

The fossil record of bird behaviour

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Abstract

Between the Middle Jurassic and Holocene, birds evolved an enormous diversity of behaviours. The distribution and antiquity of these behaviours is difficult to establish given a relatively poor fossil record. Rare crop, stomach and gut contents typically reveal diets consistent with morphology but stem-members of some lineages (including Cariamae and Coraciiformes) seem to have been different in ecology from their extant relatives. Most of our ideas about the behaviour of fossil birds are based on analogy (with skull form, limb proportions and claw curvature being used to guide hypotheses). However, this has limitations given that some extinct taxa lack extant analogues and that some extant taxa do not behave as predicted by osteology. Reductionist methods have been used to test predation style and running ability in fossil taxa including moa, *Gastornis* and phorusrhacids. Virtually nothing is known of nesting and nest-building behaviour but colonial nesting is known from the Cretaceous onwards. Rare vegetative nests demonstrate modern nest-building from the Eocene onwards. Ornamental rectrices indicate that sexually driven display drove some aspects of feather evolution and evidence for loud vocal behaviour and intraspecific combat is known for some taxa. Our knowledge of fossil bird behaviour indicates that 'modern' behaviours are at least as old as crown birds. Stem-members of extant lineages, however, may sometimes or often have differed from extant taxa.

Introduction

Birds are among the most extensively studied of organisms, a fact we owe to their convenient body size, the ease with which they can be observed in the field and laboratory, their reliance on visual signals, and their diversity. Such aspects of behaviour as migration, feeding, sexual and social display, and nesting are well documented. The construction of vegetative nests, extensive pre- and post-hatching parental care, egg brooding, mating displays and other behaviours are present within all major branches of the avian tree (Palaeognathae, Galloanserae and Neoaves), and hence were plausibly present in the common ancestor of these lineages (taxonomic names used here are illustrated in Fig. 1). We can thus predict 'modern' behaviours across fossil birds, so long as they appear reasonable on the basis of data on morphology, life appearance, habitat preference and ecology (Fig. 2). However, we face at least three problems in making such inferences.

Firstly, while speculations about such behaviours are not unreasonable, they rely on numerous assumptions, ignore the possibility that extinct species were novel in aspects of behaviour and remain unsatisfying when not backed by evidence.

Secondly, most of our ideas about the behaviour and lifestyles of fossil birds are based on morphological analogy: that is, on comparisons made between the body shapes and skull and pedal morphologies of extinct species with what we know about ecomorphological correlations in extant ones. An enormous

number of such inferences have been made (Fig. 2). This technique has limitations given that some fossil taxa lack extant parallels. Furthermore, some living birds do not behave as we might predict based on anatomy, a subject that is little discussed but demonstrated to occur within both extant (e.g. Smith & Redford, 1990), and fossil species (e.g. Munk & Sues, 1993). To point to examples among extant birds: the Palm-nut vulture *Gypohierax* has a predatory bauplan but is exclusively frugivorous, while Capercaillies (*Tetrao urogallus*) are occasional predators (Berthold, 2004).

Thirdly, all of the behaviours discussed so far have only been documented across crown-birds, leaving us speculating as to the presence and/or antiquity of these behaviours across stem taxa. Much has been inferred on the basis of what we know about non-avian theropods and extant birds, but data is scant.

In the following review, areas of evidence that provide insight into the behaviour of fossil birds are discussed in order of perceived robustness and reliability.

Crop, stomach and gut contents, coprolites and emetolites

Direct evidence for diet in fossil birds is rare (Table 1). Single records do not reliably demonstrate preferred diet and it is conceivable that stomach contents represent atypical food choice and cause of death.

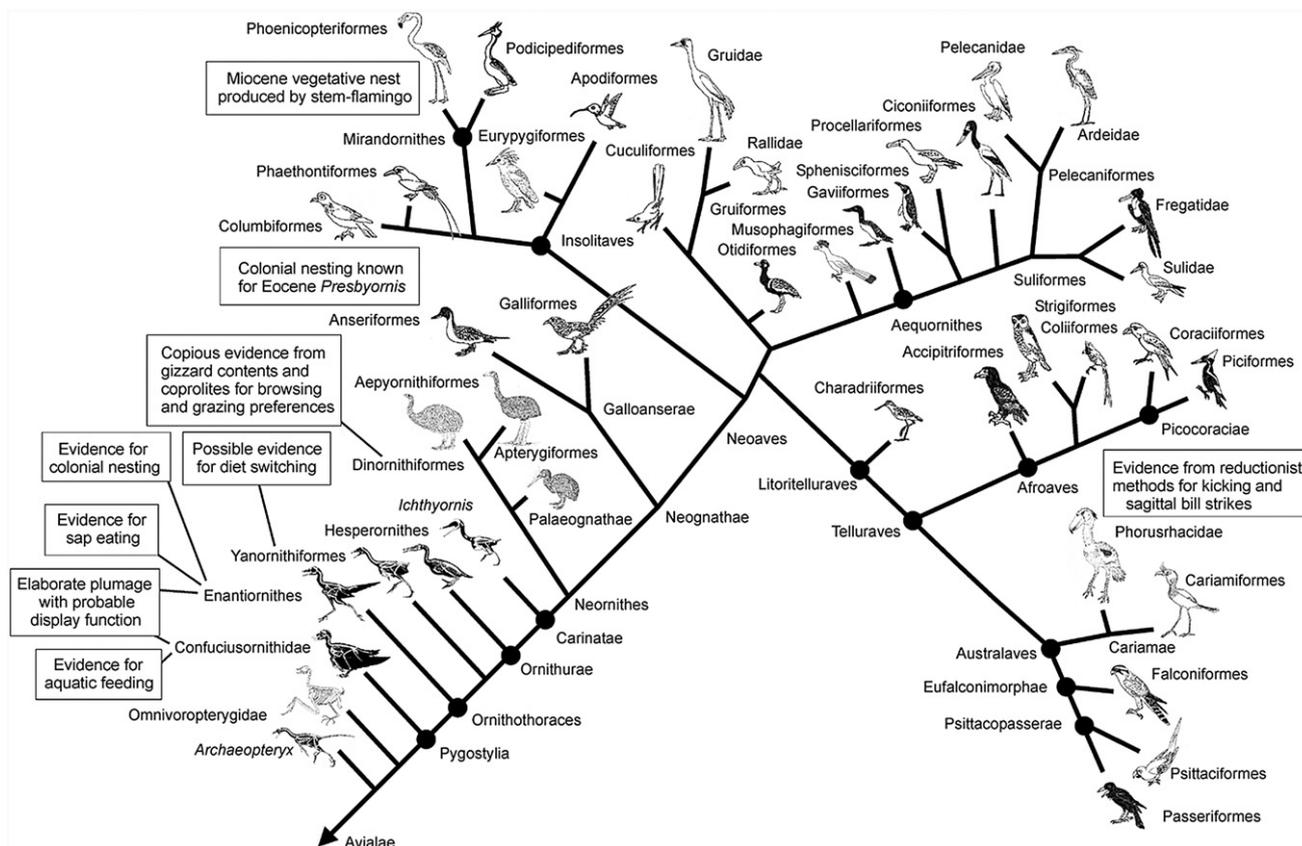


Figure 1 Simplified cladogram for Avialae, with select insights into the behaviour of fossil taxa shown adjacent to relevant taxa. Nomenclature and topology based on Naish (2012) and Yuri *et al.* (2013).

Several Cretaceous birds preserve food items. Crustacean remains in *Eoalulavis* (Sanz *et al.*, 1996) and fish in *Confuciusornis* (Dalsätt *et al.*, 2006), *Yanornis* (Zhou *et al.*, 2004) and *Baptornis* (Martin & Tate, 1976) are consistent with the assumption that stem-birds were predators of aquatic prey. However, other stem-birds reveal more diverse diets: a *Jeholornis* contains over 50 *Carpolithus* ovules (Zhou & Zhang, 2002) (Fig. 3), the holotype of *Enantiophoenix* preserves resin in its body cavity (Dalla Vecchia & Chiappe, 2002), while the presence of fish and gastroliths in *Yanornis* suggests the earliest instance of diet switching (the sometimes seasonal ability to switch from a fish-based diet to one dominated by plants; Zhou *et al.*, 2004). Gastroliths are present in other terrestrial Cretaceous birds (e.g. Zhou & Zhang, 2003; Zhou, Zhou & O'Connor, 2013) and appear to correlate with an herbivorous diet. Gastroliths appear to be absent from confuciusornithids and enantiornithines.

These records hint at a diversity in the feeding behaviour and ecology of Mesozoic birds. Furthermore, the assumption that stem-birds were predominantly or wholly animalivorous or piscivorous has been partially based on the presence of carnivory in bird ancestors. This assumption seems simplistic given that omnivory and perhaps herbivory were widespread in non-avian maniraptorans (Zanno & Makovicky, 2011): the ancestral condition for Avialae may have been omnivory.

Among Cenozoic birds, evidence of diet is similarly rare (Table 1). Stomach and gut contents mostly show the diets we would predict. There are, however, some surprises. Small stones preserved within fossil gamebirds show that a large crop was present in Late Oligocene members of the crown clade but not in Eocene stem-galliforms (Mayr, 2006). The holotype of *Strigogyps sapea* preserves plant material in its crop and stomach or gut regions (Mayr & Richter, 2011): this is interesting given that this taxon is apparently a member of Cariamae, a clade noted for predatory habits. *Strigogyps* has a proportionally small skull compared with other members of Cariamae, so may have been a herbivore or omnivore. Extant rollers (Coraciiformes) are predominantly predators of insects and small vertebrates but fruits are preserved as stomach contents in the Eocene stem-roller *Primobucco* (Mayr, Mourer-Chauviré & Weidig, 2004). Another stem-roller, *Eocoracias*, has a large (11.3 × 5.5 mm), bean-shaped seed, surrounded by grit, in its body cavity (Mayr & Mourer-Chauviré, 2000). These specimens suggest that early rollers were omnivores (or even frugivores?) and that a transition to animalivory occurred between these stem taxa and crown rollers (Clarke *et al.*, 2009). The presence of gastroliths in the Paleocene or Eocene suliform *Protoplotus* is surprising given that this taxon was apparently an aquatic predator; the gastroliths may have functioned as ballast (van Tets, Rich &

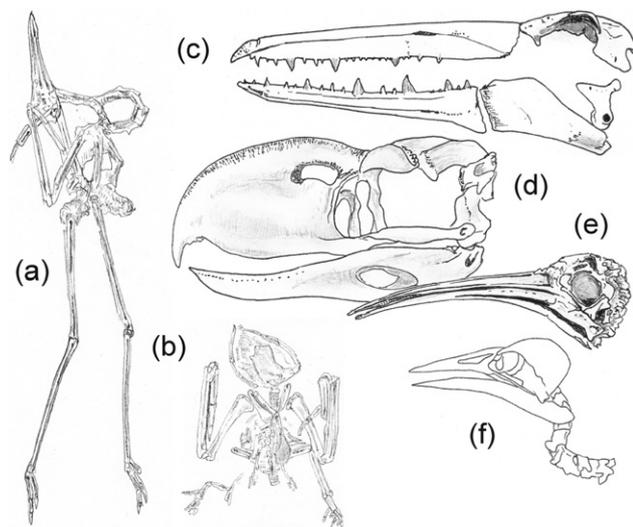


Figure 2 Numerous anatomical features present in fossil birds allow us to make inferences about behaviour. (a) Exceptionally long, slender legs in *Juncitarsus merkei* suggest wading habits. (b) The wide jaws, short feet and wing proportions of *Paraprefica kelleri* suggest that it lived in a similar way to modern potoos. (c) The long, pointed jaws, intramandibular joint and pseudoteeth of *Pelagornis chilensis* indicate that this marine bird grabbed pelagic prey. (d) The massive, hooked jaws of the cariaman *Phorusrhacos inflatus* indicate predation on vertebrates. (e) The slender, decurved jaws of *Rhychaeites messelensis* suggest probing behaviour in this Eocene ibis. (f) Jaws suited for probing and a massive retroarticular process suggest that the colliiform *Chascacocolius cacicrostris* gaped in the manner of extant starlings and icterids. Images not to scale.

Marino-Hadiwardoyo, 1989) or might provide evidence for diet switching between fish and plants.

Fossil coprolites are rare and mostly produced by recently extinct or extant taxa (Horrocks *et al.*, 2008). Coprolites produced by the moa-nalo *Thambetochen* show that these birds were folivores that consumed ferns (James & Burney, 1997). Moa coprolites (Horrocks *et al.*, 2004; Wood *et al.*, 2013) show that moa consumed herbs and were rhea- or ostrich-like in feeding ecology when in open habitats (Wood *et al.*, 2008).

Carnivorous, piscivorous and insectivorous birds eject gastric pellets or emetolites (Myhrvold, 2012). These are as yet unreported as fossils though birds themselves are the contents of two Cretaceous emetolites (Sanz *et al.*, 2001; Dalla Vecchia & Chiappe, 2002). Decomposed raptor and owl pellets, often produced by extant species, are known (e.g. Andrews, 1990; Worthy & Holdaway, 2002) and an extensive literature documents pellet form and content in extant taxa (e.g. Dodson & Wexlar, 1979; Hockett, 1996; Laroulandie, 2002).

Anomalous mollusc shells and sedimentary particles

Anomalous mollusc shells can represent direct evidence for diet. In the modern world, the remains of deep-water molluscs

(collected in or below seabird colonies) are frequently mixed with the shells of intertidal species. Lindberg & Kellogg (1982) concluded that these represent prey collected by cormorants and guillemots offshore, discharged with their droppings. Deep-water molluscs discovered within Pliocene and Pleistocene assemblages dominated by nearshore taxa may have originated in the same way. It may be possible to gain insight into the feeding preference and diving depth of extinct seabirds if specific mollusc prey could be matched to bird taxa. Lindberg & Kellogg (1982) speculated that freshwater bathymetric anomalies might exist as well. California condors (*Gymnogyps californianus*) also transport modern and Pleistocene mollusc shells (Collins, Snyder & Emslie, 2000) and may also explain anomalous occurrences of fossil molluscs.

Migratory habits were presumably widespread in fossil birds but it is difficult to document such behaviour [though insights into the migratory behaviour of ancient populations come from phylogeographic patterns: e.g. Jones *et al.* (2005)]. Quartz grains in Holocene sediments on Bermuda almost certainly represent sediment transported annually by birds (of uncertain species) from the North American mainland (Rueger, 2004) and thus preserve evidence for prehistoric migratory behaviour.

Direct evidence for predatory behaviour

The shapes of skulls, pedal phalanges and so on demonstrate predatory behaviour in numerous extinct birds (see ecomorphological correlations, below), many of which are close relatives of extant owls and raptors. However, direct fossil evidence demonstrating predatory behaviour in fossil species is rare. In cases, inferences about prey preference have been made based on associated fauna (Goodman, 1994; Mitev & Boev, 2006). A Pleistocene assemblage of broken mammal bones from Corsica, including remains of the deer *Megaloceros cazioti*, compares well in terms of the representation of skeletal elements and digestion damage with Lammergeier *Gypaetus barbatus* ossuaries (Robert & Vigne, 2002). Mammal bones from the Upper Pliocene of Taung, South Africa, have been suggested to represent the remains of prey accumulated by a large raptor, most likely Crowned eagle *Stephanoaetus coronatus* (Berger & McGraw, 2003), although scepticism remains (de Ruiter *et al.*, 2010).

The New Zealand eagle *Harpagornis* (or *Hieraaetus*) *moorei* has long been regarded as a predator of terrestrial birds, especially moa. Puncture marks on the pelvis of over 12 specimens (*Dinornis giganteus* among them) are believed to represent injuries caused by eagles (Worthy & Holdaway, 2002) in which case the eagle attacked the back and dorsal pelvis with one foot, presumably while crushing the neck base with the other.

Ecomorphological correlations

Several studies have linked morphology with behaviour or lifestyle: several aspects of rostral anatomy in particular allow

Table 1 Reported instances of crop, stomach or gut contents in the avialan fossil record

Taxon	Phylogenetic hierarchy	Geological age, horizon and location	Crop, stomach or gut contents	Reference
<i>Jeholornis prima</i>	Jeholornithidae, Jeholornithiformes, Avialae	Lower Cretaceous, Jiufotang Formation, Liaoning Province, China	>50 <i>Carpolithus</i> ovules	Zhou & Zhang (2002)
<i>Confuciusornis sanctus</i>	Confuciusornithidae, Confuciusornithiformes, Avialae	Lower Cretaceous, Jiufotang Formation, Liaoning Province, China	Single fish, cf. <i>Jinanichthys</i>	Dalsätt <i>et al.</i> (2006)
<i>Sapeornis chaoyangensis</i>	Omnivoropterygidae, Avialae	Lower Cretaceous, Jiufotang Formation, Liaoning Province, China	Seeds in crop, 'dozens of gastroliths' in stomach region	Zhou & Zhang (2003); Zheng <i>et al.</i> (2011)
<i>Enantiophoenix electrophyla</i>	Avisauridae, Enantiornithes, Avialae	Cenomanian (Upper Cretaceous), unnamed unit, Nammouira, Lebanon	Four small inclusions of amber (0.5–1.8-mm-long), suggesting sap feeding	Dalla Vecchia & Chiappe (2002)
<i>Eoalulavis hoyasi</i>	Enantiornithes, Avialae	Barremian (Lower Cretaceous), Caliza de Huérguina Formation, Cuenca, Spain	Crustacean exoskeletal elements	Sanz <i>et al.</i> (1996)
<i>Archaeorhynchus spathula</i>	Avialae	Lower Cretaceous, Yixian Formation, Liaoning Province, China	Gastroliths	Zhou <i>et al.</i> (2013)
<i>Hongshanornis longicresta</i>	Hongshanornithidae, Avialae	Lower Cretaceous, Yixian Formation, Liaoning Province, China	Mass of small seeds in crop; mass of gastroliths in gizzard	Zheng <i>et al.</i> (2011)
<i>Yanornis martini</i>	Yanornithiformes, Avialae	Lower Cretaceous, Jiufotang Formation, Liaoning Province, China	Fish in one specimen, numerous small gastroliths in another	Zhou <i>et al.</i> (2004)
<i>Baptornis advenus</i>	Baptornithidae, Hesperornithes, Avialae	Upper Cretaceous, Niobrara Chalk, Kansas, USA	Associated coprolites (or intestinal cast) containing small fish bones including <i>Enchodus</i>	Martin & Tate (1976)
<i>Dinornis giganteus</i>	Dinornithidae, Dinornithiformes, Palaeognathae, Aves	Holocene, mostly from Pyramid Valley, New Zealand	Numerous seeds, twigs, leaves and petioles (and occasional fruit) of numerous tree, vine, herb and grass or sedge species; also gastroliths	Worthy & Holdaway (2002)
<i>Emeus crassus</i>	Emeidae, Dinornithiformes, Palaeognathae, Aves	Holocene, from Pyramid Valley, New Zealand	Seeds, fruit and rare leaves of numerous plant species; also gastroliths	Worthy & Holdaway (2002)
<i>Euryapteryx geranooides</i>	Emeidae, Dinornithiformes, Palaeognathae, Aves	Holocene, from Pyramid Valley, New Zealand	Seeds, fruit and rare leaves of numerous plant species; also gastroliths	Worthy & Holdaway (2002)
<i>Anomalopteryx didiformis</i>	Emeidae, Dinornithiformes, Palaeognathae, Aves	Holocene, from New Zealand	Gastroliths	Worthy & Holdaway (2002)

<i>Palaeortyx cf. gallica</i>	Phasianidae, Galliformes, Galloanserinae, Neognathae, Aves	Upper Oligocene, Enspel Fossilagerstätte, Rheinland-Pfalz, Germany	Numerous small quartz pebbles in crop and stomach regions, also possible fibrous plant material in stomach and seeds in crop	Mayr, Poschmann & Wuttke (2006)
<i>Taubacrex granivora</i>	Galliformes, Galloanserinae, Neognathae, Aves	Upper Oligocene or Lower Miocene, Brazil	Gastroliths	Mayr (2000)
<i>Dromornis stirtoni</i>	Dromornithidae, ?Galloanserinae, Neognathae, Aves	Upper Miocene, Waite Formation, Australia	Gastroliths	Murray & Vickers-Rich (2004)
<i>Genyornis newtoni</i>	Dromornithidae, ?Galloanserinae, Neognathae, Aves	Pleistocene, unnamed unit, Lake Callabonna, Australia	Gastroliths	Murray & Vickers-Rich (2004)
<i>Ilbandornis woodburnei</i>	Dromornithidae, ?Galloanserinae, Neognathae, Aves	Upper Miocene, Waite Formation, Australia	Gastroliths	Murray & Vickers-Rich (2004)
<i>Strigogyps sapea</i>	Ameghinornithidae, Cariamae, Australaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Numerous storage cells from unidentified plant	Mayr & Richter (2011)
<i>Salmila robusta</i>	Salmilidae, Cariamae, Australaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Mass of unidentified material	Mayr (2002)
<i>Youngornis gracilis</i>	?Rallidae, Gruiformes, Neognathae, Aves	Middle Miocene, Shanwan Series, Shandong Province, China	Sand in stomach area, presumed to represent gizzard contents	Yeh (1981)
<i>Messelornis cristata</i>	Messelornithidae, Gruiformes, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Percoid fish <i>Rhenanoperca</i> preserved in area of oesophagus; seeds preserved in gut	Hesse (1990); Morio (2004)
<i>Primobucco frugilegus</i>	Coraciiformes, Picocoraciae, Afroaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Seeds	Mayr et al. (2004)
<i>Eocoracias brachyptera</i>	Eocoraciidae, Coraciiformes, Picocoraciae, Afroaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Single seed	Mayr & Mourer-Chauviré (2000)
<i>Primozygodactylus major</i>	Zygodactylidae, ?Picocoraciae, Afroaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Vitaceae and other (unspecified) seeds	Mayr (2009)
<i>Protoplotus beauforti</i>	Protoplotidae, Suliformes, Aequornithes, Neognathae, Aves	Paleocene, unnamed unit, Sumatra	Dense mass of quartz pebbles	van Tets et al. (1989); Zhou et al. (2004)
<i>?Colymboides metzleri</i>	Gaviiformes, Aequornithes, Neognathae, Aves	Lower Oligocene, Grube Unterfeld, Baden-Württemberg, Germany	Densely packed remains of small fish	Mayr (2004b)
<i>Oligocolius psittacocephalon</i>	Coliiformes, Afroaves, Neognathae, Aves	Upper Oligocene, unnamed unit, Enspel, Germany	Eight fruit stones in gastrointestinal tract, six in crop region, two in stomach or gut region	Mayr (2013)
<i>Eoglaucidium pallas</i>	Sandcoleidae, Coliiformes, Afroaves, Neognathae, Aves	Middle Eocene, Messel Formation, Germany	Annonaceae seeds	Mayr & Peters (1998)

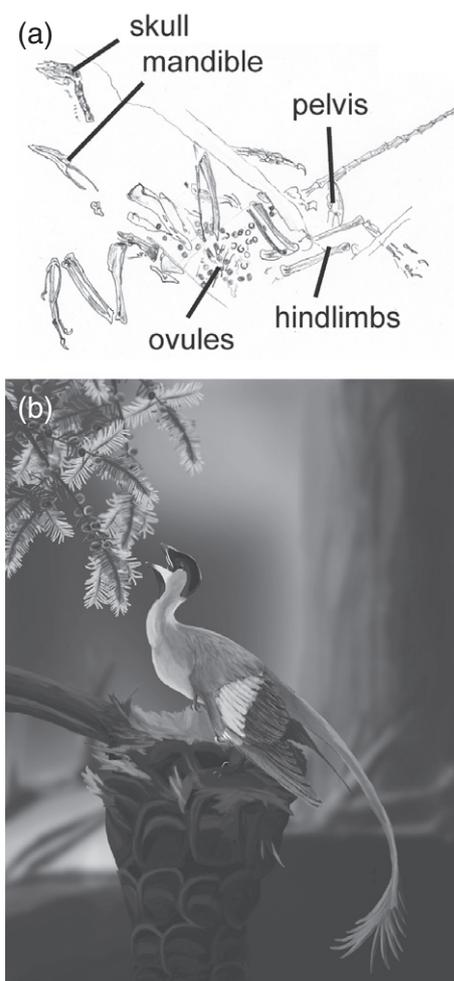


Figure 3 Fossilized stomach or gut contents can give insights into the behaviour of an extinct taxon, sometimes altering views on assumed ecology and behaviour. A caveat, however, is that data from a single specimen might be misleading. (a) Skeleton of *Jeholornis prima* from the Jiufotang Formation of Liaoning Province, China. Note numerous ovules within body cavity. Based on photograph in Zhou & Zhang (2002). (b) Seed-eating behaviour in *Jeholornis prima*. Image by Matthew Martyniuk, used with permission.

predictions with respect to lifestyle and behaviour (e.g. Hertel, 1995; Nebel, Jackson & Elner, 2005). In fossils, the form of the rhamphotheca is frequently unknown: note that, in some taxa, bill form is not reliably reflected by bony anatomy (Burton, 1974).

Toothed birds could yield tooth wear data that might provide direct evidence of diet; to date, observations have been limited to basic tooth form. The teeth of toothed birds frequently lack denticles, striations and other features that might be informative with respect to diet (the enantiornithine *Sulcavis* is an exception; O'Connor *et al.*, 2013). Among enantiornithines, dental and rostral morphologies have been suggested to indicate mud-probing, carnivory, piscivory,

insectivory and durophagy (Hou *et al.*, 2004; O'Connor *et al.*, 2013). These are reasonable inferences, but data from stomach or gut contents or tooth microwear is required.

Limb bone proportions, foot and wing morphology and overall shape and size also provide obvious indications of behaviour and numerous studies document ecomorphological correlations across extant birds (e.g. Leisler & Winkler, 1984; Winkler & Leisler, 1985; Barbosa & Moreno, 1999). These methods have been applied to fossil birds (e.g. Hinic-Frlog & Motani, 2010; Wang, McGowan & Dyke, 2011; Nudds *et al.*, 2013) but sometimes give conflicting results when applied to Mesozoic taxa (Hopson, 2001; Elzanowski, 2002). Numerous additional aspects of behaviour – including roosting habit, migratory abilities, take-off and landing techniques, anti-predator strategies, methods of intraspecific combat and mating systems – could be determined via analysis of skeletal proportions. Within galliforms, Mayr (2000) showed that migratory or semi-migratory taxa have proportionally longer wing skeletons than non-migratory taxa.

Several efforts to use claw curvature as an indicator of lifestyle have been published; the latest (Birn-Jeffery *et al.*, 2012) concluded that, while there is a general correlation between claw curvature and terrestriality or arboreality, there is overlap between the members of different ecomorphological classes, there are outliers and exceptions, and the claws of different digits can give different results.

Insights into behaviour from reductionist methods

Quantitative biomechanical studies can do more than inform us with respect to the possible loading and stress that a structure or organism underwent during life: they can generate and test specific hypotheses on behaviour. Ideally, this needs to be combined with inferences made from analogy, and with data from stomach contents, ecology and palaeoenvironment, before it can be considered reliable.

Blanco & Jones (2005), for example, tested the possible running speeds of extinct flightless birds by comparing tibiotarsal strength with that of extant ratites. By combining data on estimated body mass with limb bone lengths and bone cross-sectional data, these authors provided running speeds of 14 m s^{-1} for *Patagornis* (viz, similar to that of extant *Struthio*), 27 m s^{-1} for *Mesembriornis* and an incredible 31 m s^{-1} for *Anomalopteryx*. Because the more extreme of these speeds appear unlikely, they suggested that bone wall strength in these taxa might provide unreliable results, and that the bones were thickened for another reason. Alexander (1983) concluded that extremely thick bone walls in the tarsometatarsi of the moa *Pachyornis* provided extra strength for terrestrial locomotion. Blanco & Jones (2005) concluded that bone strength in *Mesembriornis* was linked to use of hindlimb strength in bone breaking and hence feeding behaviour. This provides a specific insight into the possible behaviour of this taxon, and one that appears plausible given the inferred similarity between smaller phorusrhacids and the extant *Sagittarius*.



Figure 4 Evidence for colonial, waterside nesting at the Upper Cretaceous Oarda de Jos site, Romania. (a) Matrix packed with eggshell fragments, bones and complete or near-complete eggs (marked with arrows). Scale bars = 10 mm. (b) Reconstruction of Oarda de Jos site. Illustrations by Julio Lacerda, used with permission.

Biomechanical modelling has most frequently been applied to cranial bones, though few such studies have been published on fossil birds. Witmer & Rose (1991) tested the inferred predatory lifestyle of *Gastornis* via a static mechanical analysis, concluding that it could exert phenomenal crushing force with its bill. They argued that these forces exceeded those required for herbivory but were more consistent with predation and scavenging. Mayr (2009) argued that the inferred bite strength is not inconsistent with a diet that might involve seeds and twigs.

Degrange *et al.* (2010) applied finite element analysis to the phorusrhacid *Andalgalornis* and reported evidence for a lack of cranial kinesis. They also found that the rostrum was poor at resisting lateral stress but performed better when placed under vertical load. Accordingly, they suggested that *Andalgalornis* avoided subduing large prey with the bill and either that it specialized on small prey that could be swallowed whole, or that it used the bill to inflict precise, sagittal strikes.

Feeding traces

Fossil bird tracks are typically identified as those of charadriiforms or charadriiform-like neornithines. Lower Cretaceous tracks from La Rioja, Spain, apparently produced by several species of different body sizes, are unusual in that many are oriented in the same direction: an observation suggesting that the birds were moving in parallel along the shoreline; gregarious behaviour among members of the same species is documented in Oligocene sediments from Spain (Lockley & Meyer, 2000). Peck and probe marks associated with bird tracks are known from the Lower Cretaceous of South Korea (Falk, Hasiotis & Martin, 2010) and appear to show a shorebird-like taxon foraging in the same manner as extant waders. Dabbling marks from the Green River Formation are associated with web-footed tracks presumably created by the anseriform *Presbyornis* (Lockley & Hunt, 1995).

Reproductive behaviour, and eggs, nests and nest mounds

Eggs and eggshell fragments produced by ground-nesting birds are well represented in the fossil record from the Lower

Cretaceous onwards (Zhou & Zhang, 2004). An eggshell and bird bone assemblage from the Upper Cretaceous of Romania (Fig. 4) shows that at least some enantiornithines nested in waterside colonies (Dyke *et al.*, 2012). Fernández *et al.* (2013) reported a similar enantiornithine nesting colony in the Upper Cretaceous of Argentina; in this case, *in situ* eggs (some containing embryonic remains) show that these birds produced scrape-like nests and planted their eggs vertically in the substrate. The latter feature indicates that enantiornithines did not turn their eggs. Colonial nesting is not otherwise known in avialans until the Cenozoic but these discoveries raise the possibility that it was widespread in pygostylians at least. Nesting colonies produced by *Presbyornis* are known from the Lower Eocene and perhaps Upper Paleocene (Leggitt, Buchheim & Biaggi, 1998). These colonies represent mass death assemblages where hundreds or thousands of birds died over a short space of time, presumably due to botulism or similar poisoning.

There has been substantial interest in reconstructing the ancestral reproductive strategy used by birds (Wesołowski, 2004). Specialists on Mesozoic dinosaurs have suggested that brooding, nest guarding and parental manipulation of eggs either evolved within non-avian theropods, or were inherited from earlier dinosaurs. According to this view, such behaviours were inherited by birds; at the same time, so was terrestrial brooding and precociality. There is support for this view (Schweitzer *et al.*, 2002; Zhou & Zhang, 2004), but it is partly based on negative evidence: that arboreal nests remain unknown for Mesozoic birds and non-avian theropods, for example, may reflect bias in the fossil record since arboreal nests are also unreported for Cenozoic birds.

Indeed, while it is assumed that fossil birds belonging to numerous lineages constructed nests similar in form to those made by living species, fossil nests are extremely rare. The burrows and nest mounds produced by megapodes have a high theoretical preservation potential and some hillocks produced by the Orange-footed megapode *Megapodius reinwardt* have been dated to over 1500 years old (Stone, 1991). Enormous mounds on New Caledonia – some 50 m across and 4–5 m high – have been interpreted as nest mounds produced by the megapode-like galliform *Sylviornis* (Mourer-Chauviré & Popin, 1985). Cave nesting sites (though not actual nests) used by California condors *Gym. californianus* have been dated to between 9585 and 22 180 years before present and

contain bones and teeth belonging to horses, bison, mountain goats, camels, and mammoths (Emslie, 1987).

A handful of fossil nests have been reported. Lambrecht (1933) described a vegetative nest from the Miocene of Germany, suggested to be that of a duck, and possible Eocene and Oligocene nests (also ascribed to ducks) have been mentioned (Boucot, 1990). Grellet-Tinner *et al.* (2012) described a twig nest and five associated eggs from the Lower Miocene of Spain, identified as that of a stem-flamingo, an identification confirmed by eggshell microstructure. The nest seems to have been a floating mat of vegetation and thus unlike the mud mounds constructed by extant flamingos; however, it is similar to the nests constructed by grebes, a group hypothesized to be the flamingo sister-clade (Van Tuinen *et al.*, 2001; Mayr, 2004a). In extant flamingos, clutch size is one, whereas it is 2–7 in grebes. This further suggests that the Spanish taxon was unlike crown-flamingos in reproductive behaviour. A cavity preserved in a piece of Eocene-age wood from the US was interpreted by Buchholz (1986) as a nest cavity produced by a modern woodpecker. While the cavity may have been produced by a bird, this precise identification is unlikely to be correct.

An enormous amount of data has been collected on egg and clutch size, incubation period and the timing of chick development in extant birds. Accordingly, it is possible to make predictions about the reproductive biology and behaviour of extinct birds when we have data on their affinities and body masses. Palmqvist & Vizcaíno (2003) made predictions about the life history of the teratornithid *Argentavis* and suggested extremely low reproductive turnover in this bird (estimated 0.78 eggs per year, estimated 484 days between clutches). They also predicted a gigantic territory size of 542 km² for *Argentavis*. As noted by Palmqvist & Vizcaíno (2003), some of these extrapolations may be erroneous since they are based on the assumption that *Argentavis* was similar to a hawk or eagle: teratornithids are most likely relatives of condors and New World vultures, but there are indications from their ecomorphology that they may have combined terrestrial behaviour with aquatic feeding as well as soaring (Campbell & Tonni, 1983; Hertel, 1995).

Inferred sociosexual display

Among extant birds, we can infer several aspects of behaviour from plumage and other epidermal structures, and from tracheal, syringeal and pedal morphology. The modified plumes, remiges and rectrices of many birds correlate with sexual display, as do the less spectacular rectricial streamers of hummingbirds, tropicbirds and others (e.g. Andersson, 1992; Veit & Jones, 2003). It seems reasonable to make similar inferences based on the existence of such extravagant structures in fossil taxa (Knell *et al.*, 2013). A frond-like rectricial array is known for *Jeholornis* (O'Connor *et al.*, 2012) while four, ribbon-shaped caudal structures that are probably feather homologs are known for *Epidixipteryx*, a member of the probable avialan clade Scansoriopterygidae (Zhang *et al.*, 2008). Similar strap-like caudal feathers, sometimes with racket-like tips, are present in confuciusornithids and some enantiornithines. These structures are similar to the display

rectrices of whydahs, motmots and paradise kingfishers and it is difficult to imagine what role they might have other than display: a widespread assumption among palaeontologists that sexual dimorphism has to be demonstrated before a given structure can be posited as one driven by sexual selection pressure ignores the existence of mutual sexual selection in extant birds and other animals, and its possible presence in fossil taxa (Hone, Naish & Cuthill, 2012).

Histological data indicates that Cretaceous birds like confuciusornithids and enantiornithines differed from crown-birds in reaching sexual maturity before they had reached adult size (Ericson *et al.*, 2007). This condition (inherited from non-avian dinosaurs) means that individuals of diverse sizes and ontogenetic stages were potentially part of the same breeding pool, in which case they were very different from modern birds. It remains unknown how this difference would have been manifested in social and reproductive behaviour: a fascinating topic for speculation.

Exchanges within the literature have focused on the hypothesis that the long tail feathers in *Confuciusornis* are limited to males: this now appears correct (Chinsamy *et al.*, 2013). Among extant birds, sexually dimorphic plumage is present in both polygamous and monogamous species (Owens & Hartley, 1998) but dimorphism in plumage length appears linked with social polygyny (Björklund, 1990). Ribbon-like feathers preserved adjacent to the back of the Middle Eocene owl *Palaeoglaux atophoron* were suggested by Peters (1988) to be ornamental. The presence of display feathers in an owl would be unusual, implying that *Palaeoglaux* was more diurnal than extant taxa. Mayr (2009), however, argued that these were an artefact. A structure interpreted as a soft cranial crest in the messelornithid *Messelornis cristata* was argued to be a misplaced patch of organic tissue by Mayr (2009).

Several additional structures may also give insights into behaviour. Tarsal spurs in fossil galliforms (e.g. Mourer-Chauviré, 1989) indicate intraspecific combat like that present in extant taxa (though note that a correlation between spur form and mating system was found unreliable by Sullivan & Hillgarth, 1993). Carpometacarpal spurs and inflated extensor processes in archaeopterygids (Mayr, 2009), the flightless pigeon *Natunaornis* (Worthy, 2001) and Pleistocene lapwings (Campbell, 2002) suggest that these taxa fought intraspecifically and/or interspecifically with their wings. A roughened area on the carpometacarpal extensor process of *Phorusrhacos* led Andrews (1901) to suggest the presence of a spur or knob used in intraspecific combat. The club-like, thick-walled carpometacarpal of the Jamaican ibis *Xenicibis* were interpreted by Longrich & Olson (2011) as weapons used in combat. Such a role is supported by the presence of healed carpometacarpal and humeral injuries in two specimens.

Approximately 60 extant bird species possess long, coiled tracheae that virtually always correlate with the production of loud, far-carrying calls (though alternative functions have been proposed; Fitch, 1999). Accordingly, it is likely that fossil birds possessing enormous coiled tracheae were also able to generate loud noises. A tracheal loop 1.25 m long, extending across the left side of the body before looping back to the

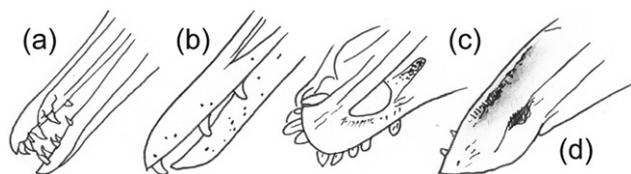


Figure 5 Specialized, anteriorly restricted, reduced dentitions in Mesozoic birds. While trophic adaptation is assumed to have driven the evolution of these teeth, it is conceivable that they played a key role in preening. (a) *Longipteryx chaoyangensis*, (b) *Longirostravis hani*, (both after O'Connor & Chiappe, 2011), (c) premaxillary dentition in *Sapeornis chaoyangensis* (after Zhou & Zhang, 2003), (d) dentary dentition in *Jeholornis prima* (after Zhou & Zhang, 2002). Not to scale.

anterior edge of the sternum, is known for some moa (Worthy & Holdaway, 2002).

Topics for consideration

Here, I would like to make some speculations about the behaviour of fossil birds that might one day be informed by fossil discoveries that would enhance our understanding of the evolutionary background to the respective aspects of behaviour.

An example concerns preening behaviour. Not only do birds with damaged plumage face problems of aerodynamics and thermoregulation, they are less attractive as mates (Clayton, 1990) and may be at increased risk of death (Clayton *et al.*, 1999). It can therefore be assumed that birds and other feathered dinosaurs have been grooming or preening their plumage ever since feathers originated. Mesozoic arthropods that were possible parasites of feathered theropods are known, and the eggs of possible Mesozoic feather parasites were reported by Martill & Davis (2001) though later suggested to be ostracod eggs (Proctor, 2003). Given that incisiform, projecting anterior teeth are present in numerous Mesozoic birds (Fig. 5), oviraptorosaurs and other coelurosaurs, it is tempting to suggest that dental reduction and evolution in birds and other coelurosaurs was driven (in part) by selection for use of the teeth in preening. This hypothesis might be testable: in mammals, microscopic 'grooming grooves' form as teeth are drawn through the pelage (Rose, Walker & Jacobs, 1981). This renders it possible that the teeth of other animals might have been marked by use in grooming or preening.

Several roosting, nesting, display and food-storage structures constructed by modern birds have a high preservation potential and belong to lineages that have long evolutionary histories, yet remain unknown as fossils. Examples include the bowers of bowerbirds, mud nests of ovenbirds, nest cavities of hornbills, giant (sometimes colonial) nests of hammerkops, weaverbirds and monk parakeets, and cache sites of corvids and woodpeckers.

Conclusions

The generally accepted tenet that forms leads to function means that palaeontologists have been able to make numerous infer-

ences about fossil bird behaviour. Furthermore, the many fossil bird species similar to extant ones likely exhibited similar behaviours. However, exceptional cases where behaviour is *not* predicted by anatomy, the evolution of novelty, and the absence of extant analogues means that there are many areas of bird palaeobehaviour where we are being misled or remain ignorant. The lack of data pertaining to fossil bird behaviour is obvious, but so is the lack of study: the application of morphometrics and reductionist methods is becoming more popular and is aiding the construction of ecomorphological hypotheses. However, simpler studies that document ecomorphological variation and link form with function and behaviour need to continue. Indeed, there is still a lack of this sort of work across many sections of the bird cladogram. However, we can still make several detailed observations about the behaviour of fossil birds and, for a few taxa at least, can make confident statements about some aspects of their behaviour.

As noted earlier, we would predict that many modern avian behaviours – including the construction of vegetative nests, extensive pre- and post-hatching parental care, and egg brooding – were present in the common ancestor of crown-birds, an animal that most likely existed during the Late Cretaceous (Lee *et al.*, in press). Stem members of some lineages may have differed morphologically and ecologically from their extant relatives but, in general, 'modern' behaviours have therefore been present throughout the Cenozoic, and at least since the latest Cretaceous. Outside of crown-birds, colonial nesting, diet switching and the use of elaborate plumage in sexual display was seemingly present in pygostylian lineages that diverged during the Early Cretaceous. In other respects, early pygostylians seem to have been archaic: they may not have turned their eggs and there is as yet no evidence for vegetative nests that pre-date the Cenozoic. Cretaceous groups like confuciusornithids and enantiornithines may have possessed a combination of both 'avian' and 'non-avian' behavioural traits, a hypothesis consistent with some aspects of their anatomy (e.g. Zheng *et al.*, 2013). However, we remain hindered by a lack of data and future discoveries may well extend the presence of 'modern' avian behaviours deeper into the Mesozoic.

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