

A global database of feeding innovations in birds

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ABSTRACT—Academic journals, as well as birding magazines and newsletters, often publish reports of novel and/or unusual feeding behaviors observed by professional and amateur ornithologists. These reports, termed “feeding innovations,” have been used to test predictions in ecology, evolution, cognition, and neuroscience. I present here the latest version of the avian innovation database that has been collated since the mid-1990s, in order to facilitate work by researchers that have up to now had access to smaller versions that contained only innovation frequencies. The database includes descriptions, key words, and references to 4,455 innovations collated for 1,689 species in 166 families, obtained by systematically examining the short notes section and, in some cases, entire issues of 216 ornithology publications over periods that varied between 2 and 84 years. The database is intended as a tool for researchers to further study behavioral plasticity, opportunism, and cognition in birds. *Received 1 September 2020. Accepted 5 March 2021.*

Key words: cognition, feeding, food type, foraging technique, innovations, unusual behaviors.

Una base de datos mundial de innovaciones alimentarias en aves

RESUMEN (Spanish)—Las publicaciones académicas, así como las revistas y boletines de pajareros, frecuentemente publican reportes de comportamientos de alimentación novedosos y/o inusuales que son observados por ornitólogos profesionales y amateurs. Estos reportes, que aquí llamo “innovaciones de alimentación”, se han utilizado para someter a prueba predicciones en ecología, evolución, cognición y neurociencia. Aquí presento la más reciente versión de una base de datos de innovaciones en aves que se ha colectado desde mediados de la década de 1990 con la meta de facilitar el trabajo de investigadores que hasta ahora han usado versiones más pequeñas que contenían únicamente frecuencias de innovación. La base de datos incluye descripciones, palabras clave y referencias de 4,455 innovaciones compiladas de 1,689 especies en 166 familias, obtenidas a través de revisiones sistemáticas de las secciones de notas cortas y, en ocasiones, de todo el contenido de 216 publicaciones de ornitología a lo largo de periodos que varían entre 2–84 años. Espero que la base de datos sirva como una herramienta para que los investigadores profundicen el estudio de plasticidad conductual, oportunismo y cognición en aves.

Palabras clave: alimentación, cognición, comportamientos inusuales, innovaciones, técnica de forrajeo, tipo de alimento.

Professional ornithologists and amateur birders occasionally report avian behaviors that seem to them surprising, unusual, and/or novel. These observations are routinely published in the short notes section of ornithology journals and birding newsletters and magazines, sometimes accompanied by comments from editors. Starting with Fisher and Hinde’s (1949) description of milk bottle opening in British tits after 1921, observations of this type have given rise to a growing literature on the role of novel behaviors in the evolution of cognition (Reader and Laland 2003). More than 3 decades ago, Kummer and Goodall (1985) proposed the term “innovation” for these behaviors, defining them as a solution to a novel problem, a novel solution to an old one, or a new ecological discovery such as a food item not previously part of the diet.

In birds, comparative analyses of taxonomic differences in the frequency of these reports have provided a useful quantitative tool to test predic-

tions in ecology, evolution, cognition, and neuroscience. Corrected for a series of potential biases (see review in Lefebvre 2011), feeding innovation frequencies have been associated with several measures of the brain (whole brain: Overington et al. 2009; forebrain: Lefebvre et al. 1997; mesopallium and nidopallium: Timmermans et al. 2000; neurotransmitter receptors: Audet et al. 2018), colonization of new environments (Sol et al. 2005a), diversification of species (Nicolakakis et al. 2003) and subspecies (Sol et al. 2005c), migration (Sol et al. 2005b), habitat and dietary generalism (Ducatez et al. 2015), cognition (tool use: Lefebvre et al. 2002; social learning: Lefebvre and Bouchard 2003), pathogen costs (Vas et al. 2011), life history traits such as lifespan and brood value (Sol et al. 2016), and extinction risk (Ducatez et al. 2020). A similar use of innovation reports from the primate literature has revealed several identical correlates (Reader and Laland 2002, Reader et al. 2011, McCabe et al. 2015, Navarrete et al. 2016) and led to the conclusion of convergent evolution of avian and primate cognition despite their more than 300 million years of phylogenetic divergence (Lefebvre et al. 2004).

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This paper presents the latest version of the avian innovation database that has been collated since the mid-1990s, in order to facilitate work by researchers that have up to now had access to smaller versions that contained only innovation frequencies (Overington et al. 2009, corrected 2011; Dryad file accompanying Ducatez et al. 2020) or who have inferred data from tables and figures that appeared in our earlier papers (see Ricklefs 2004, Garamszegi et al. 2005, 2007; Møller 2009, Soler et al. 2012, Jönsson et al. 2012, Clucas and Marzluff 2016, Møller and Xia 2020).

Methods

The contents of the short notes section and, in some cases, the entire issue of 216 ornithology publications were systematically examined over periods that varied, depending on availability, between 2 and 84 years per publication. These include publications that cover restricted clades of birds (e.g., *Wader Study*, *Colonial Waterbirds*, *Journal of Heron Biology and Conservation*, *Raptor Research*, and *Vulture News*) as well as publications that are not taxonomically specialized. It can be argued that the latter offer an unbiased coverage of all the avian clades, but it is also possible that cases involving taxa for which specialized journals exist will appear less often in generalist publications because they are submitted to specialized ones. Given these 2 possibilities, analyses using previous, smaller versions of the database have up to now included both generalist and taxonomically specialized publications.

Publications were initially searched in paper form in the Blacker-Wood Library of Zoology and Ornithology of McGill University. As more publications have become available online, more recent searches have involved electronic versions of journal archives. The list of publications examined (Supplemental Table S1), whether or not an innovation was found in it, includes the time period covered and the online reference in cases where the publication is available electronically (note that not all online sites are available publicly; in some cases, they were only accessible to us via a VPN connection to the McGill Libraries).

In some cases, the years covered include some examined in paper form at the Blacker-Wood

Library and some examined online through the site indicated. Journals and newsletters that mostly published population counts, rarities, and sightings, but no innovations, were examined for a shorter period than journals that contained novel feeding cases. Publications whose name has changed over time are entered in a single line when the electronic source is the same for all versions of the journal; when the electronic sources differ, the different names of the publication appear separately (Supplemental Table S1).

All but one of the publications are journals or newsletters, the only exception being the online site of the Bird Ecology Study Group (active from July 2005 to December 2019), published with the help of the Natural History Museum of the National University of Singapore. It is on this site that the first description of tool use in the wild by Goffin's Cockatoos (synonym: Tanimbar Corella, *Cacatua goffiniana*), one of the key species in the study of avian intelligence, was published (see Osuna-Mascaró and Auersperg 2018). Most publications are in English or contain English-language abstracts; in the latter case, online translation was used for descriptors and key words in the original language if the English abstract indicated an innovation was present. Publications in German were searched in paper form in the McGill libraries by an assistant, Simran Kurir. Early volumes of *Aquila* in Hungarian were searched by Laszlo Zsolt Garamszegi. Publications in romance languages (French, Italian, Catalan, Spanish, and Portuguese), whether in paper form or online, were searched by myself. Innovations that are only documented on video, but have not been the subject of a description in one of 216 publications covered (e.g., <https://www.smithsonianmag.com/science/these-woodpeckers-will-drill-your-skull-and-eat-your-brains-if-youre-baby-dove-180961656/>), were not included in the database.

In very rare cases, the journals that were systematically searched made reference to articles in more generalist journals (e.g., deceptive use of alarm calls by Fork-tailed Drongos [*Dicrurus adsimilis*] to take food from other species: Flower 2011; New Caledonian Crows [*Corvus moneduloides*] making tools: Hunt 1996). These references are included here, but the generalist journals were not systematically searched because we expected too few cases to be found there. High

impact generalist journals are also more likely to feature spectacular and cognitively complex innovations (e.g., tool manufacture), potentially biasing taxonomic frequency comparisons away from more mundane cases in species not expected to show “intelligent” behavior (e.g., partridges eating leeks; Williams 1984).

Only cases in the feeding domain were included in the database. This is because feeding is universal and is the basis for the first reported innovation in birds (Fisher and Hinde 1949), as well as almost all experimental tests of innovative problem-solving. When the title of an article suggested novel feeding, the paper was systematically read for key words such as “unusual,” “new,” “never seen before,” “first time,” “unreported,” “no mention in the literature,” “undocumented,” “of interest,” “noteworthy,” “opportunistic,” “clever,” “intelligent,” and “learned.” In a small number of cases, these key words were not present, but the note contrasted the behavior observed with other foods or foraging techniques used by the species or similar observations published on often related species. In such cases, key words like “other species mentioned” and “other foods mentioned” are used. In rare cases (for example, foraging on ephemeral insect swarms), no key words were present in some references, but similar observations on other species were accompanied by key words such as “opportunistic.” Cases with no key words sometimes had titles similar to those given to newsworthy events in newspapers (e.g., “Cape Wagtail eating fiddler crabs”; Begg 1981); they were included in the database.

Recent publications tend to feature more key words than older ones, as editors and reviewers now rely more on clearer statements of novelty to accept a manuscript. An example of this is Lafferty et al. (2013), where the case of Mallards (*Anas platyrhynchos*) feeding on sand crabs on the California coast is accompanied by 8 descriptors: “novel behavior and food source, potentially new behavior, forage opportunistically, recently emerged, testament to their flexibility, not reported, observation surprising, our observations are novel.” In contrast, an earlier report of Mallards preying on frogs contains only a description, but no key words (Choffat 1989). Both are included in our database.

In some cases, several observations are published in a single paper, e.g., Roadside Hawks

(*Rupornis magnirostris*) in Guatemala catching several types of prey: frogs at a newly refilled waterhole after heavy rains, insects fleeing army ants, and rodents and grasshoppers fleeing human slash-and-burn fires (Panasci and Whitacre 2000). Instances such as these are listed as a single case in the database. In other cases, separate papers report the same or similar innovations, e.g., House Sparrows (*Passer domesticus*) picking dead insects from cars; when these cases occur in different areas of the world, they are entered separately in the database.

All possible cases were double-checked for the present paper, except the few whose journals were not available online and whose paper copies could no longer be consulted in the McGill Library system due to the COVID-19 confinement and/or transfer to boxes in closed storage. These cases are presented in italics in Supplemental Table S2 and correspond to the descriptions and key words taken for our original searches starting in the mid-1990s.

During the collation of the database, it was assumed that the direct observers of the cases, and the editors and reviewers of the publications, had greater expertise in qualifying their description as unusual, unique, etc., than I or my collaborators could have. No judgment was therefore made beyond that of the original authors as to whether or not a case should be included. As Giraldeau et al. (2007) have argued, decisions to exclude or include any case or establish stricter criteria for inclusion, as suggested by Ramsey et al. (2007), are best taken *after* collection of the initial data, as users of our database are free to do. The same applies to splitting or lumping of entries that may include several observations (e.g., Panasci and Whitacre 2000, discussed above) or list separately cases that some researchers might consider sufficiently similar to warrant lumping.

Results and Discussion

This paper presents 4,455 feeding innovations found for 1,689 species of birds from 166 families (Supplemental Table S2). Each entry lists the family (in bold), species (including in italics and parentheses the name used in the Jetz et al. [2012] phylogeny if different from the currently recognized one), the number of cases (*n*) per species, a

description of the innovation followed by the key words used by the authors of the original paper, the reference of the paper, and the region of the world where it was seen. Note that nocturnal birds (Strigiformes, Apterygiformes, and Strigopidae) do not appear in Supplemental Table S2, as they were excluded from our searches from the start (Lefebvre et al. 1997) given that their feeding behaviors, innovative or not, were unlikely to be seen by ornithologists. Supplemental Table S3 is a CSV version of Table S2 intended to facilitate analyses using the database; it further lists, when applicable, any alternative family classification for a species in the Jetz et al. (2012) phylogeny.

At the family level, Accipitridae, Corvidae, Ardeidae, Laridae, Sturnidae, and Picidae, in that order, show the most innovations. At the species level, House Sparrow, Gray Heron (*Ardea cinerea*), Carrion Crow (*Corvus corone*), Bald Eagle (*Haliaeetus leucocephalus*), Peregrine Falcon (*Falco peregrinus*), Common Raven (*Corvus corax*), Cattle Egret (*Bubulcus ibis*), European Starling (*Sturnus vulgaris*), Eurasian Blackbird (*Turdus merula*), and Herring Gull (*Larus argentatus*) top the list.

The key words most often reported are variants of “no” and “not” coupled with “mention,” “report,” “record,” followed by “unusual,” by references to species “other” than the one showing the innovation and variants of the term “opportunistic.” Descriptors such as “not in HB,” “not in Ali and Ripley” (i.e., *Handbook of the Birds of India and Pakistan*), “not in BWP” (i.e., *Birds of the Western Palearctic*), “not in HANZAB” (i.e., *Handbook of Australian, New Zealand and Antarctic Birds*) refer to foods or techniques that the authors did not find in standard reference books. The terms “not in Brockmann and Barnard” and “not in Morand-Ferron” refer to cases of kleptoparasitism not mentioned in the 2 major reviews of this behavior (Brockmann and Barnard 1979, Morand-Ferron et al. 2007).

The database can be used in several ways. Innovation categories can be analyzed separately, as they were in Lefebvre et al. (2002; tool use), Morand-Ferron et al. (2007; kleptoparasitism), Overington et al. (2009; 12 categories, reduced to 2), and Ducatez et al. (2015; food type vs. technical innovations). As suggested by Ramsey et al. (2007), descriptions can be searched to exclude cases that do not show a sufficient level of

cognitive complexity for a researcher’s purpose. Different decisions concerning lumping and splitting cases can also be taken to reach whatever conclusion on innovation frequency per clade a researcher considers valid. Over a dozen potential biases have been addressed up to now in the literature on avian and primate innovations (see review in Lefebvre 2011), but future work might want to target ones that have not been quantified as yet.

In any comparative analysis using the database, it is recommended to use one or more covariates of innovation frequency to remove potential biases likely to inflate or hide intrinsic differences in innovativeness. Research effort has proven the most useful variable. It can be rapidly estimated by looking at the article count per species given in the *Zoological Record*. A useful tool for this is table S1 in Ducatez and Lefebvre (2014), which lists research effort between 1978 and 2008 for 10,064 species of birds. Poorly studied species may fail to show at least one case and thus fail to appear in the database, even if they could potentially show novel feeding behaviors in the wild. Sol (2020, pers. comm.) estimates that a minimum research effort of 50 articles is sufficient to detect at least one innovation in a species. Given this, it is safe, for example, to consider as non-innovative a species like the Southern Cassowary (*Casuarus casuarinus*), which has no reported innovations in our database: it is from a part of the world well covered by ornithology journals, Australia, and has a sufficiently high research effort, 72 articles in Ducatez and Lefebvre (2014). Conversely, a highly studied species is likely to bias innovation frequency in the opposite direction: a species on which there are 1,000 articles is more likely to be observed doing anything, be it innovative or not, than a species on which there are only 50 articles. Log transformed research effort is thus a useful confounding variable to include in any analysis.

Research effort also reflects regional differences in the number of publications, which is likely to increase innovation numbers in species that live in areas with more extensive journal coverage. For instance, Western Europe and North America have many more ornithology publications than do Asia and Africa, and this is also likely to lead to differences in the total number of papers published on species from these areas. In crows, for example, innovation frequencies in Supplemental Table S2

rank the Carrion Crow from Europe above the American Crow (*Corvus brachyrhynchos*) in North America, which ranks above the Asian Large-billed Crow (*Corvus macrorhynchos*), which in turn ranks above the African Pied Crow (*Corvus albus*). The 4 species are in the same rank order in terms of research effort (Ducatez and Lefebvre 2014), so the inclusion of this correction factor can reduce potential regional effects. A further control can be added by including region as a confounding variable in any analyses (e.g., Sol et al. 2005a).

The reliability and validity of the database have been examined in several papers (see Lefebvre 2011). When different researchers have examined the same publications and compared their decisions to include or not reports in the avian and primate databases, inter-observer agreement has been high (0.82–0.95; Lefebvre et al. 2001, Reader and Laland 2002, Nicolakakis and Lefebvre 2003). Even in the absence of key words, publication of an observation on avian feeding could in itself suggest that the case is worthy of note, as there would be no basis for the behavior to be noted and published if it were routine. Despite this possibility, our database includes one or more key terms in almost all cases and can therefore be considered conservative. In any case, our approach is strictly quantitative, relying on corrected frequencies for comparative analyses, and not using the anecdotal descriptions for interpretations of the cognitive complexity of cases, even when the original authors use terms such as “intelligent” or “insight.”

As is evident in the descriptions of the database, innovations represent a diverse set of processes, unified only by the initial observers’ belief that they are unusual and worth reporting. Some (e.g., new foods) might be a simple extension of dietary generalism (Ducatez et al. 2015), while others (e.g., tool use) may involve more complex cognitive processes. Beyond this, if the ability to generate novel solutions to a problem is one feature of fluid intelligence and behavioral plasticity, innovation rate can be assumed to yield some kind of quantitative proxy for avian intelligence, particularly for technical innovations (Overington et al. 2009). Nevertheless, it is by no means only a measure of intelligence and might more often reflect opportunism, a concept that has proven hard to define. The term “opportunistic” is

sometimes applied to animals that feed randomly, without specializing on particular food types or sizes; this is clearly not a feeding strategy that would select for intelligence. If the term “opportunism,” however, is restricted to cases where an animal searching for food A unexpectedly encounters new food B and quickly shifts its foraging to that second food, then this plasticity might offer the selective context in which enhanced cognition could provide advantages. In other words, in the same way that food storing and brood parasitism are seen as biological traits that can select for enhanced spatial memory, opportunism might select for innovativeness.

Over the years, several factors are likely to change innovation reports. Improvements in camera traps are likely to make more observable cases that might have been inhibited by human presence, in addition to multiplying observation time. Online videos are now also being used to assess novel avian behaviors ranging from taking food from the hands of humans (Møller and Xia 2020) to consuming alcohol (Tryjanowski et al. 2020). Radar analyses have also revealed new coordinated prey searching movements over several kilometers by seabirds, but for now the methods are not precise enough to identify birds at the species level (Assali et al. 2020).

Finally, the concept of innovation now appears to be sufficiently mainstream for recent papers on the possible role of phenotypic plasticity in the foraging ecology of corellas and Galahs (*Eolophus roseicapilla*) in urban Melbourne to state that it *did not* (my emphasis) involve innovation (Lill and Polley 2020, Polley and Lill 2020). This is in contrast to an earlier study on Little Raven (*Corvus mellori*) by the same research group, in which they concluded that innovative feeding *did* (my emphasis) play a role in Little Raven urbanization in the same city (Lill and Hales 2015). This type of opposition between negative and positive statements is one of the controls that Byrne and Whiten (1987) used in their survey of primate tactical deception, asking their informants which species had been seen performing possible instances of deception, but also which species had *not* despite years of observation in the field. Negative observations like those of Lill and coauthors need to be more frequent, to help guard against confirmatory biases in innovation reports that

might be more often expected in large-brained, urbanized species such as Galahs and corellas.

The current extended focus on conservation might further increase observations of unusual foraging by endangered species, even if general trends suggest that endangered taxa are less innovative than those of least concern (Ducatez et al. 2020). One recent example of this is the population of Malherbe's Parakeet (*Cyanoramphus malherbi*) brought to predator-free Maud Island, which has increased from 11 captive-bred individuals to 97 birds from 2007 to 2009 (Ortiz-Catedral et al. 2012), in part due to flexible foraging on 14 previously unreported plant species (Ortiz-Catedral and Brunton 2009). Innovativeness is thus an important tool to understand the way behavioral plasticity can contribute to survival and reproductive success in normal (Cole et al. 2012, Cauchard et al. 2013) or novel (Sol et al. 2005a) conditions, but also to offer hope for threatened taxa.

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