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Extraordinary large brains in tool-using New Caledonian crows (*Corvus moneduloides*)

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Abstract

A general correlation exists between brain weight and higher cognitive ability in birds and mammals. In birds this relationship is especially evident in corvids. These animals are well-known for their flexible behavior and problem-solving abilities, and have relatively large brains associated with a pallial enlargement. At the behavioral level, New Caledonian crows stand out amongst corvids because of their impressive object manipulation skills both in the wild and in the laboratory. However, nothing is known about the relative size of their brains. Here we show that NC crows have highly encephalised brains relative to most other birds that have been studied. We compared the relative brain size of five NC crows with combined data for four passerine species (7 European carrion crows, 2 European magpies, 3 European jays and 4 domestic sparrows) and found that NC crows had significantly larger brains. A comparison only with the seven carrion crows also revealed significantly larger brains for NC crows. When compared with brain data for 140 avian species from the literature, the NC crow had one of the highest degrees of encephalisation, exceeding that of the 7 other Corvidae in the data set.

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Avian species belonging to the order Passeriformes have relatively large brains in comparison to the other birds [38]. This is especially true for the Corvidae family. It has been suggested that the encephalisation in Corvidae is related to their flexible behavior and considerable learning abilities [4,24,43,41,49]. *Corvus* species, in particular, are highly innovative (for review see Ref. [34] and Table 1 in Ref. [32]), can manufacture tools (*Corvus moneduloides* [20]), spontaneously solve novel problems (*Corvus corax* [18,19]; *C. moneduloides* [55]), use tactical deception (*C. corax* [6]) and can learn from conspecifics (*C. corax* [13]). In fact, there is increasing evidence that they independently evolved brains and associated cognitive abilities similar to those of primates [12,39]. The New Caledonian crow (NC crow hereafter, *C. moneduloides*, Fig. 1) stands out amongst corvids because of its impressive tool manufacturing skills in the wild [20–23]. NC crows have also exhibited considerable

problem-solving skills in the laboratory comparable to those of nonhuman primates [55–57].

A large number of studies show that higher cognitive abilities correlate with larger relative brain size in both mammals [2,16,51] and birds [24,32,34,37,38,41]. To see if this was the case with NC crows, we first compared the relative brain weight of the NC crow with that of four other Passeriformes (European carrion crow *Corvus c. corone*, European magpie *Pica pica*, European jay *Garrulus glandarius* and domestic sparrow *Passer domesticus*) using the same histological procedure (individual body weight and brain weight of perfused birds). As data for comparably treated birds are lacking, we also compared our NC crow brain data with fresh brain weights for a wide range of avian species using the largest set of data available [38].

Our study material consisted of the perfused brains of five NC crows, seven European carrion crows, two European magpies, three European jays and four domestic sparrows. All the birds were captured in their original habitat and weighed immediately after catching to determine body weights. The five NC crows were kept in an outdoor aviary for one week before being

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Fig. 1. New Caledonian crow holding a leaf-stem tool.

euthanized. The crows were provided with food twice daily and permanent, clean water while in the aviary.

All the 21 birds above were euthanized with an overdose of pentobarbiturate then weighed again. After cardiac arrest was confirmed they were perfused with physiological saline solution to wash out the blood, followed by Bodian's fluid to fix the brain [46]. The brains were removed immediately following the perfusion process to ensure that they were not significantly different from fresh brain weights [50]. Thus, a correction for shrinkage due to fixation was not necessary.

Brain weight scales allometrically with body weight [7,48,53], therefore allometric methods were used. The relationship between brain and body weight is represented best by the allometric formula: $\log y = \log b + a \log x$ where y represents the brain weight, b the intercept of the allometric regression with the abscissa, x the body weight and a the slope of the regression [48].

We compared the brain weight of NC crows to that of other birds by carrying out three regression analyses. Ideally these analyses would be conducted taking into account phylogenetic relationships [17]. Unfortunately, no character-based phylogeny has been published for *Corvus* and thus no phylogenetic corrections are possible. The first regression used material from our collection, which consisted of 21 brains from 5 passerine species. Portmann [38] provides the largest published set of fresh brain and body weights, containing data for 140 individual species (given as species means without error statistics). Thus, we also combined our brain data for the NC crow with those of Portmann's to see how brain size of the NC crow compared to birds in general. We carried out the remaining two regressions using this data set. The first of these two regressions included

all of Portmann's 140 species and our NC crow data, and the second included only Corvidae species. Portmann's data set included seven Corvidae species [47]: the common raven (*C. corax*), the European carrion crow (*Corvus c. corone*), the rook (*Corvus frugilegus*), the European magpie (*P. pica*), the jackdaw (*Corvus monedula*), the red billed chough (*Pyrrhocorax pyrrhocorax*) and the European jay (*Garrulus glandarius*).

To analyze the differences in relative brain size between the 5 New Caledonian crows and the 16 other perfused passerines (from our own collection, see above), we calculated allometric encephalisation indices (E). To calculate the indices we divided the actual brain size of an individual by its predicted brain size obtained from the regression [50]. All points on the regression line represent an E of 1.0, so an E of 2.0 would mean that a brain was twice as heavy as the predicted weight based on the data. We used the t -test to compare encephalisation indices.

To detect outliers in the two regressions using Portmann's [38] data we examined the studentized residuals. Studentized residuals are distributed as a t distribution with $n - 3$ degrees of freedom for simple regression [3]. Therefore, we can approximately determine if an individual residual is statistically significant or not. In other words, we can test if the corresponding observation conforms to the regression model that describes the other observations.

The five NC crows had a mean body weight of 277.25 ± 29.87 g (mean \pm S.D.) and a mean perfused brain weight of 7.56 ± 0.77 g. The mean encephalisation index (1.103 ± 0.158) for the 5 NC crows was significantly greater than the mean for the 16 other passerines (0.974 ± 0.072 ; $t = -2.603$, d.f. = 19, $p = 0.017$, Figs. 2 and 3). The mean encephalisation index for the NC crows was also significantly greater than that for the seven European carrion crows (0.939 ± 0.047 ; $t = 2.641$, d.f. = 10, $p = 0.025$).

When data for the NC crow was plotted with Portmann's 140 species (Fig. 4), 9 species had studentized residuals larger than $t = 1.656$ (the 1-tailed 0.05 significance level for a positive studentized residual in the regression; d.f. = 138). The nine species consisted of a woodpecker (Piciformes), five parrots (Psittaci-

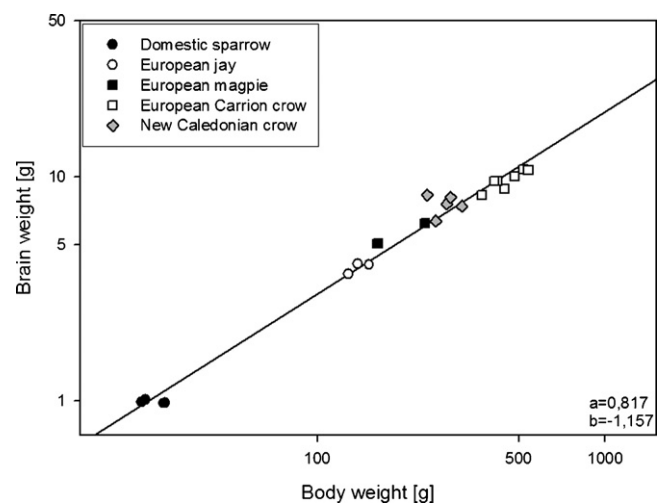


Fig. 2. Double logarithmic plot of brain weight vs. body weight for 21 individuals from 5 passerine species.

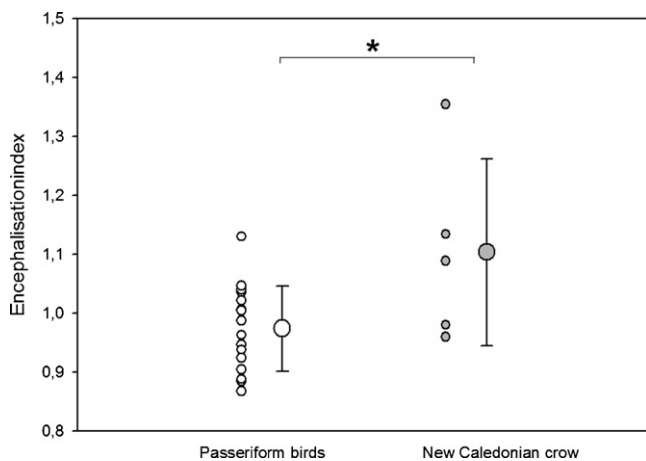


Fig. 3. Encephalisation indices for 16 individuals from 4 passerine species (European carrion crow, European magpie, European jay, domestic sparrow) compared to the indices for 5 NC crows. Individual data with mean and standard deviation are given. * $p = 0.017$. The error bars are offset from the data points for clarity.

formes), an owl (Strigiformes) and two Corvidae (the NC crow and the common raven). The NC crow had the fourth highest relative brain weight (Fig. 4). Only two Psittaciformes species (the blue and yellow macaw, *Ara arana*, and the red and green macaw, *Ara chloroptera*) and the black woodpecker (*Dryocopus martius*) had a larger studentized residual (t_s : NC crows = 2.064; *A. arana* = 2.728; *A. chloroptera* = 2.673; *D. martius* = 2.077). When data for the NC crow were plotted with those for the seven other Corvidae in Portmann's data set, the NC crow was a significant outlier; it was the only species with a t_s -value (2.164) higher than $t = 2.015$ (the 1-tailed 0.05 significance level for a positive studentized residual in the regression; d.f. = 5). These results suggest that the degree of encephalisation in the NC crow is inconsistent with that observed in birds generally and in its close relatives in particular.

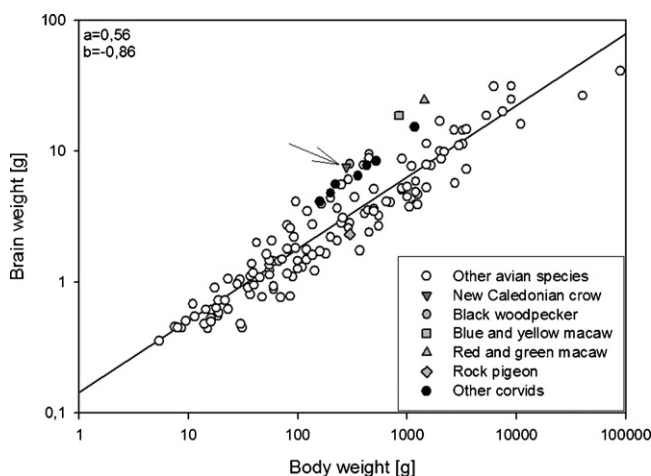


Fig. 4. Double logarithmic plot of brain weight vs. body weight for 141 avian species. Data for the NC crow are the authors' and those for all other species are taken from Portmann (1947). One symbol indicates one species. The arrow indicates the symbol for the NC crow. Given that pigeons are commonly used in behavioral and neuroscience studies, the position of the rock pigeon (*Columba livia*) is also shown.

The present study reveals that the brains of NC crows are probably relatively larger than those of other birds, except for a small number of non-passerine species. Therefore, NC crows' exceptional skills are associated with one of the highest encephalisation values in avian species studied so far. This is consistent with studies that show a positive correlation between brain (component) size and brain (component) function (e.g., Refs. [4,24,44,40,54]). A large number of findings using dozen of species make it likely that ecoethological adaptations and higher cognitive abilities correlate with larger brain size in both mammals [2,16,51] and birds [24,33,37,38,43].

Early on in comparative neuroanatomy, birds were considered to be poorly encephalised and only capable of instinctive behavior [11]. This was mostly because they were thought to lack a cortex but have a hypertrophied striatal area [1]—an opinion that was also reflected in the older terminology of the avian brain [31,35]. It is now generally accepted that most of the avian telencephalon consists of a pallium that is structurally different from, but homologous to, that of mammals [14,29,39]. This paradigm shift also resulted in a new nomenclature of the avian forebrain [28,45].

Brain size of a species (or an individual) is only relevant within a comparative framework. Brain and body weights of newly captured wild animals are ideal, but these data are rare. Portmann [37,38] published a large contingent of brain/body-weight data that covered 140 avian species. Ebinger and collaborators have published such data on rock doves, wild mallards and wild turkeys [8–10] and Rehkämper et al. [43] and Boire and Baron [5] on several other orders of birds (e.g., Galliformes, Passeriformes). Iwaniuk and collaborators have also published avian brain and body-weight data for a large number of species and individuals [25–27]. Most of the brain data are based on endocranial volumes. These data allow a detailed comparison across species and provide new insights into the evolution of the avian brain. However, endocranial volumes and fresh brain weights are not directly comparable. Therefore, we used Portmann's and Rehkämper et al.'s fresh brain/body-weight data to compare the brain weight of NC crows with that for a wide range of other avian species.

Large brains can result from a mosaic-like pattern of selective relative growth of brain components [26,42]. In non-passerines like woodpeckers, total brain size is disproportionally increased by a progressive development of the cerebellum [54]. This is quite different from passerines and (non-passerine) parrots, where encephalisation has largely occurred by an increase of the pallium. Parrots are also capable of impressive cognitive abilities and complex social interactions [36], and both parrots and corvids possess much larger nidopallium and mesopallium proportions than other birds [24,52,43].

Both the nido- and the mesopallium of birds are associative forebrain areas [30,39] that are involved in cognitive functions like flexibility, working memory, and context integration [14,15]. The ability of NC crows to solve complex novel problems demonstrates considerable behavioral flexibility [55–57]. Thus, their impressive skills would seem to require cognitive abilities that are known to be processed within the avian mesopallium and nidopallium. Enlargement of these pallial

components and therefore, concomitantly, of total brain weight is a possible explanation for the high degree of encephalisation that we found in NC crows.

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