behavioural bout expressed by either of these birds did not influence their behavioural lateralization, which did not display any side bias. In other words, the significant left-sided bias observed

at a populational level could not be attributed to either one of these crows. Moreover, Tracy and Spike themselves did present different individual tendencies, as a categorical breakdown of their actions revealed. In reality, Spike alone showed significantly lateralized bouts, with a strong left-sided bias emerging during object manipulation. More surprisingly, a weaker albeit still significant right-sided bias characterized his active and explorative behavioural bouts. Such results echo those found in other avian species (e.g., flamingos) where males displayed stronger lateral preferences within given behavioural categories (Regaiolli, Spiezio, Ottolini, Sandri, & Vallortigara, 2021b) – but we have yet to formally test for the existence of a similar trend within the New Caledonian crow, as these results may have just been mirroring the intriguing possibility that laterality could vary within individuals.

Another perspective we hope to see future studies explore is that laterality, even if not as strong as in tool behaviour, could (a) be found across several behavioural categories, (b) get reversed from one domain to the other, thus reflecting a complex form of cerebral lateralization and behavioural control (Rogers, 2021; Rogers et al. 2013), and (c) overall vary in strength, with task features acting as predictors (Hunt et al. 2006). Bird locomotion, for instance, has already been thoroughly discussed; results show not only strong individual footedness preferences in a species like the Japanese jungle crow (*Corvus macrorhynchos*) (Izawa et al. 2005), but also highlight the need to take into account any evolutionarily relevant environmental factors that may shape these trends (Brown & Magat 2011b; Davies & Green 1991; Güntürkün et al. 1988). To completely rule out the existence of similar locomotor preferences in the New Caledonian crow, our lack of significant results within this behavioural category should be sought once again across ecologically different populations, as we know that crow groups reside in a wide range of territories on New Caledonia (Abdelkrim et al. 2012). Furthermore, the lack of lateralization within our categories of “activity & exploration”, “locomotion”, and “maintenance” may have been due to the large spectrum of behaviours that each category covers, and a more detailed analysis per behaviour would be welcomed, if one could obtain sufficient data points. As the video clips used here were originally taken to study tool behaviour, they may have introduced an additional bias regarding the types of behaviours expressed in our data.

Overall, our study supports the tight connection between laterality and the evolution of tool-making skills that has previously been argued by others (Haslam et al. 2019; Hunt, 2000b, Hunt et al., 2001, 2006; Mosquera et al. 2012). What is yet uncertain is which came first. One major theory proposes that being a tool-using species is a driving factor in the evolution of laterality, as tool use causes the brain to become more strongly

lateralized (Cashmore et al. 2008; Hunt et al. 2001; MacNeilage, 2014; Martinho et al. 2014; Mosquera et al. 2012; Steele & Uomini, 2005; Uomini, 2009; Uomini & Ruck 2018; Weir et al. 2004). Alternatively, tool-making skills could emerge in already lateralized species thanks to hemispheric specialization in vertebrates, which enhances the simultaneous processing of two tasks that draw on different hemispheres (Rogers, 2017; Versace & Vallortigara 2015). The lateralization of tool-use and tool-making skills would then be further supported through the learning process and an individual's lifelong practice (Biro et al. 2006; Boesch, 1991; Sousa et al. 2009; Uomini et al. 2020).

Given the individual laterality profiles suggested by our findings, the present study advocates for comparison, already at the species level – i.e., between populations, between individuals and between those two units. In order to achieve such a goal, the focal subjects need to be individually identified, for instance *via* the trapping and marking of birds with a leg ring, a wing tag or even a harness-mounted transceiver tag (Caffrey, 2002a; Hunt, 2016; Rutz et al. 2012a, 2012b; St Clair et al. 2016), keeping in mind the extreme time and luck required to catch crows (Caffrey, 2002b; Hunt, personal communication 2016; Uomini, personal observation), or simply by focusing our work on already labelled populations if we wish to avoid the anxiety-inducing, fitness-reducing procedures involved in capture and marking (Burley et al. 1982; Pietz et al. 1993). Moreover, a long-term monitoring would allow researchers to both take a special interest for individual behaviour outside of tool use and manufacture and follow the evolution of behavioural trends across generations. For instance, it seems that social life plays a crucial role in a New Caledonian crow's life, as already suggested by the peculiar structure of a highly-tolerant family unit – however, in this domain like in many others, studies remain scarce (Holzhaider et al. 2011; Kenward et al. 2004). In other words, there is an urgent need to biologically and ecologically better understand the New Caledonian crow, whose tool manufacture skills, unlike any other non-human species, present hominid-like features (Hunt & Gray 2004a; Hunt & Uomini 2016), if we wish to ever pursue this promising comparative road and perhaps uncover new co-evolutionary paths leading to the emergence of language.

Acknowledgements

NU was supported by the Max Planck Society and a grant from the Templeton World Charity Foundation (<https://www.templetonworldcharity.org/>) #0271. The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of Templeton World Charity Foundation, Inc. We are grateful to Anne B. Clark and Andria Kroner for sharing their unpublished work on several crow species including Mariana crows. Thanks are due to Neil Smith for collecting half of the video data in the field. We thank two anonymous reviewers for their helpful comments.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by Templeton World Charity Foundation: [Grant Number 0271].

Author contributions

CM conceived the study. CM and NU designed the study. NU collected video data. CM coded video data and performed all analyses. CM wrote the paper and prepared the supplementary material, with inputs from NU. All authors approved the final manuscript.

Ethics statement

All research activities complied with national and international ethical standards for wild animal observation (The Ornithological Council (Fair et al. 2010), the Association for the Study of Animal Behaviour (2012), the American Psychological Association (2010), and the International Primatological Society (2014)), and were carried out under permits from the *Direction de l'Environnement*, Province Sud, New Caledonia and with ethical approval from the Max Planck Society's Ethics Council (2016 and #2018_34). The authors report there are no competing interests to declare.

Data availability statement

The R script and associated data can be downloaded from the following OSF repository: https://osf.io/7x8ur/?view_only=bd2b0663f7da495683e6c93beb04b595.

ORCID

Cyrielle Mack  <http://orcid.org/0000-0002-4190-1329>

Natalie Uomini  <http://orcid.org/0000-0002-9898-6415>

References

- Abdelkrim, J., Hunt, G. R., Gray, R. D., & Gemmell, N. J. (2012). Population genetic structure and colonisation history of the tool-using New Caledonian crow. *PLoS One*, 7(5), e36608. doi:10.1371/journal.pone.0036608
- Alfredsson, J. (2012). Innovative tool-modifications and tool selectivity in New Caledonian crows (*Corvus moneduloides*). Master thesis, Umeå University, Department of Psychology.

- Allen, L. L., Morrison, K. L., Scott, W. A., Shinn, S., Haltiner, A. M., & Doherty, M. J. (2018). Differences between stance and foot preference evident in osprey (*Pandion haliaetus*) fish holding during movement. *Brain and Behavior*, 8(11), 1–5. doi: 10.1002/brb3.1126
- American Psychological Association. (2010). Guidelines for Ethical Conduct in the Care and Use of Nonhuman Animals in Research. <http://www.apa.org/ethics/code/index.aspx> Last accessed 24 May 2021.
- Association for the Study of Animal Behaviour. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, 83, 301–309. doi:10.1016/j.anbehav.2011.10.031
- Auersperg, A. M., Von Bayern, A. M., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011). Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS One*, e20231, 6(6).
- Baciadonna, L., Zucca, P., & Samour, J. (2021). Laterality preferences at rest and predatory behaviour of the Gyrfalcon (*falco rusticolus*): An alpha predator of the sky. *Laterality*, 1–15. doi:10.1080/1357650x.2021.1958831
- Baragli, P., Scopa, C., Felici, M., & Reddon, A. R. (2021). Horses show individual level lateralisation when inspecting an unfamiliar and unexpected stimulus. *PLoS One*, 16(8), e0255688. doi:10.1371/journal.pone.0255688
- Barré, N., Tron, F., Chartendrault, V., Okahisa, Y., Sato, N. J., Legault, A., & Theuerkauf, J. (2013). Breeding seasons of landbirds in New Caledonia. *The Wilson Journal of Ornithology*, 125(2), 384–398. doi:10.1676/12-110.1
- Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn> Last accessed 24 May 2021.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. doi:10.18637/jss.v067.i01
- Beck, B. B. (1982). Chimpocentrism: Bias in cognitive ethology. *Journal of Human Evolution*, 11(1), 3–17. doi:10.1016/S0047-2484(82)80027-4
- Berkelaar, M. (2020). lpSolve: Interface to 'Lp_solve' v. 5.5 to Solve Linear/Integer Programs. R package version 5.6.15. <https://CRAN.R-project.org/package=lpSolve> Last accessed 24 May 2021.
- Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool Use by wild chimpanzees at bossou, Guinea: Case studies in Nut cracking and leaf folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 476–508). Tokyo: Springer-Verlag. doi:10.1007/4-431-30248-4_28.
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L. J., & Vallortigara, G. (1996). Right-pawedness in toads. *Nature*, 379, 408. doi:10.1038/379408a0
- Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioural brain lateralization in fishes, reptiles, and amphibians. *Neuroscience and Behavioral Reviews*, 22, 411–426. doi:10.1016/S0149-7634(97)00050-X
- Blazevich, A. J., & Gill, N. D. (2006). Reliability of unfamiliar, multijoint, uni- and bilateral strength tests: Effects of load and laterality. *The Journal of Strength & Conditioning Research*, 20(1), 226–230. Retrieved from https://journals.lww.com/nsca-jscr/Abstract/2006/02000/RELIABILITY_OF_UNFAMILIAR_MULTIJOINT_UNI_AND.37.aspx
- Bluff, L. A., Kacelnik, A., & Rutz, C. (2010a). Vocal culture in New Caledonian crows *Corvus moneduloides*. *Biological Journal of the Linnean Society*, 101(4), 767–776. doi:10.1111/j.1095-8312.2010.01527.x

- Bluff, L. A., Troscianko, J., Weir, A. A., Kacelnik, A., & Rutz, C. (2010b). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society B: Biological Sciences*, 277(1686), 1377–1385. doi:10.1098/rspb.2009.1953
- Boesch, C. (1991). Handedness in wild chimpanzees. *International Journal of Primatology*, 12(6), 541–558. doi:10.1007/bf02547669
- Brown, C., & Magat, M. (2011a). Cerebral lateralization determines hand preferences in Australian parrots. *Biology Letters*, 7(4), 496–498. doi:10.1098/rsbl.2010.1121
- Brown, C., & Magat, M. (2011b). The evolution of lateralized foot use in parrots: A phylogenetic approach. *Behavioral Ecology*, 22(6), 1201–1208. doi:10.1093/beheco/arr114
- Brown, E. D., & Veltman, C. J. (1987). Ethogram of the Australian magpie (*Gymnorhina tibicen*) in comparison to other Cracticidae and *Corvus* species. *Ethology*, 76(4), 309–333.
- Burley, N., Krantzberg, G., & Radman, P. (1982). Influence of colourbanding on the conspecific preferences of zebra finches. *Animal Behaviour*, 30, 444–455. doi:10.1016/S0003-3472(82)80055-9
- Caffrey, C. (2002a). Marking crows. *North American Bird Bander*, 26, 146–150.
- Caffrey, C. (2002b). Catching crows. *North American Bird Bander*, 26, 137–145.
- Cashmore, L., Uomini, N., & Chapelain, A. (2008). The evolution of handedness in humans and great apes: A review and current issues. *Journal of Anthropological Sciences*, 86(2008), 7–35. Retrieved from http://www.isita-org.com/jass/Contents/2008_vol86/03_Cashmore.pdf
- Chapelain, A., Pimbert, P., Aube, L., Perrocheau, O., Debunne, G., Bellido, A., & Blois-Heulin, C. (2015). Can population-level laterality stem from social pressures? Evidence from cheek kissing in humans. *PLoS One*, 10(8), e0124477. doi:10.1371/journal.pone.0124477
- Chapelain, A. S., & Hogervorst, E. (2009). Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behavioural Brain Research*, 196(1), 15–29. doi:10.1016/j.bbr.2008.07.012
- Cnotka, J., Güntürkün, O., Rehkämper, G., Gray, R. D., & Hunt, G. R. (2008). Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*). *Neuroscience Letters*, 433(3), 241–245. doi:10.1016/j.neulet.2008.01.026
- Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, 20(1), 37–46. doi:10.1177/001316446002000104
- Corballis, M. C. (1998). Evolution of language and laterality: A gradual descent? *Cahiers de Psychologie Cognitive/Current Psychology of Cognition*, 17(6), 1148–1155.
- Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton: Princeton University Press.
- Davies, M. N., & Green, P. R. (1991). Footedness in pigeons, or simply sleight of foot? *Animal Behaviour*, 42(2), 311–312. doi:10.1016/S0003-3472(05)80562-7
- Fair, J. M., Paul, E., Jones, J., Clark, A. B., Davie, C., & Kaiser, G. (2010). *Guidelines to the use of wild birds in research (3rd ed.)*. The Ornithological Council special publication. <http://naturalhistory.si.edu/BIRDNET/guide/index.html> Last accessed 24 May 2021.
- Fairlie, J., & Uomini, N. (2022 accepted). Tool use by New Caledonian crows can inform cognitive archaeology: A case study using observational action coding. In L. Overmann, F. Coolidge, & T. Wynn (Eds.), *Oxford Handbook of cognitive archaeology*. Oxford: Oxford University Press.
- Faraway, J. J. (2006). *Extending the linear model with R. Generalized linear, mixed effects and nonparametric regression models*. Boca Raton: Chapman & Hall.

- Favaro, L., Ozella, L., & Pessani, D. (2014). The vocal repertoire of the african penguin (*Spheniscus demersus*): structure and function of calls. *PloS one*, 9(7), e103460. doi:10.1371/journal.pone.0103460
- Fitch, W. T., & Braccini, S. N. (2013). Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Annals of the New York Academy of Sciences*, 1288(1), 70–85. doi:10.1111/nyas.12071
- Fox, J., & Weisberg, S. (2019). *An {R} companion to Applied regression* (3rd ed.). Thousand Oaks: Sage Publications.
- Frasnelli, E. (2013). Brain and behavioral lateralization in invertebrates. *Frontiers in Psychology*, 4, 00939. doi: 10.3389/fpsyg.2013.00939
- Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left–right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience & Biobehavioral Reviews*, 36(4), 1273–1291. doi:10.1016/j.neubiorev.2012.02.006
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. doi:10.1111/2041-210X.12584
- Gamer, M., Lemon, J., & Puspendra Singh, I. F. (2019). irr: Various Coefficients of Interrater Reliability and Agreement. R package version 0.84.1. <https://CRAN.R-project.org/package=irr> Last accessed 24 May 2021.
- Godinho, L., Marinho, Y., & Bezerra, B. (2020). Performance of blue-fronted Amazon parrots (*amazona aestiva*) when solving the pebbles-and-seeds and multi-access-box paradigms: Ex situ and in situ experiments. *Animal Cognition*, 23(3), 455–464. doi:10.1007/s10071-020-01347-6
- Goodwin, D., & Gillmor, R. (1986). *Crows of the World* (2nd ed.). Seattle: University of Washington Press.
- Greenberg, N. (1977). An ethogram of the blue spiny lizard, *sceloporus cyanogenys* (reptilia, lacertilia, iguanidae). *Journal of Herpetology*, 11(2), 177–195. doi:10.2307/1563139
- Güntürkün, O., Delius, J., & Kesch, S. (1988). Absence of footedness in domestic pigeons. *Animal Behaviour*, 36(2), 602–604. doi:10.1016/S0003-3472(88)80032-0
- Hallgren, K. A. (2012). Computing inter-rater reliability for observational data: An overview and tutorial. *Tutorials in Quantitative Methods for Psychology*, 8(1), 23–34. doi:10.20982/tqmp.08.1.p023
- Harrison, R. M., & Nystrom, P. (2008). Handedness in captive bonobos (*Pan paniscus*). *Folia Primatologica*, 79(5), 253–268. doi:10.1159/000113539
- Haslam, M., Fujii, J., Espinosa, S., Mayer, K., Ralls, K., Tinker, M. T., & Uomini, N. (2019). Wild sea otter mussel pounding leaves archaeological traces. *Scientific Reports*, 9(1), 1–11. doi:10.1038/s41598-019-39902-y
- Heinrich, B., & Marzluff, J. (1992). Age and mouth color in common ravens. *The Condor*, 94, 549–550. doi:10.2307/1369233
- Hellige, J. B. (1993). *Hemispheric asymmetry: What's right and What's left*. Cambridge: Harvard University Press.
- Herculano-Houzel, S. (2009). The human brain in numbers: a linearly scaled-up primate brain. *Frontiers in Human Neuroscience*, 3. doi:10.3389/neuro.09.031.2009
- Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010a). The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour*, 147(5–6), 553–586. doi:10.1163/000579510(12629536366284
- Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010b). Social learning in New Caledonian crows. *Learning & Behavior*, 38(3), 206–219. doi:10.3758/LB.38.3.206

- Holzhaider, J. C., Sibley, M. D., Taylor, A. H., Singh, P. J., Gray, R. D., & Hunt, G. R. (2011). The social structure of New Caledonian crows. *Animal Behaviour*, 81(1), 83–92. doi:10.1016/j.anbehav.2010.09.015
- Hopkins, W. D., & Cantero, M. (2003). From hand to mouth in the evolution of language: The influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science*, 6(1), 55–61. doi:10.1111/1467-7687.00254
- Hothorn, T., Hornik, K., van de Wiel, M. A., & Zeileis, A. (2006). A lego system for conditional inference. *The American Statistician*, 60(3), 257–263. doi:10.1198/000313006X118430
- Hothorn, T., Hornik, K., van de Wiel, M. A., & Zeileis, A. (2008). Implementing a class of permutation tests: The coin package. *Journal of Statistical Software*, 28(8), 1–23. doi:10.18637/jss.v028.i08
- Humle, T., & Matsuzawa, T. (2009). Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 71(1), 40–48. doi:10.1002/ajp.20616
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379(6562), 249–251. doi:10.1038/379249a0
- Hunt, G. R. (2000a). Tool use by the New Caledonian crow *Corvus moneduloides* to obtain cerambycidae from dead wood. *Emu-Austral Ornithology*, 100(2), 109–114. doi:10.1071/MU9852
- Hunt, G. R. (2000b). Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1441), 403–413. doi:10.1098/rspb.2000.1015
- Hunt, G. R. (2016). Social and spatial reintegration success of New Caledonian crows (*Corvus moneduloides*) released after aviary confinement. *The Wilson Journal of Ornithology*, 128(1), 168–173. doi:10.1676/1559-4491-128.1.168
- Hunt, G. R., Abdelkrim, J., Anderson, M. G., Holzhaider, J. C., Marshall, A. J., Gemmill, N. J., & Gray, R. D. (2007). Innovative pandanus-tool folding by New Caledonian crows. *Australian Journal of Zoology*, 55(5), 291–298.
- Hunt, G. R., Corballis, M. C., & Gray, R. D. (2001). Laterality in tool manufacture by crows. *Nature*, 414(6865), 707–707. doi:10.1038/414707a
- Hunt, G. R., Corballis, M. C., & Gray, R. D. (2006). Design complexity and strength of laterality are correlated in New Caledonian crows' pandanus tool manufacture. *Proceedings of the Royal Society B: Biological Sciences*, 273(1590), 1127–1133. doi:10.1098/rspb.2005.3429
- Hunt, G. R., & Gray, R. D. (2004a). The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271 (suppl_3), S88–S90. doi:10.1098/rsbl.2003.0085
- Hunt, G. R., & Gray, R. D. (2004b). Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 7(2), 114–120. doi:10.1007/s10071-003-0200-0
- Hunt, G. R., & Gray, R. D. (2006). Tool manufacture by New Caledonian crows: Chipping away at human uniqueness. *Acta Zoologica Sinica*, 52(Supp), 622–625.
- Hunt, G. R., Holzhaider, J. C., & Gray, R. D. (2012). Prolonged parental feeding in tool-using New Caledonian crows. *Ethology*, 118(5), 423–430. doi:10.1111/j.1439-0310.2012.02027.x
- Hunt, G. R., & Uomini, N. (2016). A complex adaptive system may be essential for cumulative modifications in tool design. *Japanese Journal of Animal Psychology*, 66(2), 141–159. doi:10.2502/janip.66.2.2

- International Primatological Society. (2014). Code of best practices for field primatology. <http://www.internationalprimatologicalsociety.org/policy.cfm> Last accessed 24 May 2021.
- Izawa, E. I., Kusayama, T., & Watanabe, S. (2005). Foot-use laterality in the Japanese jungle crow (*Corvus macrorhynchos*). *Behavioural Processes*, 69(3), 357–362. doi:10.1016/j.beproc.2005.02.001
- Jacobs, I., von Bayern, A. M., & Osvath, M. (2021). Tools and food on heat lamps: Pyrocognitive sparks in New Caledonian crows? *Behaviour*, 1(aop), 1–12. doi:10.1163/1568539X-bja10138
- Kacelnik, A., Chappell, J., Weir, A. A. S., & Kenward, B. (2006). Cognitive adaptations for tool-related behaviour in New Caledonian crows. In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 515–528). Oxford: Oxford University Press.
- Kaplan, G., & Rogers, L. J. (2021). Brain size associated with foot preferences in Australian parrots. *Symmetry*, 13(5), 867. doi:10.3390/sym13050867
- Karenina, K., & Giljov, A. (2022). Lateralization in feeding is food type specific and impacts feeding success in wild birds. *Ecology and Evolution*, 12(2), e8598. doi:10.1002/ece3.8598
- Kenward, B., Rutz, C., Weir, A. A., Chappell, J., & Kacelnik, A. (2004). Morphology and sexual dimorphism of the New Caledonian crow *Corvus moneduloides*, with notes on its behaviour and ecology. *Ibis*, 146(4), 652–660. doi:10.1111/j.1474-919x.2004.00299.x
- Kenward, B., Rutz, C., Weir, A. A., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour*, 72(6), 1329–1343. doi:10.1016/j.anbehav.2006.04.007
- Klump, B., van der Wal, J. E., St Clair, J. J., & Rutz, C. (2015). Context-dependent ‘safe-keeping’ of foraging tools in New Caledonian crows. *Proceedings of the Royal Society B: Biological Sciences*, 282(1808), 20150278.
- Krippendorff, K. (1980). *Content analysis: An introduction to its methodology*. Beverly Hills: Sage Publications.
- Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, 33(1), 159–174. doi:10.2307/2529310
- MacNeilage, P. F. (2013). Vertebrate whole body-action-asymmetries and the evolution of right handedness: A comparison between humans and marine mammals. *Developmental Psychobiology*, 55(6), 577–587. doi:10.1002/dev.21114
- MacNeilage, P. F. (2014). Evolution of the strongest vertebrate rightward action asymmetries: Marine mammal sidedness and human handedness. *Psychological Bulletin*, 140(2), 587–609. doi:10.1037/a0034298
- Marchant, L. F. (2018). Handedness. In W. Trevathan, M. Cartmill, D. Dufour, C. Larsen, D. O’Rourke, K. Rosenberg, & K. Strier (Eds.), *The International encyclopedia of Biological anthropology*. Hoboken: John Wiley & Sons.
- Martinho IIIA., Burns, Z. T., von Bayern, A. M., & Kacelnik, A. (2014). Monocular tool control, eye dominance, and laterality in New Caledonian crows. *Current Biology*, 24(24), 2930–2934. doi:10.1016/j.cub.2014.10.035
- McGrew, W. C. (2013). Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120422. doi:10.1098/rstb.2012.0422
- McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *American Journal of Physical Anthropology: The Official Publication of the American*

- Association of Physical Anthropologists*, 104(S25), 201–232. doi:[10.1002/\(SICI\)1096-8644\(1997\)25+<201::AID-AJPA8>3.0.CO;2-6](https://doi.org/10.1002/(SICI)1096-8644(1997)25+<201::AID-AJPA8>3.0.CO;2-6)
- Meguerditchian, A., Cochet, H., & Vauclair, J. (2011). From gesture to language: Ontogenetic and phylogenetic perspectives on gestural communication and its cerebral lateralization. In A. Vilain, J.-L. Schwartz, C. Abry, & J. Vauclair (Eds.), *Advances in interaction studies: Vol. 1. Primate communication and human language: Vocalisation, gestures, imitation and deixis in humans and non-humans* (pp. 91–119). Amsterdam: John Benjamins Publishing Company.
- Miletto Petrazzini, M. E., Sovrano, V. A., Vallortigara, G., & Messina, A. (2020). Brain and behavioral asymmetry: A lesson from fish. *Frontiers in Neuroanatomy*, 14, 11. doi:[10.3389/fnana.2020.00011](https://doi.org/10.3389/fnana.2020.00011)
- Miller, E. H. (1988). Description of bird behavior for comparative purposes. In R. F. Johnston (Ed.), *Current ornithology* (pp. 347–394). Boston: Springer. doi:[10.1007/978-1-4615-6787-5_9](https://doi.org/10.1007/978-1-4615-6787-5_9)
- Miller, R., Schiestl, M., Whiten, A., Schwab, C., & Bugnyar, T. (2014). Tolerance and social facilitation in the foraging behaviour of free-ranging crows (*Corvus corone corone*; *C. c. cornix*). *Ethology*, 120(12), 1248–1255.
- Mosquera, M., Geribàs, N., Bargalló, A., Llorente, M., & Riba, D. (2012). Complex tasks force hand laterality and technological behaviour in naturalistically housed chimpanzees: Inferences in hominin evolution. *The Scientific World Journal*, 2012, 514809. doi:[10.1100/2012/514809](https://doi.org/10.1100/2012/514809)
- Nakagawa, S., Johnson, P. C., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14(134), 20170213. doi:[10.1098/rsif.2017.0213](https://doi.org/10.1098/rsif.2017.0213)
- Nettle, D. (2003). Hand laterality and cognitive ability: A multiple regression approach. *Brain and Cognition*, 52(3), 390–398. doi:[10.1016/S0278-2626\(03\)00187-8](https://doi.org/10.1016/S0278-2626(03)00187-8)
- Osvath, M., Kabadayi, C., & Jacobs, I. (2014). Independent evolution of similar complex cognitive skills: the importance of embodied degrees of freedom. *Animal Behavior and Cognition*, 1(3), 249–264. doi:[10.12966/abc.08.03.2014](https://doi.org/10.12966/abc.08.03.2014).
- Pereira, M. E., & Fairbanks, L. A. (1993). *Juvenile primates: Life history, development, and behavior*. Chicago: University of Chicago Press.
- Pietz, P. J., Krapu, G. L., Greenwood, R. J., & Lokemoen, J. T. (1993). Effects of harness transmitters on behavior and reproduction of wild mallards. *The Journal of Wildlife Management*, 57, 696–703. doi:[10.2307/3809068](https://doi.org/10.2307/3809068)
- Prieur, J., Lemasson, A., Barbu, S., & Blois-Heulin, C. (2019). History, development and current advances concerning the evolutionary roots of human right-handedness and language: Brain lateralisation and manual laterality in non-human primates. *Ethology*, 125(1), 1–28. doi:[10.1111/eth.12827](https://doi.org/10.1111/eth.12827)
- Prieur, J., Pika, S., Barbu, S., & Blois-Heulin, C. (2018). A multifactorial investigation of captive gorillas' intraspecific gestural laterality. *Laterality: Asymmetries of Body, Brain and Cognition*, 23(5), 538–575. doi:[10.1080/1357650X.2017.1410167](https://doi.org/10.1080/1357650X.2017.1410167)
- Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology*, 17(6), R199–R201. doi:[10.1016/j.cub.2007.02.008](https://doi.org/10.1016/j.cub.2007.02.008)
- Radford, A. N., & Du Plessis, M. A. (2006). Dual function of allopreening in the cooperatively breeding green woodhoopoe, *phoeniculus purpureus*. *Behavioral Ecology and Sociobiology*, 61(2), 221–230. doi:[10.1007/s00265-006-0253-6](https://doi.org/10.1007/s00265-006-0253-6)

- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/> Last accessed 24 May 2021.
- Regaiolli, B., Bolcato, S., Ottolini, G., Vallortigara, G., Pievani, D., & Spiezio, C. (2021a). Preliminary investigation of foot preference for a string-pulling task in zoo macaws. *Applied Animal Behaviour Science*, 238, 105307. doi:10.1016/j.applanim.2021.105307
- Regaiolli, B., Spiezio, C., Ottolini, G., Sandri, C., & Vallortigara, G. (2021b). Behavioural Laterality in two species of flamingos: Greater flamingos and Chilean flamingos. *Laterality*, 26(1-2), 34–54. doi:10.1080/1357650x.2020.1781877
- Rodgers, R. M., & Cain, K. E. (2019). No evidence for side preference or handedness in a New Zealand rail species with habitual foot-usage, the pukeko. *Behavioural Processes*, 167, 103910. doi:10.1016/j.beproc.2019.103910
- Rogers, L. J. (1980). Lateralisation in the avian brain. *Bird Behavior*, 2(1), 1–12. doi:10.3727/015613880791573835
- Rogers, L. J. (2017). A matter of degree: Strength of brain asymmetry and behaviour. *Symmetry*, 9, 57.
- Rogers, L. J. (2021). Brain lateralization and cognitive capacity. *Animals*, 11(7), 1996. doi:10.3390/ani11071996
- Rogers, L. J., & Andrew, R. (2002). *Comparative vertebrate lateralization*. Cambridge: Cambridge University Press.
- Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains: The biology and behaviour of brain asymmetries*. Cambridge: Cambridge University Press.
- Ruby, D. E., & Niblick, H. A. (1994). A behavioral inventory of the desert tortoise: development of an ethogram. *Herpetological Monographs*, 8, 88–102.
- Ruck, L., & Uomini, N. (2021). Artefact, praxis, tool and symbol. In A. Lock, & N. Gontier (Eds.), *Oxford Handbook of symbolic evolution* (pp. 1–38). New York: Oxford University Press. doi:10.1093/oxfordhb/9780198813781.013.19
- Rutledge, R., & Hunt, G. R. (2004). Lateralized tool use in wild New Caledonian crows. *Animal Behaviour*, 67(2), 327–332. doi:10.1016/j.anbehav.2003.07.002
- Rutz, C., Bluff, L. A., Reed, N., Troscianko, J., Newton, J., Inger, R., ... Bearhop, S. (2010). The ecological significance of tool use in New Caledonian crows. *Science*, 329(5998), 1523–1526. doi:10.1126/science.1192053
- Rutz, C., Burns, Z. T., James, R., Ismar, S. M., Burt, J., Otis, B., ... St Clair, J. J. (2012b). Automated mapping of social networks in wild birds. *Current Biology*, 22(17), R669–R671. doi:10.1016/j.cub.2012.06.037
- Rutz, C., Ryder, T. B., & Fleischer, R. C. (2012a). Restricted gene flow and fine-scale population structuring in tool using New Caledonian crows. *Naturwissenschaften*, 99(4), 313–320. doi:10.1007/s00114-012-0904-6
- Rutz, C., & St Clair, J. J. (2012). The evolutionary origins and ecological context of tool use in New Caledonian crows. *Behavioural Processes*, 89(2), 153–165. doi:10.1016/j.beproc.2011.11.005
- Schleidt, W. M., Yakalis, G., Donnelly, M., & McGarry, J. (1984). A proposal for a standard ethogram, exemplified by an ethogram of the bluebreasted quail (*coturnix chinensis*). *Zeitschrift für Tierpsychologie*, 64(3–4), 193–220. doi:10.1111/j.1439-0310.1984.tb00360.x
- Simmons, K. E. L. (1964). Feather maintenance. In A. L. Landsborough Thomson (Ed.), *New dictionary of birds* (pp. 278–286). London: Nelson.
- Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): acquisition patterns and handedness. *Animal Cognition*, 12(S1), 115–125. doi:10.1007/s10071-009-0278-0

- Stanton, L. A., Sullivan, M. S., & Fazio, J. M. (2015). A standardized ethogram for the felidae: A tool for behavioral researchers. *Applied Animal Behaviour Science*, 173, 3–16. doi:10.1016/j.applanim.2015.04.001
- St Clair, J. J., Klump, B. C., van der Wal, J. E., Sugawara, S., & Rutz, C. (2016). Strong between-site variation in New Caledonian crows' use of hook-tool-making materials. *Biological Journal of the Linnean Society*, 118(2), 226–232. doi:10.1111/bij.12757
- St Clair, J. J., & Rutz, C. (2013). New Caledonian crows attend to multiple functional properties of complex tools. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120415. doi:10.1098/rstb.2012.0415
- Steele, J., & Uomini, N. (2005). Humans, tools and handedness. In V. Roux & B. Bril (Eds.), *Stone knapping: The necessary conditions for a uniquely hominid behaviour* (pp. 217–239). Cambridge: McDonald Institute for Archaeological Research.
- Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in non-human vertebrates. Laterality: Asymmetries of body. *Brain and Cognition*, 18(5), 536–575. doi:10.1080/1357650X.2012.723008
- Sugawara, S., Klump, B. C., St Clair, J. J., & Rutz, C. (2017). Causes and consequences of tool shape variation in New Caledonian crows. *Current Biology*, 27(24), 3885–3890. doi:10.1016/j.cub.2017.11.028
- Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R., & Gray, R. D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PLoS One*, 5(2).
- Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution*, 2(2), 175–183. doi:10.1007/BF02436405
- Tommasi, L., & Vallortigara, G. (1999). Footedness in binocular and monocular chicks. *Laterality*, 4, 89–95. doi:10.1080/713754325
- Trosciano, J., Von Bayern, A. M., Chappell, J., Rutz, C., & Martin, G. R. (2012). Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. *Nature Communications*, 3(1), 1–7. doi:10.1038/ncomms2111
- Uomini, N., Fairlie, J., Gray, R. D., & Griesser, M. (2020). Extended parenting and the evolution of cognition. *Philosophical Transactions of the Royal Society B*, 375(1803), 20190495. doi:10.1098/rstb.2019.0495
- Uomini, N. T. (2009). The prehistory of handedness: Archaeological data and comparative ethology. *Journal of Human Evolution*, 57(4), 411–419. doi:10.1016/j.jhev.2009.02.012
- Uomini, N. T., & Meyer, G. F. (2013). Shared brain lateralization patterns in language and acheulean stone tool production: A functional transcranial Doppler ultrasound study. *PLoS One*, 8(8), e72693. doi:10.1371/journal.pone.0072693
- Uomini, N. T., & Ruck, L. (2018). Manual laterality and cognition through evolution: An archeological perspective. *Progress in Brain Research*, 238, 295–323. doi:10.1016/bs.pbr.2018.06.015
- Vallortigara, G., & Rogers, L. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, 28(4), 575–589. doi:10.1017/S0140525X05000105
- Vallortigara, G., & Versace, E. (2017). Laterality at the neural, cognitive, and behavioral levels. In J. Call (Ed.), *APA Handbook of comparative psychology: Vol. 1. Basic concepts, methods, neural substrate, and behavior* (pp. 557–577). Washington D.C.: American Psychological Association.
- Ventolini, N., Ferrero, E. A., Sponza, S., Della Chiesa, A., Zucca, P., & Vallortigara, G. (2005). Laterality in the wild: Preferential hemifield use during predatory and

- sexual behaviour in the black-winged stilt. *Animal Behaviour*, 69(5), 1077–1084. doi:[10.1016/j.anbehav.2004.09.003](https://doi.org/10.1016/j.anbehav.2004.09.003)
- Versace, E., & Vallortigara, G. (2015). Forelimb preferences in human beings and other species: Multiple models for testing hypotheses on lateralization. *Frontiers in Psychology*, 6, 233. doi:[10.3389/fpsyg.2015.00233](https://doi.org/10.3389/fpsyg.2015.00233)
- Weir, A. A., Kenward, B., Chappell, J., & Kacelnik, A. (2004). Lateralization of tool use in New Caledonian crows (*Corvus moneduloides*). *Proceedings of the Royal Society of London Series B: Biological Sciences*, 271(suppl_5), S344–S346. doi:[10.1098/rsbl.2004.0183](https://doi.org/10.1098/rsbl.2004.0183)
- Ying, J. (2019). *Evidence for active control of tongue lateralisation in Australian English// and its acoustic consequences* [Doctoral dissertation]. Western Sydney University, Penrith.