Brains, tools, innovation and biogeography in crows and ravens

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Abstract

Background: Crows and ravens (Passeriformes: Corvus) are large-brained birds with enhanced cognitive abilities relative to other birds. They are among the few non-hominid organisms on Earth to be considered intelligent and well-known examples exist of several crow species having evolved innovative strategies and even use of tools in their search for food. The 40 Corvus species have also been successful dispersers and are distributed on most continents and in remote archipelagos.

Results: This study presents the first molecular phylogeny including all species and a number of subspecies within the genus Corvus. We date the phylogeny and determine ancestral areas to investigate historical biogeographical patterns of the crows. Additionally, we use data on brain size and a large database on innovative behaviour and tool use to test whether brain size (i) explains innovative behaviour and success in applying tools when foraging and (ii) has some correlative role in the success of colonization of islands. Our results demonstrate that crows originated in the Palaearctic in the Miocene from where they dispersed to North America and the Caribbean, Africa and Australasia. We find that relative brain size alone does not explain tool use, innovative feeding strategies and dispersal success within crows.

Conclusions: Our study supports monophyly of the genus Corvus and further demonstrates the direction and timing of colonization from the area of origin in the Palaearctic to other continents and archipelagos. The Caribbean was probably colonized from North America, although some North American ancestor may have gone extinct, and the Pacific was colonized multiple times from Asia and Australia. We did not find a correlation between relative brain size, tool use, innovative feeding strategies and dispersal success. Hence, we propose that all crows and ravens have relatively large brains compared to other birds and thus the potential to be innovative if conditions and circumstances are right.

Keywords: Biogeography, Brain, Cognition, Crow, Systematics, Tool use

Background

Crows are large passerine birds that are considered intelligent because of their flexible behaviour, problem-solving abilities and social learning [1,2]. Several species show a number of fascinating innovations including tool use in their foraging, the best-known example being that of the New Caledonian crow (C. moneduloides) [3-5]. Such innovations in foraging are not only unique but are also expected to require increased cognitive abilities, which have been shown to be related to a brain size relatively larger than that of other birds [1,4,6]. Thus, the combination of opportunistic behaviour and intelligence should make corvids highly adaptable, competitive and potentially good colonizers of new environments [7,8].

The family Corvidae (crows, jays, magpies and allies) contains 117 species [9] distributed across most continents except Antarctica. Within the family, crows (genus Corvus) make up about one third of the species diversity (40 species) and they occur on all continents except South America and Antarctica as well as in remote archipelagos such as Hawaii, Micronesia and Melanesia [10]. The Corvidae is part of the core Corvoidea radiation that contains more than 750 species. Recent studies have argued that the core Corvoidea originated in an
archipelago environment north of Australia in the late Oligocene/early Miocene and dispersed via the historically complex Indo-Pacific archipelagos to the rest of the world [11]. Thus, we may expect that some or all of the core Corvodoidea’s member groups could have been preadapted for dispersal and colonization and in the case of *Corvus*, it can be expected that this combined with large brains and the increased associated cognitive abilities would make them ideal dispersers and colonizers across the planet [8].

Species-level systematics within *Corvus* has been based largely on morphological data [12] or very sparse sampling for molecular phylogenies e.g. [13-15] and even vocalizations have been used to infer phylogeny e.g. *C.

Species-level systematics within *Corvus* has been based largely on morphological data [12] or very sparse sampling for molecular phylogenies e.g. *C. enca* and *C. mellori*, [16,17]. A molecular phylogeny based on extensive taxon sampling is required to establish systematic relationships within *Corvus* so that questions pertaining to historical biogeography, brain size and the evolution of innovative foraging habits and tool use might be addressed. Additionally, a robust and densely sampled phylogeny will provide a framework for future work on plumage evolution and various aspects of macroecology and macroevolution.

In the present study, we present a molecular phylogeny including all extant crow species and a number of subspecies sometimes assigned species rank [10]. We use the phylogeny to assess systematic relationships and to elucidate historical biogeographical patterns by dating the phylogeny and estimating ancestral areas across the tree. Furthermore, taking into account the *Corvus* phylogeny, we test whether (i) brain size is correlated with the ability to disperse to and colonize islands and (ii) brain size correlates with innovative feeding behaviour and tool use within crows.

**Methods**

**Taxon sampling and laboratory procedures**

We sampled all forty extant species of *Corvus* [9] (Table 1). Where possible we included multiple individuals and, for widespread species, multiple subspecies (e.g. *Corvus enca*, *Corvus macrorhynchos*, *Corvus corone* and *Corvus frugilegus*). We also included some well-documented closely related genera to test for monophyly of *Corvus*: *Garrulus*, *Pica*, *Nucifraga* [14]. *Lanius* was used to root the tree.

Two nuclear gene regions, ornithine decarboxylase (ODC) introns 6 to 7 (chromosome 3), and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) intron-11 (chromosome 1), and two mitochondrial markers NADH dehydrogenase subunit 2 (ND2) and subunit 3 (ND3) were sequenced and used to estimate phylogenetic relationships. Primer pairs used for amplification were: ND2: Lmet [18]/H6312 [19]; ND3: ND3-L10755/ND3-H11151 [20]; ODC: OD6/OD8 [21], G3P14b [22]. For the old museum specimens we only sequenced the mitochondrial genes. Corresponding laboratory procedures for study skins are detailed in Inrestedt et al. [23]. Additional internal primers were designed for this study, ND3-covR1: GTCAATAGT-GAAACAGGATTCG; ND3-CovF1: TTTTCAATTC-GATTCTTTGATTAG; ND2-CovR1: CTGGAAGACTGACATGCA; ND2-CovF2: CCCCTATACTCTCAAATCTCACA; ND2-CovR2: CCTGTAGGACTTCTTGGAATC; ND2-CovF3: CTAGGACTATGCGCATTTCACTT; ND2-CovR3: AGATAGAGGAGGAGGCTATAATT; ND2-CovF4: CTGAATAAGGACTAAACCAAACACAA; ND2-CovR4: ATGTGGTGAGGATTGTGCT; ND2-CovF5: CCAACTAAACTG-CATGAAACAAA; ND2-CovR5: GTGGGAATC; ND2-CovF6: TCACACTGCGCCTCTTCTTTCACA. Purified PCR products were cycle-sequenced using the Big Dye terminator chemistry (ABI, Applied Biosystems) in both directions with the same primers used for PCR amplification and run on an automated AB 3100 DNA sequencer. Sequences were assembled with SeqMan II (DNASTAR). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are provided in Table 1.

**Alignment and phylogenetic analyses**

Sequence alignment was performed using MegAlign. The concatenated alignment consisted of 2346 base pairs (bp) and the lengths of the individual alignments were GAPDH: 299 bp, ODC intron-6 and 7: 611 bp, NADH dehydrogenase subunit 2: 1041 and NADH dehydrogenase subunit 3: 395 bp. Coding genes (ND2 and ND3) were checked for the presence of stop codons or insertion/deletion events that would have disrupted the reading frame. We used Bayesian inference [24,25], as implemented in MrBayes 3.1.2 [26,27] to estimate phylogenetic relationships. The most appropriate substitution models were determined with MrModeltest 2.0 [28], using the Akaike information criterion [29,30]. Bayesian analyses for the concatenated data set were performed allowing the different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary between the six partitions (GAPDH, ODC, 1st, 2nd, 3 rd codon positions for mtDNA and tRNA), i.e. mixed-models analyses [27,28]. Two independent runs initiated from random starting trees were performed for each data set, and in all MrBayes analyses, the Markov Chain Monte Carlo (MCMC) was run using Metropolis-coupling, with one cold and three heated chains, for 10 million (individual analyses) to 20 million (combined analysis) iterations with trees sampled every 100 iterations. The number of iterations discarded before the chains had reached their
| Species                     | Origin of sample | Voucher number | GAPDH | ODC | ND3 | ND2 |
|-----------------------------|------------------|----------------|-------|-----|-----|-----|
| *Corvus albicollis*         | South Africa     | FMNH 447947    | JQ024104 | JQ024061 | JQ023991 |
| *Corvus albus*              | South Africa     | FMNH 443790    | JQ023921 | JQ024013 | JQ024060 | JQ023990 |
| *Corvus bennetti*           | Australia        | ANWC 332922    | JQ023900 | JQ024082 | JQ024019 | JQ023945 |
| *Corvus bennetti*           | Australia        | ANWC 52018     | JQ023901 | JQ024083 | JQ024020 | JQ023946 |
| *Corvus brachyrhynchos*     | USA              | UWBM 86268     | JQ023920 | JQ024102 | JQ024039 | JQ023966 |
| *Corvus capensis*           | Abyssinia        | FMNH 370464    | JQ023977 |
| *Corvus caurinus*           | USA              | UWBM 58841     | JQ023915 | JQ024097 | JQ024034 | JQ023961 |
| *Corvus corax*              | Denmark          | ZMUC 131662    | JQ023891 | JQ024073 |
| *Corvus corone cornix*      | Denmark          | ZMUC 143486    | JQ023894 | JQ024076 | JQ024013 | JQ023939 |
| *Corvus corone corone*      | Denmark          | ZMUC 138386    | JQ023892 | JQ024074 | JQ024010 | JQ023936 |
| *Corvus coronoides coronoides* | Australia, QLD | ANWC 32675    | JQ023908 | JQ024090 | JQ024027 | JQ023953 |
| *Corvus coronoides coronoides* | Australia, NSW | ANWC 49539    | JQ023911 | JQ024093 | JQ024030 | JQ023956 |
| *Corvus coronoides coronoides* | Australia, NSW | ANWC 29239    | JQ023904 | JQ024086 | JQ024023 | JQ023949 |
| *Corvus coronoides coronoides* | Australia, ACT | ANWC 34200    | JQ023910 | JQ024092 | JQ024029 | JQ023955 |
| *Corvus coronoides perplexus* | Australia, WA | ANWC 31774    | JQ023906 | JQ024088 | JQ024025 | JQ023951 |
| *Corvus coronoides perplexus* | Australia, WA | ANWC 31706    | JQ023905 | JQ024087 | JQ024024 | JQ023950 |
| *Corvus coronoides perplexus* | Australia, WA | ANWC 50365    | JQ023902 | JQ024084 | JQ024021 | JQ023947 |
| *Corvus coronoides perplexus* | Australia, WA | ANWC 31869    | JQ023907 | JQ024089 | JQ024026 | JQ023952 |
| *Corvus coronoides perplexus* | Australia, WA | ANWC 50476    | JQ023912 | JQ024094 | JQ024031 | JQ023957 |
| *Corvus crassirostris*      | Ethiopia         | NRM 551730     | JQ024002 | JQ023927 |
| *Corvus cryptoleucus*       | USA              | UWBM 80762     | JQ023917 | JQ024099 | JQ024036 | JQ023963 |
| *Corvus dauricus*           | Mongolia         | UWBM 58041     | JQ023913 | JQ024095 | JQ024032 | JQ023958 |
| *Corvus edithae*            | Kenya            | FMNH 370461    | JQ024056 | JQ023986 |
| *Corvus enca celebensis*    | Sulawesi         | RMNH 60561     | JQ024042 | JQ023969 |
| *Corvus enca compiler*      | Borneo           | RMNH 60563     | JQ024059 | JQ023989 |
| *Corvus enca pusillus*      | Palawan          | RMNH 100023    | JQ024043 | JQ023970 |
| *Corvus florensis*          | Flores           | RMNH 85140     | JQ024046 | JQ023973 |
| *Corvus frugilegus frugilegus* | Denmark  | ZMUC 143511    | JQ024011 | JQ023937 |
| *Corvus frugilegus pastinator* | China         | NRM 570731     | JQ024068 | JQ023999 |
| *Corvus fusciapillus*       | New Guinea       | AMNH 300970    | JQ024048 | JQ023975 |
| *Corvus hawaiiensis*        | Hawaii           | AMNH 196263    | JQ023982 |
| *Corvus imparatus*          | Mexico           | AMNH 706673    | JQ023978 |
| *Corvus insularis*          | New Britain      | AM 060592      | JQ023888 | JQ024070 | JQ024007 | JQ023932 |
| *Corvus jamaicensis*        | Jamaica          | AMNH 155238    | JQ024052 | JQ023981 |
| *Corvus kubayi*             | Micronesia       | NRM 570711     | JQ024003 | JQ023928 |
| *Corvus leucognaphalus*     | Hispaniola       | NRM 570710     | JQ024004 | JQ023029 |
| *Corvus macracanthus japonensis* | Japan    | NRM 570732     | JQ024069 | JQ024000 |
| *Corvus macracanthus levaillantii* | N. Siam | NRM 570733     | JQ024067 | JQ023998 |
| *Corvus macracanthus mandschuricus* | Russia | UWBM 47167    | JQ023918 | JQ024100 | JQ024037 | JQ023064 |
| *Corvus macrorynchus philippinus* | Philippines | ZMUC 104586    | JQ024054 | JQ023984 |
| *Corvus meeki*              | Bougainville     | AMNH 221033    | JQ024058 | JQ023988 |
| *Corvus mellori*            | Australia        | ANWC 45128     | JQ023895 | JQ024077 | JQ024014 | JQ023940 |
| *Corvus mellori*            | Australia        | ANWC 52403     | JQ023903 | JQ024085 | JQ024022 | JQ023948 |
| *Corvus mellori*            | Australia        | ANWC 34099     | JQ023909 | JQ024091 | JQ024028 | JQ023954 |
apparent target distributions (i.e. the length of the “burn-in" period) was graphically estimated using AWTY [31,32] by monitoring the change in cumulative split frequencies, and by the loglikelihood values and posterior probabilities for splits and model parameters. We used GARLI 0.95 [33] to perform maximum likelihood analyses on the concatenated data set. Five independent analyses of 50 million generations were performed. Nodal support was evaluated with 100 non-parametric bootstrap pseudoreplications.

| Taxon                  | Location         | Accession Numbers                           | Accession Numbers |
|------------------------|------------------|---------------------------------------------|-------------------|
| Corvus minutus*        | Cuba             | AMNH 501484                                 | JQ024051 JQ023980 |
| Corvus monedula        | Denmark          | ZMUC 143533                                 | JQ023893 JQ024075 JQ024012 JQ023938 |
| Corvus monedulaoides*  | New Caledonia    | FMNH 268468                                 | JQ024040 JQ023967 |
| Corvus nasicus*        | Cuba             | NRM 570734                                  | JQ024066 JQ023997 |
| Corvus orru            | Australia        | ANWC 32239                                  | JQ023898 JQ024080 JQ024017 JQ023943 |
| Corvus orru            | Australia        | ANWC 50885                                  | JQ023899 JQ024081 JQ024018 JQ023944 |
| Corvus ossifragus      | USA              | UWBM 86680                                  | JQ023914 JQ024096 JQ024033 JQ023960 |
| Corvus palmarum*       | Hispaniola       | FMNH 352731                                 | JQ024050 JQ023979 |
| Corvus palmarum        | Hispaniola       | AMNH DOT 16134                              | JQ023922 JQ024105 JQ023992 |
| Corvus pectoralis*     | China            | AMNH 261595                                 | JQ024053 JQ023983 |
| Corvus pectoralis*     | China            | NRM 570709                                  | JQ024005 JQ023930 |
| Corvus rhipidurus*     | Niger            | FMNH 370467                                 | JQ024057 JQ023987 |
| Corvus ruficollis*     | Iran             | FMNH 284717                                 | JQ024055 JQ023985 |
| Conus sinaloe          | Mexico           | UWBM 81200                                  | JQ023916 JQ024098 JQ024035 JQ023962 |
| Conus splendidens      | Singapore        | UWBM 83598                                  | JQ023919 JQ024101 JQ024038 JQ023965 |
| Conus tasmanicus boreus| Australia        | AM 0.70670                                  | JQ023889 JQ024071 JQ024009 JQ023934 |
| Conus tasmanicus boreus| Australia        | AM 0.70687                                  | JQ023890 JQ024072 JQ024008 JQ023933 |
| Conus tasmanicus tasmanicus | Australia | ANWC 44920                                  | JQ023896 JQ024078 JQ024015 JQ023941 |
| Conus tasmanicus tasmanicus | Australia | ANWC 45902                                  | JQ023897 JQ024079 JQ024016 JQ023942 |
| Conus tristis*         | New Guinea       | NRM 543594                                  | JQ024006 JQ023931 |
| Conus tristis*         | New Guinea       | RMNH 22732                                  | JQ024049 JQ023976 |
| Conus typicus*         | Sulawesi         | RMNH 101686                                 | JQ024045 JQ023972 |
| Conus unicolor*        | Sulawesi         | AMNH 673967                                 | JQ024041 JQ023968 |
| Conus validus*         | Halmahera        | RMNH 140643                                 | JQ024047 JQ023974 |
| Conus violaceus*       | Seram            | RMNH 140590                                 | JQ024044 JQ023971 |
| Conus woodfordi        | Solomon Islands  | UWBM 63090                                  | JQ023959 |
| Conus woodfordi        | Solomon Islands  | AMNH DOT6705                                 | JQ023923 JQ024106 JQ024062 JQ023993 |

Outgroups

| Taxon                  | Location         | Accession Numbers                           | Accession Numbers |
|------------------------|------------------|---------------------------------------------|-------------------|
| Nucifraga canyocatactes | Sweden           | ZMUC 138408                                 | JQ023924 JQ024107 JQ024064 JQ023995 |
| Garrulus garrulus      | Denmark          | ZMUC 136378                                 | JQ024063 JQ023994 |
| Pica pica              | Denmark          | ZMUC 144204                                 | JQ023925 JQ024108 JQ024065 JQ023996 |
| Lanius collaris        | Cameroonian/Tanzania | GenBank/ZMUC 138905 | FJ357916 EU272112 JQ024001 JQ023926 |
| Dicurus bracteatus/hottentottus | New Guinea/Philippines | GenBank | EF052813 EU272113 GG145422 GQ415384 |
| Sturnus vulgaris        | Sweden           | GenBank                                     | EF441231 EF441253 GU816823 DJ146346 |
| Menura                 | Australia        | GenBank                                     | EF441220 EF441242 AY542313 AY542313 |
| Pitta angolensis       | Tanzania         | GenBank                                     | AY365969 DQ785940 GU816799 GU816827 |
| Acanthisitta           | New Zealand      | GenBank                                     | EU726202 EU726220 AY325307 AY325307 |

Acronyms are: AM, Australian Museum, Sydney, Australia; AMNH, American Museum of Natural History, USA; ANWC, Australian National Wildlife Collection, Canberra, Australia; FMNH, Field Museum of Natural History, Chicago, USA; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; UWBM, University of Washington, Burke Museum, Seattle, USA; ZMUC, Zoological Museum, University of Copenhagen, Denmark. Asterisks after taxon names indicate that sequences were obtained from toe-pads of old museum specimens.
Dating analyses
To estimate the relative divergence times within Corvus, we used BEAST v.1.6 [34-36] and assigned the best fitting model, as estimated by MRMODELTEST 2.0 [28], to each of the four partitions. We assumed a Yule Speciation Process for the tree prior and an uncorrelated log-normal distribution for the molecular clock model [35,37]. We used default prior distributions for all other parameters and ran MC3 chains for 50 million generations. The program Tracer [38] was used to assess convergence diagnostics. To obtain absolute date estimates we calibrated the tree using secondary calibration points derived from Barker et al. [39] who used various approaches to date the all Passeriformes tree. Thus we used the age of Acanthisittidae versus other passerines at 76 ± 8 My SD (age within 95% confidence intervals = 62.8–89.2 My) and the split between Menura noveahollandiae and all other oscines 63 ± 2 My SD (confidence intervals = 59.7–66.3 My). In order to apply these calibration points, some additional taxa were included in the dating analyses (see Table 1). We also compared our age estimates with the classic mitochondrial 2% rule [40].

Biogeographical analysis
We used Bayes-LAGRANGE [41] to assess ancestral patterns within Corvus. In a Maximum-Likelihood biogeographical analysis [42,43] as implemented in the software LAGRANGE [42], ancestral areas are optimized onto internal nodes. LAGRANGE enables maximum likelihood estimation of the ancestral states (range inheritance scenarios) at speciation events by modelling transitions between discrete states (biogeographical ranges) along phylogenetic branches as a function of time. With the Bayes-LAG RANGE approach it is possible to optimize on multiple trees whereby topological uncertainty is taken into account. We sampled 2000 trees (by thinning the chain stochastically) from the MCMC BEAST output, and ran LAGRANGE on all of them. The frequency of ancestral areas for clades was then recorded and plotted as marginal distributions on the majority-rule consensus tree derived from the MCMC. The major advantage of the Bayes-Lagrange method is that the marginal distributions for the alternative ancestral areas at each node in the tree are the product of both the phylogenetic uncertainty in the rest of the tree and the uncertainty in the biogeographical reconstruction of the node of interest.

We assigned species distributions to one or more of nine geographical areas for the Bayes-LAG RANGE analysis basing these on evidence of historical relationships of tectonic plates and terranes in the Indo-Pacific [44,45]: Neartctic, Caribbean, Palaeartic, Africa, Indomalaya (including the Philippines), Wallacea, Australo-papua and the Pacific. The analysis was carried out using the maxareas (= 2) option in LAGRANGE. However, we also ran additional analyses exploring the importance of changing the maxareas (setting maxareas = 3 and 4).

Brain size, tool use and innovation
Data on brain size, which are considered a good proxy for cognition and intelligence [46], and body mass, were taken from Mlikovsky [47] and Iwanuik & Nelson [48]. Although the data are drawn from two sources, the data have been converted to reflect inner brain case volumes and are therefore directly comparable. These two datasets together include brain size data for 29 Corvus species [47,48]. By comparing the brain sizes for those species that are represented in both datasets it is clear that most discrepancies between the two datasets are explained by the size of the bird individuals measured. Therefore we believe that the measurements from the two datasets can be analysed combined. For a few species information on body mass was lacking in which case we used data from the CRC Handbook [49]. We compared the data on body mass used in our analyses [47-49] with body mass data provided in Handbook of Birds of the World [10] and found the data to be in agreement. After ln transforming the data we regressed brain size against body mass for 30 out of 40 species of Corvus. We also ran separate analyses based on the two datasets from Mlikovsky [47] and Iwanuik & Nelson [48] to account for potential differences in measuring body mass and brain size. We compiled data on tool use and innovative foraging behaviour from studies by Lefebvre et al. [4], Overington et al. [50] and Bentley-Condit & Smith [51]. Additionally, we searched the Handbook of Australian, New Zealand and Antarctic birds [52] for data on Australian crows. Altogether we found that 10 out of 40 Corvus species have a documented record of using tools and that 17 out 40 species use innovative foraging behaviour. We note that opinions differ on what it means to be a “real” tool user and that some species are only known to use tools in captivity (Corvus frugilegus). However, this only underscores the high plasticity of this behaviour among Corvus species.

To investigate whether tool use, innovative foraging strategy and colonization of islands was associated with relative larger brain size across Corvus species, we ran a phylogenetic generalized least squares model (PGGLS) in a phylogenetic framework using R version 2.10.1 [53] and the CAPER R package [54,55] as well as the APE package [56]. This statistical approach fits a linear model, taking into account phylogenetic non-independence. We tested the correlation of In transformed brain size and In transformed body mass as explanatory variables, with potential effect of tool use, innovation or island/continent distribution.
Results

Molecular phylogenetics and dating

Model based analyses performed on the concatenated dataset (six partitions: GAPDH, ODC, 1st, 2nd, 3 rd codon positions for mtDNA and tRNA; maximum likelihood (ML): –ln 16528.5601, Bayesian inference (BI) harmonic mean: –ln 15872.64) yielded a 50% majority-rule consensus tree (BI) that was topologically congruent with the Maximum Likelihood tree (Figure 1), (for well-supported nodes receiving posterior probabilities >0.95 or bootstrap values >70%). Scores of the best likelihood trees were within 0.05 likelihood units of the best tree recovered in each of the other four GARLI runs, suggesting that the five runs had converged.

We find that the genus *Corvus* is monophyletic and furthermore recovered eight well-supported sub-clades that contain members more or less restricted to biogeographical regions. The basal members (Clades I-III) are distributed across the Holarctic region, the Caribbean and Africa. The Caribbean members are found in two well-supported separate clades (Clades II and III) but resolution between the clades and *Corvus capensis* remain unresolved. Clade IV consists of the Eurasian *Corvus frugilegus* and *Corvus hawaiiensis*. The western and eastern subspecies of *C. frugilegus* represent a deep split in concordance with a previous study on this species complex [15]. Clade V consists of all the African *Corvus* species (except *C. capensis*) and the Holarctic *C. corax*. Clade VI consists of Holarctic species that are separated in two distinct well-supported clades, one clade of Nearctic species (*C. caurinus* and *C. brachyrhynchos*) and one clade of Palaearctic species (*C. corone* and *C. pectoralis*). Clade VII contains all the Australo-Papuan and Wallacean taxa except the Wallacean *Corvus floresiens*. The latter species remains unresolved relative to Clades VII and VIII. Within Clade VII we also find some Pacific taxa. One subclade within Clade VII contains all Australian taxa and we also recover a well-supported Australo-Papuan clade. The relationships of the Wallacean species, however, remain unresolved at the base of Clade VII except that there is good support for a sister relationship between *C. unicolor* and *C. typicus*. Clade VIII includes the widespread *C. macrorhynchos*, the Indomalayan *C. splendens* and the Micronesian *C. kubaryi*.

Our BEAST dating analysis supports a mid-Miocene origin of *Corvus* dating to around 17.5 Mya (age within 95% HPD confidence intervals = 14.05–21.19 My). Our chronogram was consistent with the “2% rule” (uncorrected pairwise distances) for the rate of mitochondrial DNA sequence divergence per million years for young nodes (Pliocene to present) but suggested somewhat younger diversification times than those that BEAST determined as of Miocene age, which could be expected due to saturation in the mitochondrial genes [57]. According to the 2% rule the origin of *Corvus* dates to about 11 Mya. Knowledge of a *Corvus* fossil from North America dating back to the late Miocene [58] does not add much further insight because the author was unable to assign a systematic position. However, assuming that the fossil is closely related to the other North American taxa it supports our age estimates based on secondary calibration points.

Biogeographical analysis

The Bayes-LAGRANGE analysis (Figure 2) finds the origin of *Corvus* and its closest relatives (*Pica, Nucifraga, Garrulus*) to be within the Holarctic region. The origin of *Corvus*, however, is Palaearctic, although some deep branches lead to taxa distributed in North America and the Caribbean. Colonization of Africa took place in the Pliocene, and colonization of Wallacea took place in the late Miocene and led to further colonization of Australo-Papua around 5 Mya. We find evidence for four colonization events of the Pacific from Asia and Australia. The Caribbean was colonized twice. One Caribbean clade is sister to a clade of North American taxa (Clade III) indicative of colonization from there. However, the ancestral area analysis postulates a Palaeartic/Caribbean origin for the other Caribbean clade (II).

Brain size and tool use

We find a highly significant correlation between body mass and brain size in *Corvus* (*P < 0.001 Figure 3) both for the combined dataset and when analyzing the individual datasets from Mlikovsky [47] and Iwanuik & Nelson [48]. This suggests that there are no significant differences in relative brain size between large and small *Corvus* species. Our analysis (Phylogenetic Generalized Least Squares) taking covariance between taxa into account, finds no correlation between brain size, tool use (*P = 0.67*) and innovative behaviour (*P = 0.69*), and no correlation between brain size and the ability to colonize islands (*P = 0.46*) (Figure 3C). Seemingly, all members of *Corvus* have the same relative brain size and species of all sizes have innovative foraging strategies/use tools and have been able to colonize islands.

Discussion

Systematics and biogeography

The early history of the classification of the family Corvidae has been summarized by Goodwin [12] but is restricted to morphology. We present the first complete molecular species level phylogeny for the crows and ravens (*Corvus* spp) including several subspecies of widespread species (Figure 1). Most notably, we demonstrate that what is currently classified as the Australian Raven *C. coronoides*, comprises two clades, one in the...
Figure 1. The 50% majority-rule consensus tree of the *Corvus* obtained from the Bayesian analysis of the combined dataset (GAPDH, ODC, ND2 and ND3). Above the branch is the posterior probability (only values above 0.95 are shown, asterisks indicate 1.00 posterior probabilities). Below the branch is the maximum likelihood bootstrap value (only values above 70% are shown) from 100 pseudoreplicates. Clades I-VIII are discussed in the text.
west (C. c. perplexus) and one in the east (C. c. coronoides). They are geographically isolated from each other only by approximately 100 km of apparently unsuitable habitat across the continent’s south coast at the Great Australian Bight. We propose that these two taxa be elevated to species rank. In contrast, populations of C. tasmanicus, geographically isolated from each other by >500 km, were not reciprocally monophyletic. Currently recognized as two subspecies, their isolation and divergence is presumably very recent. In accordance with a previous study including samples from throughout the Palaearctic, we show that C. frugilegus may also
represent two distinct species, one in the western Palearctic and one in the eastern Palearctic [15]. *C. macrorhynchos* is found to be paraphyletic such that the Philippine *C. macrorhynchos philippinus* is sister to a clade comprising all other *C. macrorhynchos*, which occur in East Asia, and *C. kubaryi*. However, denser taxon sampling for *C. macrorhynchos* and population sampling for other widespread species (e.g. *Corvus enca* and *Corvus orru*) is needed to properly revise taxonomic issues at species and subspecies levels.

Our dating analysis suggests that the radiation of *Corvus* began in the mid-Miocene and our ancestral area analysis indicates a Palearctic origin (Figure 2). This is consistent with the two most basal members, *Corvus monedula* and *Corvus dauuricus* (Clade I) being Eurasian and with the closest extant relatives of *Corvus* distributed in Eurasia and North America (*Pica* and *Nucifraga*). This results in a signature of a Holarctic origin for *Corvus* and its closest relatives. We infer that two clades independently colonized the Caribbean islands in the late Miocene (Clades II and III). One Caribbean clade (II) has a long branch that leads to *C. leucognaphalus*, *C. jamaicensis* and *C. nasicus* and our analyses suggest a Palaearctic/Caribbean origin. This could be interpreted as evidence for long distance ocean dispersal similar to that inferred in other passerine bird groups that have crossed the Atlantic e.g. *Turdus* [59]. Two alternative interpretations of the Caribbean having been colonized from North America are possible (i) extinction of a North American ancestor, (ii) an ancestral form was widely distributed in the Holarctic (like *Corvus corax*) and gave rise to independent colonizations to the Caribbean followed by isolation of the North American population and a second colonization to the Caribbean (Clade III).
The other Caribbean species (C. palmarum and C. minutus; Clade III) are sister to three North American species (C. ossifragus, C. sinaloae and C. imparatus). This provides evidence for colonization by C. palmarum and C. minutus of the Caribbean from North America.

Relationships of an African species, C. capensis, were difficult to ascertain but it seems to represent a single Miocene colonization of Africa from the Palearctic. C. capensis does not seem closely related to members of Clade V, which includes all other taxa that have colonized Africa and radiated within the continent. Clade VII of Indo-Pacific species has sequentially colonized Southeast Asia, Wallacea, Australo-Papua and the Pacific islands. However, the Hawaiian crow (C. hawaiiensis) is not a member of this clade, instead it clusters with the Palearctic C. frugilegus (Clade IV) and so we infer it to have colonized Hawaii from East Asia. This is unexpected because the Hawaiian biota generally evolved through colonization from America whereas that of the rest of the Pacific was mostly colonized from Asia and Australo-Papua [60]. For the Corvus radiation, Asia has been the main source area for colonization of the Pacific as opposed to Australo-Papua, which is only the source area for one out of four Pacific lineages. Overall, the ancestral area analysis provides a rather clear pattern of separate colonizations of all continents except South America from the Palearctic/(Nearctic).

**Brain size, tool use and colonization**

Tool use is rare in the animal kingdom and is considered restricted to primates [61], Cetaceans [62], and some birds (e.g. Psittaciformes and Passeriformes) [1]. By far the most well-known tool using bird is the New Caledonian crow (Corvus monedulae) and several studies have demonstrated this island endemic crow's ingenious abilities to use sticks to probe for larvae [5,63]. It is well established in the literature that cognitive abilities correlate with larger relative brain size, and that the family Corvidae have unusually large brains compared to other birds [64,65]. Particularly, the New Caledonian crow's ability to use tools has been explained by its extraordinary large brain [6]. However, in the study by Cnotka et al. [6] phylogenetic relationships among crows were unknown and they were therefore unable to make appropriate phylogenetic corrections.

Several members of the genus Corvus use a variety of natural tools or advanced innovative strategies when foraging [summarized in 4]. Until now, innovative feeding techniques have been reported for 17 of the 40 species of Corvus and tool use for 10 of the 40 Corvus species (Additional file 1: Table S1). There is only one tool using species (Corvus ossifragus) that is not known to have foraging innovations and it should be noted that tool-use is usually seen as species typical and often hard-wired as evidenced by experiments on young woodpecker finches [66] and young New Caledonia crows [67], both of which “know” about tools from the start without having to learn about them.

Our analyses on body mass and brain size demonstrate that there is a significant correlation between the two variables, meaning that all crows have the same large relative brain size (similar body mass/brain size ratio). However, our comparative analyses on brain size and innovative feeding/tool use strategies within Corvus, corrected for phylogenetic relationships, reveal no correlation between the variables. This could be interpreted in two ways. Either brain size has little to do with innovative foraging strategies/tool use and thus other factors are more important in determining whether or not crows use tools or innovative feeding strategies. Alternatively, all crow species have large brains relative to other birds and thus have the potential to use tools or other innovative feeding strategies. Given that a number of studies have already demonstrated a link between cognitive abilities and brain size in both birds [3,4] and mammals [68,69] and that it is well-established that corvids have larger brains than many other birds [1,4], it seems the most likely hypothesis that all crows have the potential to develop innovative foraging strategies and to use tools in their search for food and there could be many reasons why this potential is only realised in some species across the Corvus tree. However, it has also been argued that total brain size may not be the ideal proxy for cognition and that measures should be taken to explore particular brain regions to explain innovation and tool-use [70]. We do not consider this study the final word on the topic, but merely a first attempt to combine phylogeny with functional traits associated with cognition and innovation in crows.

The most persistent hypothesis of large brains and corresponding enhanced cognition is that they evolved as an adaptation to handle novel or altered environmental conditions [71]. Island environments may prove particularly challenging as they, depending on the size and nature of the island, may provide fewer available niches, inferior access to food and new unknown dangers. On the other hand, a new island colonizer, could also find itself in an environment free of closely related competitors and free of inhibitors leading to occupancy of a wider range of habitats – ecological release [72,73]. A combination of these two extreme scenarios, however, could to some extent counteract each other, which may explain the lack of correlation between relative brain size and island colonisations in crows and ravens.

**Conclusion**

The analyses based on molecular sequence data from all recognized crow and raven species (genus: Corvus) demonstrate that the genus is monophyletic and that it
originated in the Palearctic in the Miocene. From the centre of origin crows dispersed to North America and the Caribbean, to Africa and to Australasia, with several independent colonizations of remote Pacific islands. Our analysis comparing brain size and colonization of islands within Corvus found no correlation and we therefore conclude that colonization of islands by crows cannot be explained by brain size. We did not find a correlation between brain size, tool use and innovative foraging strategies as otherwise suggested by other studies e.g. [6,8]. Thus, there seems no reason to believe that brain size alone has any influence on tool use, innovative foraging strategies and colonization ability within the crow lineages. Rather it would appear that large brains had already evolved in the ancestor of crows, leading to a generally high cognitive ability to deal with new challenges for crows and other corvid lineages.

Additional file

Additional file 1: Table S1. List of taxa used in the comparative analyses. Distribution is either insular or continental. Body mass (D) according to Dunning body mass (I) according to Iwanuik & Nelson and body mass (M) according to Milkovich. Brain size according to Milkovich and Iwanuik & Nelson. Feeding innovation according to Lefebvre et al. Bentley-Condit & Smith and Higgins et al. Feeding innovations according to Lefebvre et al. Bentley-Condit & Smith and Overington et al. [4,7,47-51].

Competing interests
The authors have no competing interests.

Authors’ contributions
KAJ designed the study, carried out the lab work, performed the phylogenetic analyses, and drafted the manuscripts. PHF carried out additional comparative analyses. MI assisted with lab work. All authors read, commented upon and approved the manuscript.

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