Evolution of nest site use and nest architecture in birds and their non-avian ancestors (submitted final revision)

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Abstract

The evolution of nesting site use and nest architecture in the non-avian ancestors of birds remains poorly understood because nest structures do not preserve well as fossils. Nevertheless, the earliest dinosaurs probably buried eggs below ground and covered them with soil so that heat from the substrate fueled embryo development, whilst some later dinosaurs laid clutches that were partially exposed where adults could incubate them and protect them from predators and parasites. The nests of euornithine birds - the precursors to modern birds - were probably partially open but the neornithine birds - or modern birds - were probably the first to build fully exposed nests. The shift towards smaller, open cup nests over time has been accompanied by shifts in reproductive traits, with females having one rather than two functioning ovaries as in crocodilians and non-avian dinosaurs. The evolutionary trend among extant birds and their non-avian ancestors has been toward them building nests requiring greater cognitive abilities to build in a greater diversity of sites and providing more care for significantly fewer, increasingly altricial, offspring. The highly-derived passerines reflect this trend with most species building small, architecturally complex, nests in open sites and investing significant parental care into altricial young.

Keywords:
birds, crocodilians, dinosaurs, evolution, nest architecture, nest sites, nests

Introduction

There are over 10,000 extant species of birds worldwide and they use a variety of nest designs and nest sites (Fang et al. 2018). Nests are structures built with the express purpose of containing eggs and/or offspring, whilst nest sites refer to the location of nest sites (Hansell, 2005). Here we review the evolution of nest site selection and nest architecture by extant birds and their non-avian ancestors, whilst also considering the evolution of birds themselves. However, our understanding of the use of nest sites and nest architecture by ancient birds and their non-avian ancestors is incomplete because nests and their substrates do not preserve well as fossils (Deeming 2015).

Despite an increasing number of fossilised clutches of dinosaur eggs being found (Norell et al. 1994; Varricchio and Jackson 2004; Dhiman et al. 2023), the fossilised remains of nests remain rare, particularly for early dinosaurs such as sauropodomorphs (Figure 1). Based on clutch forms and eggshell porosity, sauropods primarily buried their eggs beneath the ground (Sander et al. 2008). As their nests were filled with muddy flood plain deposits, and thus in conditions not conductive to fossilization, discernible traces of their nests are only rarely preserved (Reisz et al. 2012). Pedogenic and diagenetic processes probably destroyed the nests of the earliest dinosaurs, yet our understanding has recently increased because of new fossils and the development of new analytical approaches (Grellet-Tinner et al. 2006; Brusatte et al. 2015; Hogan & Varricchio, 2023).

* Figure 1

Extant birds (clade Avialae) fall within Theropoda, the clade that includes all carnivorous dinosaurs, such as small species such as *Troodon* and *Velociraptor* and large species such as *Allosaurus* and *Tyrannosaurus* (Brusatte et al. 2015). Birds are hypothesized to be derived from within the less inclusive clade Pennaraptora, representing birds and their close relatives the troodontids, dromaeosaurids, and oviraptorosaurs (Xu et al. 2014; Brusatte et al. 2015). It is thought that birds (Avialians) evolved from pennaraptorans approximately 165-150 million years ago during the Jurassic period and had begun to diversify by the early Cretaceous, as confirmed by 120-130-million-year-old fossils found in China (Zhou et al. 2003; Xu et al. 2014). Enantiornithines were the dominant Avialian group during the Cretaceous as modern birds, members of the clade Neornithes, largely represent a post-Cretaceous radiation (Brussatte et al., 2015). Enantiornithines were decimated during a mass extinction event at the end of the Cretaceous period, as were the non-avian dinosaurs, but the neornithine survivors rapidly diversified and there are now over 10,000 bird species worldwide (Brussatte et al., 2015).

Evolution of nests and nest site use by non-avian ancestors

Early non-avian dinosaurs

Our understanding of the reproductive biology of the earliest dinosaurs remains relatively poor (Upchurch 1995; Grellet-Tinner and Chiappe 2004), yet the ecological context of fossil remains provide important insights into both the nesting sites and also the dispersion of nest sites. Saurischians are thought to be the earliest known clade of dinosaurs, and are thought to have laid unpigmented white eggs (Wiemann et al. 2015) below ground and covering them with substrate so that eggs were incubated by environmental heat sources such as soil moisture and thermoradiance, without any heat from incubating parents (Grellet-Tinner et al. 2006; Sander et al. 2008; Reisz et al. 2012). Incomplete skeletons of the sauropodomorph *Massospondylus*, which is a genus of prosauropod dinosaur from the early Jurassic Period, deposited a single layer of tightly packed eggs below ground (Reisz et al. 2012, 2013). Meanwhile, the fossilised remains of thousands of the nests of sauropods, who are believed to have descended from the prosauropoda, were found distributed within little over one square kilometre at Auca Mahuevo, Argentina, suggesting that hundreds of individuals nested colonially in that area (Chiappe et al. 1998). As the remains of vegetation were found in some of the nests then it is thought very probably that they used the heat from decomposing leaves to help incubate their clutches of 30-40 eggs (Chiappe et al. 1998). Titanosaur sauropod clutches of Europe (Sander et al., 2008) and India (Dhiman et al., 2023) were buried underground. There is evidence that sauropods repeatedly nested at a site with a peculiarly warm hydrothermal geology, which would have also facilitated incubation (Grellet-Tinner and Fiorelli 2010). Such behaviour can still be found in the extant megapodes, although the behaviour is a convergent trait evolved from ancestors which used body heat for incubation (Dekker and Brom 1992). For example, Australian brush-turkeys (*Alectura lathami*) bury their eggs in mounds of decomposing leaves, which provide heat sources for incubation (Eiby and Booth 2008, 2009), and Polynesian megapodes (*Megapodius pritchardii*) select nest sites which provide geothermal warming for incubation (Göth and Booth 2005).

The subterranean development of eggs of the earliest dinosaurs had important implications for nest architecture, egg characteristics, sex determination and parental care. Nests were simple scrapes or holes in the ground and the eggs were probably laid '*en masse*' in one ovideposition event, similar to modern reptiles, before being covered with substrate. The eggs were subspherical and had modular ornamentation that enabled air to flow easily in the nests and the eggshells were perforated by many pore canals as a result of high moisture content within nests (Grellet-Tinner et al. 2006). Deeming (2006) showed that compared to the eggs of extant birds, dinosaur eggs are thought to have had relatively thicker eggshells after controlling for egg size, with more pores which would have meant that water vapour conductance was significantly higher as well relative to shell size and thickness. The absence of parental incubation meant that dinosaur eggs were not turned, whilst all extant birds, except for megapodes and the three-banded courser (Kemp and MaClean 1973), turn them on a regular basis.

The eggs of the earliest dinosaurs were probably white (Wiemann et al. 2015, 2018) because they were buried and neither were exposed to potentially harmful UV light, nor were they visible to conspecifics or predators (Lahti and Ardia 2016; Hogan & Varricchio, 2023). It is probable that any role of the parents after egg laying was to protect the nest site and the benefits of group defence may explain why sauropods were colonial nesters (Chiappe et al. 1998). We are unaware of any studies quantifying the predation rates upon the nests of non-avian dinosaurs, yet it is intuitive that predators did prey upon the eggs of dinosaurs, where they were buried or not. Ruxton et al. (2014) estimated that the eggs of sauropods took 65-82 days to hatch and suggested that the small egg sizes and clutch sizes of sauropods, based on their enormous body sizes, were a result of high nest predation rates. The eggs of later dinosaurs were, however, coloured and speckled and such colouration and patterning is probably the result of the later dinosaurs beginning to leave their eggs unburied and incubating them themselves, so that the oviraptor probably sat on dark blue eggs which are better camouflaged than plain white eggs (Wiemann et al. 2018).

Nesting traces from Auca Mahuevo may indicate that these Argentinian clutches were incubated subaerially (Chiappe et al. 2004; Jackson et al., 2004; Sander et al. 2008), but this contradicts the high porosity eggshell indicative of buried incubation (Vila et al. 2010). The fossil evidence suggests that dinosaurs within the clade Pennaraptora began to lay their eggs closer to ground level so the eggs were partially exposed thereby representing an important shift in nest sites by the avian ancestors (Varricchio and Jackson 2016; Hogan & Varricchio, 2023). The shift to nesting fully above ground was gradual because taphonomic evidence suggests that these dinosaur nesters, such as oviraptorosaurs and troodontids (Pennaraptora), were probably the first dinosaurs to incubate their eggs (Tanaka et al. 2015). The shift from completely burying eggs below ground t having partially- or fully-exposed eggs is covered in more detail by Hogan & Varricchio (2023).

Late non-avian dinosaurs

The shift to partially exposed eggs is hypothesized to have been associated with changes in parental care (Tanaka et al. 2015). The discovery of oviraptorosaur and troodontid skeletons positioned atop of their eggs (see summary in Varricchio and Jackson 2016; Bi et al. 2020) indicates that they were incubating those eggs similarly to modern birds (Neornithes). However, it is thought that oviraptorid eggs were paired and arranged sub-horizontally up to three layers deep and as the parents do not appear to rotate them, then it was improbable that parents could effectively incubate all the eggs at once (Yang et al. 2019). Oviraptorids may have represented an intermediary phylogenetic precursor to incubation seen in extant birds (Grellet-Tinner et al. 2006) or a divergent behaviour (Yang et al. 2019). The increase in parental care among these dinosaurs may have contributed to the evolutionary radiation of pennaraptoran theropods (Hogan & Varricchio, 2023).

The increasing amount of care provided by parents for their offspring is encapsulated by the transition by which parents guarded their buried eggs through to incubating eggs and thus directly providing warmth for the embryos and protecting them against predators. The discovery of many well-preserved nests in Montana, North America, are therefore notable. The fossilised nests and eggs of either a dromaesaurid or a caenagnathid (Ornithoraptora) in the Two Medicine Formation from the late Cretaceous period indicate that the nest was in a sparsely vegetated area of freshly-deposited sand, implying it was close to an active river channel (Zelenitsky and Therrien 2008). A *Troodon* nest in the same rock formation indicates a bowl-shaped depression with a distinct rim which contained a tightly-packed clutch of 24 eggs. The size and shape of the nest, relatively tight clutch arrangement, and low organic carbon content of the overlying mudstone suggested the eggs were incubated by parents and not by environmental heat sources (Varricchio et al. 1999).

Troodon (Paraves) provides a crucial evolutionary link between their earlier crocodilian sister taxa in the Archosauria and their later avian relatives (Avialae) as whilst *Troodon* maintained partially buried eggs, probably without egg rotation similarly to crocodilians, their open nests, partially exposed eggs and parental incubation are similar to extant birds (Neornithes: Varricchio et al. 1999, 2008). The more compact clutches of both troodontids and some enatiornithines, suggest an intermediate role for the former and the persistence of buried eggs from non-avian dinosaurs thru Mesozoic birds (Varricchio and Jackson 2016), as is outlined more fully in Hogan and Varricchio (2023). Modeling of *Troodon* incubation suggests that contact incubating partially buried eggs would still confer an energetic advantage and provides “evidence for a possible evolutionary path from guarding behavior to thermoregulatory contact incubation” of modern birds (Hogan and Varricchio 2021).

The location and architecture of nests were probably influenced by clutch sizes, which appear to have declined over time from non-dinosaur archosaurs, through non-avian dinosaurs and on to extant birds (Brusatte et al., 2015). This pattern is probably due, at least in part, to more basal dinosaurs having two functioning ovaries, consistent with modern crocodilians (Varricchio et al. 1997; Grellet-Tinner et al. 2006). In contrast, evidence for pennaraptoran theropods suggests they retained two ovaries and oviducts but that they functioned in an avian fashion. Important specimens include clutches exhibiting egg-pairing and gravid oviraptorosaurs associated with two eggs (Sato et al. 2005, Jin et al. 2019). Modern birds have one ovary whilst crocodilians, sister taxa as the other extant archosaurs, have retained two ovaries. Fossil discoveries of some of the earliest birds (Avialae) in the form of the long bony-tailed *Jeholornis* and two enantiornithine birds, in rock formations from the early Cretaceous period at Jehol Biota in China, show they had one functioning ovary (Zheng et al. 2013). Thus, the shift from two ovaries to one occurred close to the origin of flight. This may represent an exaptation (Gould and Vrba, 1982) as eggs represent payloads that impact flight performance (Lee et al., 1996).

As derived theropod dinosaurs began to incubate partially exposed eggs, they also had pigmented eggs which were laid during several visits to nests presumably over several days. Wiemann et al. (2018) used high-resolution Raman microspectroscopy to show that although ornithischian and sauropod eggs were white, the later dinosaurs laid coloured and maculated eggs. These pennaraptoran theropods retained two ovaries each functioning in an avian-like manor, thus an adult would produce two eggs per day or greater intervals (Varricchio et al. 1997) so that, for illustration, a clutch of thirty eggs were laid over a minimum period of fifteen days. The later theropod dinosaurs are hypothesized to only have begun to incubate eggs after the final eggs were laid, so that clutches hatched synchronously (Varricchio et al 1999; Prum 2002).

The shift to incubating partially exposed eggs is hypothesized to have resulted in dinosaurs providing increasing amounts of care for offspring. Several adult oviraptorid fossils (Maniraptora) in Mongolia were lying on top of clutches of eggs and thus are interpreted to have been incubating eggs similarly to extant birds (Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999). Although Mesozoic birds (Enantiornithes and Ornithuromorpha) were probably too heavy to contact incubate their eggs (Deeming and Mayr 2018; but see Varricchio and Barta 2015), evidence suggests that non-avian ancestors provided increasing amounts of care for their precocial offspring. Dial (2003) hypothesised that shifts in nest elevation, architectural complexity and parental care were associated with decreasing clutch size and increasing altricial ontogeny. The evolution of increasingly sophisticated patterns of parental care was driven by the mutual reinforcement of different components of parental care and offspring behaviours; the evolution of food provisioning caused or enabled parents to select safer nest sites and also resulted in increased levels of sibling competition, which further selected for increased provisioning (Gardner and

Smiseth 2011). Nesting in increasingly safer nest sites was, therefore, associated with increasing altricial care and offspring begging behaviours.

Enantiornithines

The enantiornithines were the dominant Avialae during the Cretaceous period, and were contemporary with the dinosaurs. They are now extinct, but during the Mesozoic era, they were the most abundant and diverse group. Virtually all of the enantiornithines had clawed fingers on their wings and retained teeth but otherwise, had a similar morphology to modern birds (Brusatte et al. 2015). They are also commonly resolved as the sister to the Ornithuromorpha, the clade within which all living birds are nested (Wang et al., 2021). Our knowledge of their nests is poor (Mayr 2017), although several fossils provide useful insights (Varricchio and Barta 2015; Varricchio and Jackson 2016).

First, fossils from Argentina show that enantiornithine birds nested among sand dunes, close to an ephemeral water course in an arid landscape, and the eggs were laid either singly or sometimes in pairs and were half-buried in sand with their pointed end downwards which is hypothesized to have precluded egg turning (Figure 2: Fernández et al. 2013). Mongolian specimens also show eggs emplaced on end within substrates either singly as in Argentina or in clutches, with two preserved with poorly intact adults atop (Varricchio and Barta 2015; Varricchio and Jackson 2016). Second, fossils found in Romania suggest that they nested colonially (Dyke et al. 2012). There has, nevertheless, been disagreement over the nesting sites of perhaps the most famous Paravian, *Archaeopteryx*, because whilst some argue that they laid eggs below ground where they would have been incubated by environmental heat sources similarly to those used by crocodilians (Stephan 1987), others argue that they nested above ground (Wellnhofer 2009).

Fossil evidence suggests that enantiornithine birds buried their eggs in substrate (Mayr 2017) which means it was the primitive nest sites of birds and that nesting free of substrate was a derived characteristic that evolved in the euornithines (Figure 1). No fossils of the nests of early ornithuromorphs have been found (Mayr 2017) but they were probably simple scrapes lined with plant material, with such nests still being used by some of the basal neornithine birds such as galloanserines and paleognaths (Fang et al. 2018).

Fossil evidence suggests that enantiornithe birds provided some primitive forms of care to their offspring and although Varricchio and Barta (2015) assumed that as they sat on their partially exposed eggs, they may have been guarding their eggs as opposed to incubating them. The egg shapes of the enantiornithines and ornithuromorphs also differed because enantiornithine birds laid narrow and elongated eggs that resembled the eggs of the non-avian theropod dinosaurs, whereas ornithurine birds laid eggs that were comparatively larger and also less elongated (Mayr 2017).

* Figure 2

Despite the presence of enantiornithine birds, non-avian dinosaurs were the dominant vertebrate group during the Cretaceous period although their fate took a dramatic downturn during the mass extinction event that occurred at the end of the Cretaceous period, some 66 million years ago. It is widely agreed that some form of catastrophic event occurred although there is disagreement over what the event was and the severity of its effect because one school of thought suggests that dinosaurs and archaic birds were declining well before the mass extinction event. There is, however, a consensus that the mass extinction event was caused by the Chicxulub asteroid which caused rapid and catastrophic changes in environmental conditions via the inducement of earthquakes, wildfires, tsunamis and acid rainfall (Brusatte et al. 2015). There is also a consensus that neither dinosaurs nor the archaic birds were declining prior to the mass extinction event and pertinently, Longrich et al. (2011) provided evidence of a diverse avifauna, representing enantiornithes, ichthyornithes, hesperornithes and an apsaravis-like bird, in the fossil record of western North America shortly before the mass extinction event occurred. As none of these groups are known to have survived into the Paleogene, then they probably perished very rapidly during the Chicxulub asteroid impact. The enantiornithines were the dominant bird group during the Cretaceous period but after they had been decimated during the mass extinction event alongside the dinosaurs the neornithes, which are considered to be the first modern birds, radiated out and filled the spaces that the enantiornithine birds left behind (Longrich et al. 2011; Brusatte et al. 2015).

Neornithes

Neornithes, known widely as modern birds, are the most recent common ancestor of all living birds (class Aves) and their descendants. They are usually divided into two superorders; the Paleognathae which consists of flightless ratites and tinamous, and the Neognathae which contains all other birds (Dyke & van Tuinen, 2004; Mayr, 2017). Evidence from fossils suggests that neornithine birds nested free of sediment and in more open locations than either the enantiornithine birds or non-avian dinosaurs and it is proposed that their relatively open nest sites associated with increased parental care helped them survive the mass extinction event (Varricchio and Jackson 2016; Mayr 2017). It has also been suggested that nesting above ground meant that during the periods of rapid environmental changes in the aftermath of the Chicxulub asteroid, neornithine parents could flexibly alter incubation patterns and thus maintain the viability of their embryos to a much greater extent than could the enantiornithine birds and dinosaurs, both of which were variably incubated by environmental heat sources (Mayr 2017). Neornithe birds are also thought to have provided increased amounts of care to hatched offspring, which is highly likely to have increased their progeny's *per capita* survival (Mayr 2017).

It has been suggested that neornithine birds were the earliest groups to lay eggs which required regular turning to develop (Deeming 2015; Mayr 2017). Egg turning is thought to have evolved in conjunction with an increase in protein-rich albumen in eggs, because regular egg turning is required to prevent the albumen inside eggs from stratifying which, in turn, limits water and protein uptake by embryos (Mayr 2017). Current support for this comes from the extant megapodes, which bury their eggs below ground and so do not turn them, but also have very low amounts of albumen within their eggs. Irrespective of the amount of albumen in eggs, megapodes are some of the only extant birds with 'superprecocial' chicks that receive no further care after the chicks leave the nest and, as the offspring of enantiornithine birds were precocial, then it is likely to have been the plesiomorphic pattern of offspring development in Neornithes. With the further exception for young brood parasitic black-headed ducks *Heteronetta atricapilla*, which receive no care from their foster parents, all other extant birds provide at least some care for their hatched offspring.

In summary, the early dinosaurs (Saurischians) laid and buried relatively large clutches of white eggs which were incubated by environmental heat sources (Grellet-Tinner et al. 2006; Brusatte et al. 2015). Birds are the only extant tetrapods that lay their eggs above ground and incubate the eggs themselves, thus suggesting that nesting above ground evolved relatively late within the ornithuromorpha, the clade that includes modern birds (Varricchio and Jackson 2016; Hogan and Varricchio, 2023). It has been suggested that the shift to nesting above-ground resulted in an increase in the relative volume of albumen within eggs (Deeming 2002) and the beginnings of offspring being increasingly dependent on their parents, as seen in altricial offspring. Further, it is probable that the early ornithuromorphs laid eggs in nests built on the ground, outside of burrows, and began to protect their offspring from adverse weather conditions and predators (Mayr 2017). It is probable that the neornithine birds were the first to lay their eggs in fully exposed nest sites and provide care for their offspring as is widespread in extant birds (Brusatte et al. 2015). There has, therefore, been a trend in dinosaurs and ancestral birds towards nest sites becoming progressively more open, and thus free of sediment, and parents laying pigmented eggs and providing increasing amounts of care for their offspring, which has continued amongst the extant birds.

Evolution of nest site use and nest architecture by extant birds

The evolution of nest sites among extant birds has received relatively little attention and until relatively recently, our understanding was based on studies that have focused on single families of birds. Although several review articles have described aspects of the evolution of nest site selection by extant passerines (Collias 1964, 1997; Collias and Collias 1984), they have largely consisted of interesting, but ultimately anecdotal, observations and so our understanding of the evolution of nest sites by extant birds has remained relatively poor.

Our understanding of the evolution of nest sites, nests structures, and methods of material attachment in all of the 242 avian families was greatly enhanced by a landmark study of the world’s bird families (Figure 3: Fang et al. 2018). In the families of extant birds, 60% nest in trees, 20% nest in non-tree vegetation, and the remaining 20% nest on the ground, in river banks or on cliffs. In terms of nest structure, meanwhile, cup nests are by far the most common, whilst domed nests, platform nests and nests in tree holes are less common. Finally, 80% of families attach their nests to substrate via basal attachment, with the three other attachment types, namely lateral, horizontally forked and pensile each being used by less than 10% of families (Fang et al. 2018).

* Figure 3

Fang et al. (2018) also showed that nest sites in trees evolved quite early in extant birds, whilst nest sites in non-tree vegetation, on cliffs and on a variety of water bodies evolved later. The trend of passerines nesting in non-tree vegetation is one of the most important evolutionary transitions in extant birds, with co-evolutionary analyses showing that nesting in non-tree vegetation came after the appearance of cup nests. Ancestral state reconstruction techniques showed that extant birds began nesting in trees, on water bodies, on cliffs and in riverbanks after cavity and platform nests evolved from scrape nests. Further, although scrape nests are always located on the ground, scrape or non-scrape nests and nests either on the ground or above the ground are traits that evolved independently of each other (Fang et al. 2018).

Hole nests in the ground

A few species of megapodes, such as the Australian brush-turkey, build mounds in which to incubate eggs via environmental heat sources (Göth and Booth 2005), which is similar to the early non-avian dinosaurs. The evolution of hole nests in the ground for species other than megapodes have received no research attention but they probably protect the occupants from strong winds (Collias 1997).

Tree cavities

Nests in tree holes, meanwhile, provide the occupants with protection from wind and rainfall, whilst also having lower nest predation rates than species nesting outside of holes (Collias 1997), as was shown in passerines in Arizona, North America (Martin and Li 1992). Nests in holes suffer relatively low predation rates and are protected from adverse weather conditions but whilst primary cavity nesting species such as woodpeckers are able to excavate their own holes, secondary cavity nesting species such as chickadees and tits are incapable of excavating their own holes and are therefore reliant upon holes either excavated by primary cavity nesting species or created by rotting trees. The distribution of secondary cavity nesting species is therefore heavily reliant upon the presence of primary cavity nesters and, for example, there are very few secondary cavity nesting species in Australia or New Guinea where woodpeckers are absent (Cockle et al. 2011a). The reliance of secondary cavity nesting species on holes excavated by primary cavity nesting species means that both intraspecific and interspecific competition for hole nesting sites is intense (von Haartman 1957; Alerstam and Hogstedt 1981). A disadvantage of hole nesting, however, is that incubating birds may be trapped in the nest by a predator either remaining at the entrance or being small enough to enter the hole, thereby preventing escape (Collias 1997). This may explain why extant birds have shifted from hole nesting to open nesting over time.

Domed nests

In terms of nest architecture, domed nests are the most similar to cavity nests because they both have small entrance holes and yet are protected on all sides. Some species whose ancestors nested in tree holes may have shifted to nest in more open sites using domed nests. For example, a study of the African lovebird genus *Agapornis* showed that the shift from nesting inside tree holes to building domed nests in cavities was derived from the parrots lining their tree hole nests and progressively building more complex nest structures (Eberhard 1998). Elsewhere, the shift from nesting inside tree holes to constructing vegetative nests outside of tree holes has occurred at least three times during the evolution of the synallaxine and furnariine ovenbirds and was probably adaptive because it served as an ecological release that enabled them to exploit a wider variety of breeding habitats (Zyskowski and Prum 1999; Irestedt et al. 2006).

Domed nests provide birds with similar, but perhaps lower, levels of protection from adverse weather conditions in comparison to cavities, because the nests are relatively insubstantial when compared to the protection provided by tree trunks. However, the birds are able to build such domed nests in a much wider variety of locations (Newton 1994). Domed nests have been identified as an ancestral nest type in passerine birds (Prum 1993; Zyskowski and Prum 1999; Price and Griffith, 2017) because basal passerine families such as the New Zealand wrens (Acanthisittidae) build enclosed nests in crevices and the broadbills (Eurylaimidae) construct domed nests with side entrances (Prum 1993). Furthermore, the suboscine ovenbirds (Furnariidae) build a diversity of nest types and the two lineages where the species building primitive tree hole nests have evolved to build more complex domed nests (Zyskowski and Prum 1999) that offer considerable flexibility because domed nests can be built wherever the parents wish to build them (Collias 1997).

The primary function of domed nests has been debated. One suggestion is that they reduce the risk of predation in comparison to open cup nests and, in support of this idea, a comparative analysis of the Old-World babblers (Timaliidae) showed that species building domed nests bred closer to the ground than species building cup-shaped nests (Hall et al. 2015). It was argued that the evolution of domed nests was dependent on the transition to nesting either on or close to the ground and that the roof provided greater protection against the increased level of predation risk on the ground (Hall et al. 2015). Nevertheless, field studies have shown that some species with domed nests suffer high levels of nest predation, with 72% of long-tailed tit (*Aegithalos caudatus*) nests predated annually (Hatchwell et al. 2013), although that study did not assess the distribution of the height of lost nests above ground and so the trend may not be universal. Meanwhile, comparative studies of tropical and temperate passerine birds showed that species with domed and non-domed nests had similar predation rates (Martin et al. 2017; Unzeta et al., 2020), thus suggesting that the primary function of domed nests is not to minimise predation risk.

An alternative idea is that the architecture of birds' nests has evolved in response to environmental conditions (Perez et al., 2020). Species building domed nests were found to more commonly occur in arid than in non-arid regions of Australia (Duursma et al. 2018), although another study of Australian birds found no such pattern (Medina 2019). Instead, species building domed nests were found to have smaller distributions than species building non-domed nests, suggesting that domed nests were lost through evolutionary time as birds in Australia expanded to occupy less arid regions (Figure 4: Medina 2019).

Moreover, the domed nests of sharp-tailed sparrows (*Ammodramus caudacutus*) helped prevent their eggs being lost when flooding events occurred on saltmarshes (Humphries et al. 2007), providing further support for the idea that domed nests serve primarily to create optimal nest microclimates rather than cover against predation. However, it is prudent to consider that the costs and benefits of domed nests may differ between species, and geographic regions, and further studies that simultaneously quantify nest predation rates and the extent to which domed nests protect birds from adverse weather conditions are needed to determine their function/s.

* Figure 4

Open cup nests

Open cup nests are the other major nest type in extant birds, and they evolved from domed nests within passerine birds (Price and Griffith, 2017). The passerines rapidly evolved and expanded during the Cenozoic period possibly because they could build open cup nests in a wide variety of nesting sites, and they also had smaller body sizes and strong flying capabilities (Collias and Collias 1984; Collias 1997). The majority of plant species also went extinct during the mass extinction event between the Cretaceous and Paleogene eras but when vegetation began to recolonise the planet, plants such as shrubs rapidly became available as both nesting substrates and materials for passerine birds which were rapidly diversifying at the same time. Newly evolved plants thus provided a plethora of new potential nesting sites for passerine birds for both domed and open cup nests and may have permitted passerines to utilize previously occupied ecological space and thus not compete with Piciform and Coraciiform birds that nest in cavities in trees that were probably limited in availability (Martin and Li, 1992). Specifically, passerine birds had evolved small body sizes and could select a wide variety of nest sites, which is hypothesized to have enabled them to occupy new niches. The piciform and coraciiform birds that were larger hole-nesting species required large, somewhat decayed trees which were likely to have been in limited supply, while passerines could occupy essentially unlimited elevated nesting sites from small shrubs to trees (Collias and

Collias 1984; Collias 1997). Open cup nests are therefore considered to be the most adaptable nest type, and having adaptable nest types is a trait that is argued to be a key innovation which enabled passerines to diversify (Collias 1997). The offspring of birds have evolved to become increasingly altricial over time and in the passerines, their offspring are born naked, blind and helpless and are therefore utterly dependent on their parents during the early stages of their lives. The open cup nests that are so prevalent in passerines (Fang et al., 2018) may be best able to provide a location in which to raise altricial offspring (Collias and Collias 1984; Collias 1997) and this possibility requires further research attention.

Meanwhile, studies show that open cup nests evolved from burrow nests excavated in substrate in swallow species (Winkler and Sheldon 1993) and that species of Old-World babblers evolved to construct open nests higher off the ground than species with domed nests (Hall et al. 2015). In turn, patterns of allometric scaling suggest that the provision of structural support, as opposed to environmental conditions, determine nest architecture in Australian passerines (Heenan and Seymour 2011). However, a study of 36 species of Australian passerine species showed that they adaptively vary their use of insulating materials in their nests in relation to spatial variation in rainfall. Specifically, birds inhabiting warm climates used poorly insulating materials in regions with high rainfall but not in regions of low rainfall, whilst birds inhabiting cool climates use well insulated materials regardless of the amount of rainfall, so that the composition of nest material mitigates spatial variation in weather conditions throughout Australia (Heenan et al. 2015). Open cup nests therefore provide more exposed conditions for parents and offspring but open cup nesting species protect themselves from adverse environmental conditions by adaptively using materials that provide insulation.

It may have been thought likely that nest architecture, nest sites, and the method of attachment may have evolved in parallel with each other, yet they evolved independently of each other (Fang et al., 2018). Basal attachment is the most common form of attachment, presumably because it is the easiest way of supporting nests and works with gravity, although other forms of attachment evolved because they only evolved in lineages with domed or cup nests (Fang et al. 2018). In Melophagoidea, there is a link between size and method of attachment, with larger species being less probably to have suspended nests (Medina, 2019). The evolution of domed or cup shaped nests could have driven the evolution of non-basal methods of attachment or vice versa, but co-evolutionary analyses showed that the evolution of domed or cup shaped nests preceded the evolution of non-basal methods of attachment rather than vice versa (Fang et al. 2018). Finally, methods of nest attachment in avian families were more similar to distantly, rather than closely, related families, suggesting that nest attachment methods are highly conserved (Fang et al. 2018).

The studies above have generally focused on single families of birds and whilst informative, interspecific studies involving more species from across the avian phylogeny are needed. In the past decade or so, studies have used data from hundreds and sometimes thousands of species from entire continents or globally to examine the evolution of nest sites or nest architecture in relation to the sex of the building parent/s (Mainwaring et al. 2021), egg characteristics (Stoddard et al. 2017; Nagy et al. 2019), host use by brood parasites (Antonson et al. 2020) and conservation threats (Tobias and Pigot 2019). The landmark study by Fang et al. (2018) examined the evolution of nest sites, nests structures, and methods of material attachment in all of the 242 avian families and therefore provided unparalleled insights into the evolution of nest sites and nest architecture in extant birds. Nevertheless, we need more data on the nest sites and nest architecture of the world's bird species, because we are lacking sufficient descriptions for many species from South America and Africa, and this hinders the results obtained from phylogenetically controlled comparative analyses. Meanwhile, it is also important to consider that whilst such comparative studies have proven insightful, they are also open to bias because, for example, different studies may produce quantitatively different results because of variation in the interpretation of the raw data collected from online data sources.

Conclusions

Non-avian dinosaurs transitioned from incubating eggs fully buried to partially buried, conditions maintained in enantiornithines, the dominant birds of the Mesozoic. Modern birds evolved to build smaller and more elaborate but still open cup shaped nests in a greater variety of nest sites, which has been accompanied by an increasing amount of care being provided for fewer, more altricial offspring. In particular, nests changed substantially when the Enantiornithes went extinct and the earliest birds

(Neornithes) exploited and thus filled the niches they left behind. Prior to the end-Cretaceous mass extinction event, most neornithine nests are hypothesized to have been scrape or platform nests, and the earliest modern birds evolved to build more complex nest structures than ever seen before, which in turn enabled them to use nesting sites that included trees, shrubs, cliffs, on water bodies and in river banks (Fang et al. 2018). It also included the use of cavities and the transition from cavities to domed nest in passerines. Passerine birds, in particular, took advantage newly evolved plants to build small open cup nests in increasingly exposed locations, which may have enabled passerines to utilize previously occupied ecological space and thus not compete with parrots (Psittaciiform), kingfishers (Coraciiform) and woodpecker (Piciform) birds that nest in cavities in trees that were probably limited in availability. In the passerines, there have been multiple transitions from domed nests to open cup nests and cavity nests.

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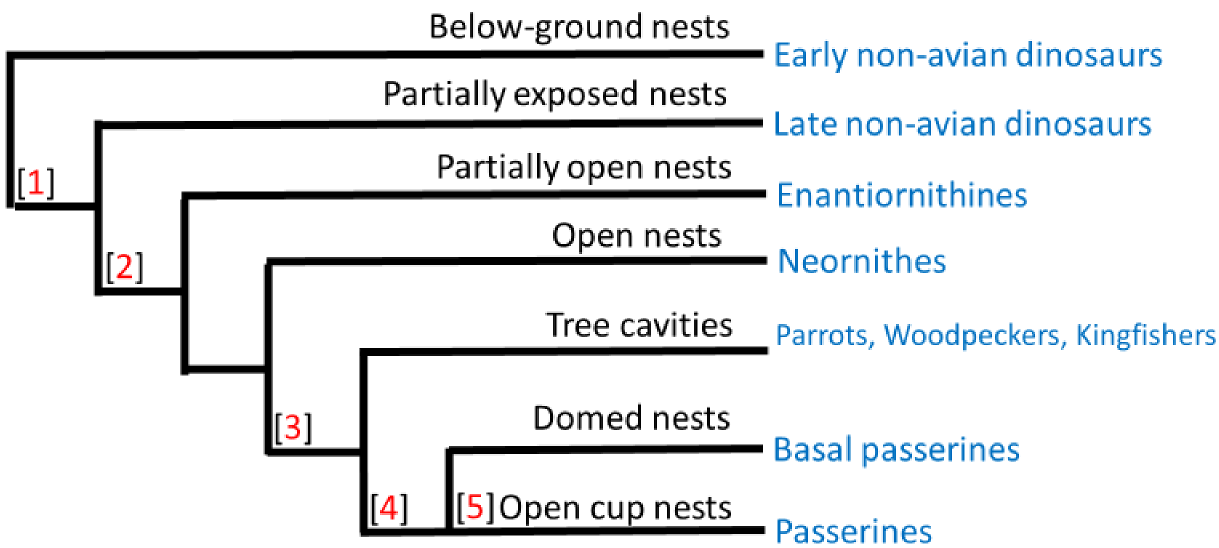
Figure 1. The evolution of nest characteristics in birds and their non-avian ancestors.



[1]From laying eggs blow ground to above ground. [2] From ground nesting to open nesting (platforms/scrapes/cups). [3] From open nesting to cavity nesting. [4] From cavities to domed nests in passerines. [5] Multiple transitions from domed to open/cavity nests in passerines

Figure 2. The fossilised remains of in-situ eggs of Mesozoic birds (Neornithes) from the Late Cretaceous in Patagonia, Argentina. Reproduced with permission from Fernández et al. (2013).

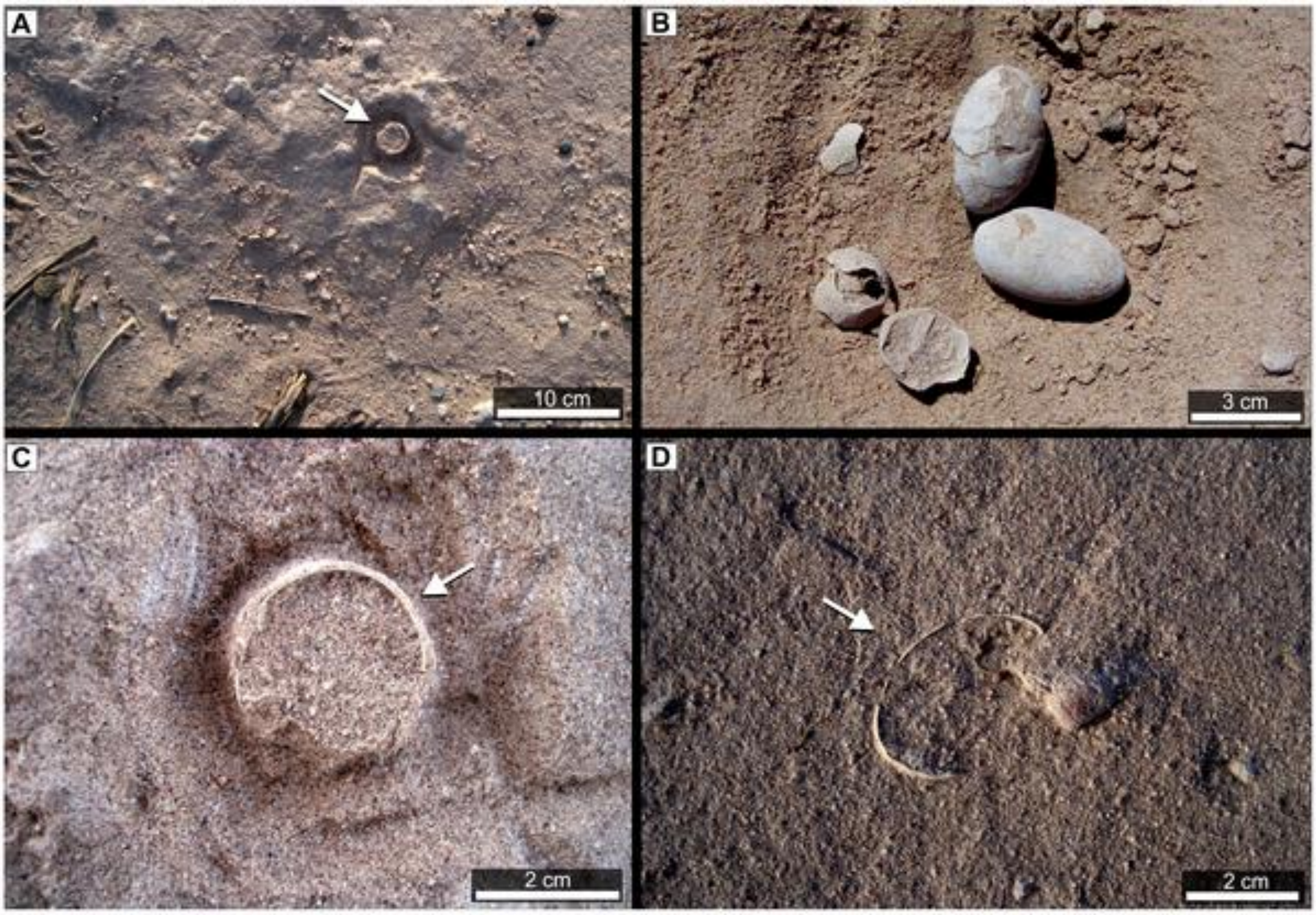


Figure 3. The phylogenetic distribution of (a) nest structure, (b) nest site and (c) nest attachment amongst extant bird families. Filled coloured circles at the tips and nodes of the trees show nest character states in extant families and their ancestors, respectively; circles filled with multiple colours show families or ancestral taxa with multiple character states; and blue rings indicate the two major adaptive radiations in extant birds. Reproduced with permission from Fang et al. (2018).

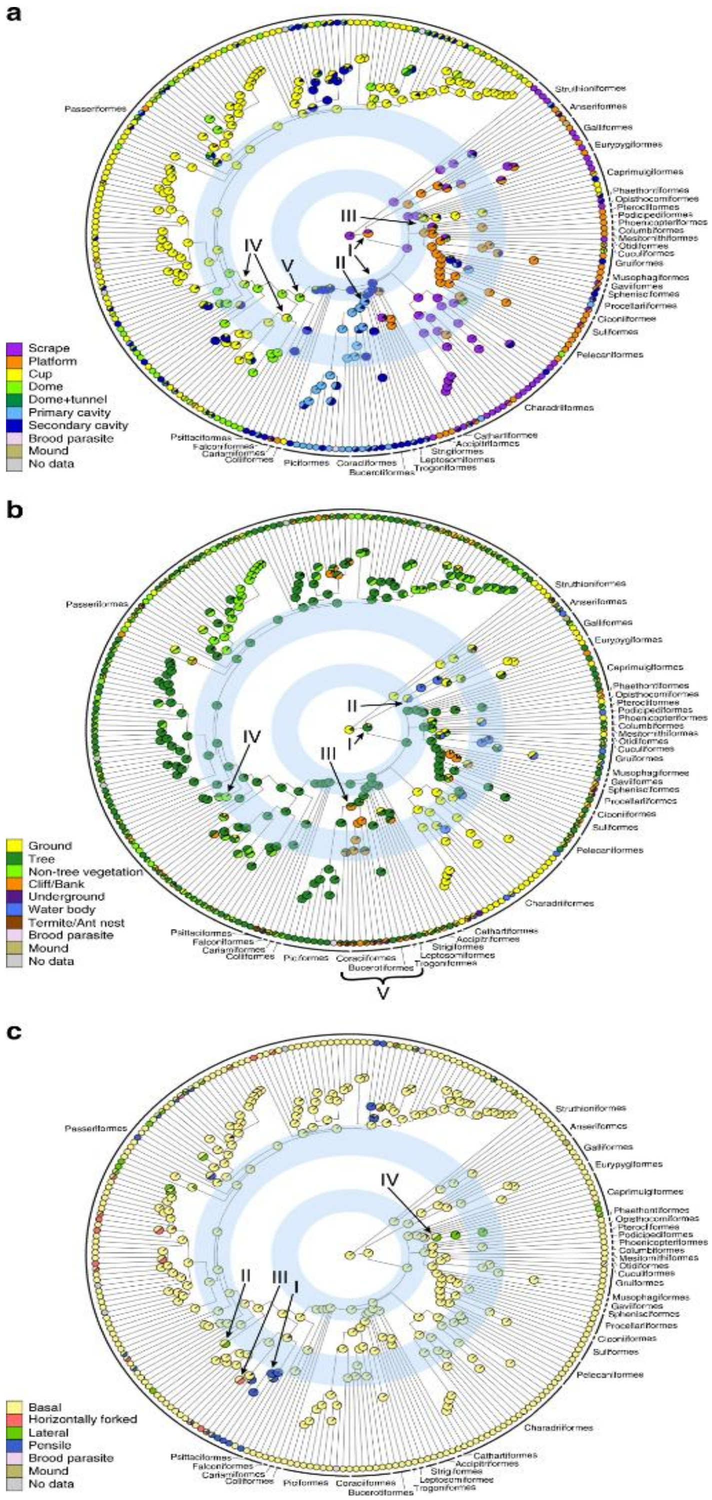


Figure 4. Australian passerines with open and closed nests are distributed across ranges with similar (a) minimum temperatures and (b) maximum radiation levels, but species with open nests have (c) larger ranges and (d) broader niches than species with domed nests. Note that the black dots represent raw data values and the colour dots represent average values per group. Reproduced with permission from Medina (2019).