Theories for Behavior in Deinonychosaurs and the Evolution of Avian Monogamy

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Velociraptor mongoliensis. Art Credit: Fred Wierum/Wikimedia, CC BY

Abstract

In popular culture and scientific literature alike, the Deinonychosauria are frequently depicted as pack-hunters like wolves or lions. This is largely based on taphonomic interpretation of *Deinonychus antirrhopus* bonebeds that seem to show multiple individuals, presumably a pack, preying on the herbivore *Tenontosaurus*. However, some feel that varanids are a better proxy for deinonychosaur behavior, and that the bonebeds are better explained by varanid-like behavior. But neither wolves nor varanids are the closest relatives of the deinonychosaurs. Rather, birds are their closest relatives, as well as the group to which deinonychosaur brains are most similar. Therefore, avian behavior is likely the best proxy for deinonychosaur behavior. Accipitrids, seriemas, and kiwis may be the best analogues for deinonychosaurs as they occupy similar niches and have potentially similar biology and life history. Additionally, avian monogamy, including long-term monogamous behavior present in accipitrids and kiwis, may have originated in dinosaurs as a response to the energy requirements of endothermy combined with the demands of their oviparity.

"Clever Girl"

"Try to imagine yourself in the Cretaceous Period. You get your first look at this 'six foot turkey' as you enter a clearing. He moves like a bird, lightly, bobbing his head…You stare at him, and he just stares right back. And that's when the attack comes. Not from the front, but from the side, from the other two raptors you didn't even know were there. Because Velociraptor's a pack hunter, you see, he uses coordinated attack patterns and he is out in force today." – Dr. Alan Grant, *Jurassic Park*, 1993

In popular culture, dromaeosaurs and troodontids are often portrayed as highly intelligent and social pack hunters, much like wolves or lions. This idea was especially made popular by the portrayal of *Deinonychus* (erroneously referred to as *Velociraptor*, or just simply "raptors") in the 1993 blockbuster, *Jurassic Park* and its sequels, and dromaeosaurids (the family that includes *Deinonychus* and *Velociraptor*) are usually portrayed as pack hunters in other media as well, along with (occasionally) their less famous sister clade, the troodontids. This portrayal has traditionally been supported by many paleontologists. But how much of this portrayal is rooted in actual science, and how much is probably mere fantasy? This paper will review the evidence and theories for and against pack hunting in deinonychosaurs, make comparisons with living organisms, including birds of prey and crocodilians, and will attempt to construct an idea of how deinonychosaurs may have behaved and hunted, and how the biology and behaviors of these dinosaurs may relate to the evolutionary origin of avian social behavior.

The Deinonychosauria

Deinonychosaurs were generally small, fleet footed, carnivores, closely related to birds, and sporting an enlarged sickle shaped claw on the second digit of each foot, for which the Deinonychosauria are named. The group is defined as containing all theropods more closely related to dromaeosaurs than to birds, which is to say the Dromaeosauridae and the Troodontidae, which are usually recovered as sister taxa. The Deinonychosauria in turn are a sister group to the Avialae, the group containing modern birds and all other theropods closer related to them than to dromaeosaurs. An analysis done in 2012 confirmed the monophyly of the Deinonychosauria (Turner, 2012). However, another study in 2013 found troodontids to be closer to birds than to dromaeosaurs, which would classify troodontids as members of the Avialae, and render the Deinonychosauria obsolete and synonymous with the Dromaeosauridae. However, according to that same study, while it is slightly less likely than a troodontid-bird pairing, a dromaeosaur-troodontid pairing is still plausible (Gotefroit, 2013). In any case, both dromaeosaurs and troodontids are very close to the origin of birds, and for the purposes of this paper, the monophyly of *Deinonychosauria* will be assumed.

The Avialae and Deinonychosauria form a clade called the Paraves within the Coelurosauria, a branch of tetanuran theropod dinosaurs which includes the Paraves, along with the oviraptorids, compsognathids, ornithomimosaurs, and tyrannosaurs, with tyrannosaurs branching off near the base of the coelurosaur lineage (Fowler, 2011).
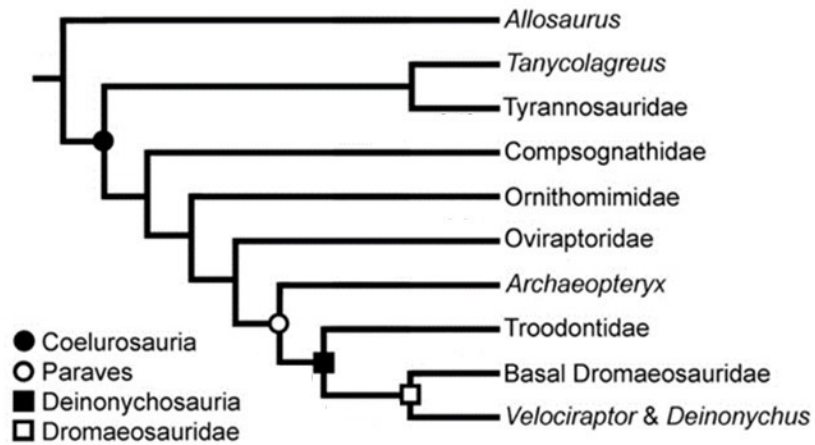
Figure 1. Modified from Fowler, 2011. Cladogram of coelurosaur relationships with *Allosaurus* as an outgroup. The clade Avialae is represented by *Archaeopteryx*.

Origin and Criticism of the Pack Hunting Hypothesis

Deinonychus antirrhopus skeletal mount on display at the Field Museum of Natural History, Chicago, IL, USA. Photo Credit: Jonathan Chen CC BY-SA 4.0

The pack hunting hypothesis for deinonychosaurs originated with *Deinonychus antirrhopus*. *Deinonychus* was discovered by John Ostrom in 1964 in the early Cretaceous Cloverly Formation in what is now Montana (Ostrom, 1969). *Deinonychus* is also known from the Antlers

Formation in what is now Oklahoma (Brinkman, 1998), the Cedar Mountain Formation of Utah (Brinkman, 1998), and teeth which may represent *Deinonychus* have been recovered from the Arundel Clay in Maryland (Lipka, 1998), suggesting that *Deinonychus* had a very wide geographic range. *Deinonychus* grew to be around 11 ft in length (Parsons, 2009), and its name, meaning "Terrible Claw", was given for the enlarged sickle shaped claw on the second digit of the hind limb.

In multiple localities in the Cloverly formation, remains of *Deinonychus* have been found alongside the remains of the large herbivorous ornithopod, *Tenontosaurus*. In some instances, only *Deinonychus* teeth were found in association with the *Tenontosaurus* remains, and the number of teeth suggests multiple individuals. And at YPM site 64-75, the skeletal remains of multiple *Deinonychus* were preserved alongside the remains of the herbivore upon which they were presumably attempting to feed when they met their demise (Maxwell, 1995). This evidence strongly suggests that *Deinonychus* frequently preyed upon *Tenontosaurus* and gave rise to the idea that they hunted said prey in packs. However, while finding the remains of multiple *Deinonychus* together could indicate an ill-fated pack hunting event, the only definitive facts the fossils reveal is that they died together, and there is no hard evidence that they actually lived together.

In the Antlers formation of Oklahoma, *Deinonychus* remains have also been found in association with *Tenontosaurus*, and as Brinkman mentions, *Tenontosaurus* was presumably too large for a single *Deinonychus* to successfully hunt, and the frequent association of the two genera as predator and prey could suggest pack hunting behavior to aid in taking such large prey (Brinkman, 1998).

The pack hunting hypothesis is not without its opposing arguments, however. In a study done on *Deinonychus* by Roach and Brinkman in 2007, they argued that instead of evidence of pack hunting, the multiple *Deinonychus*, probably four individuals, preserved with *Tenontosaurus* at YPM site 64-75 could represent the end result of a feeding frenzy, similar to the feeding habits of modern Komodo Dragons (*Varanus komodoensis*). Komodo Dragons are solitary hunters, but rarely feed alone, as when one lizard makes a kill, others are usually quick join in. Larger dragons assert dominance over smaller ones, and cannibalism frequently occurs. Roach and Brinkman cite evidence for intraspecific competition within *Deinonychus*, and a reassessment of the taphonomy of the site suggests that the individuals of *Deinonychus* were probably not fully grown and may have been cannibalized by members of their own species. Roach and Brinkman do not contest that *Deinonychus* regularly fed on herbivores many times larger than themselves, nor do they contest that *Deinonychus* seems to have at least occasionally fed in groups. However, they suggest behavior more like unto a shark, Komodo Dragon, or crocodile. Either a single *Deinonychus* made a kill and others arrived afterward to join in the feast, or multiple solitary *Deinonychus* congregated into a mob and killed the herbivore, as well as some of their conspecifics (Roach, 2007). It is important to note that a mob is not the same as a pack. A pack is coordinated, cooperative, and may exist as a permanent unit outside of hunting, as seen in wolves, while a mob is uncoordinated and always temporary.

Roach and Brinkman also raise a valid point about dromaeosaur behavior as it relates to phylogeny. Advanced wolf-like pack hunting behavior in extant species exists only in mammals. *Deinonychus* and its relatives are diapsids, and among diapsids, examples of similarly advanced behavior are rare. They point out that crocodilians and varanid lizards are solitary, and any group

behavior is generally uncoordinated, and feeding frenzies and cannibalism are common occurrences. Predatory birds are also usually solitary hunters, and frenzy-type behavior is known from some species such as vultures. The only bird known to engage in organized pack hunting behavior is the Harris Hawk (*Parabuteo unicinctus*), with packs engaging in coordinated attacks, and consisting of a mated pair and their offspring (Roach, 2007) (Mannan, 1991). A few species of other birds practice coordinated hunting but don't form packs. Aplomado falcons (*Falco femoralis*) hunt as mated pairs in a coordinated fashion with both individuals playing predetermined roles (Hector, 2010). And rarely, Golden Eagles (*Aquila chrysaetos*) have been observed to cooperate with each other to bring down larger prey. These appear to have been extreme circumstances (Roach, 2007), though Golden Eagles hunting both large prey and small prey as mated pairs have also been observed (Fothergill, 2007) (San Diego Zoo, 2011). It is understandably doubtful then, that dromaeosaurs were engaging in wolf-like hunting behavior, considering there is little precedent for such in any of their extant relatives, though coordinated hunting behavior within mated pairs cannot be ruled out.

However, there is additional evidence that could lend support to the dromaeosaur pack-hunting hypothesis or at least suggest a higher degree of gregariousness or high level of intraspecific tolerance. Perhaps some of the most compelling evidence comes from a deinonychosaur trackway site in the Lower Cretaceous Tianjialou Formation from Junan County, Shandong Province, China. The track site preserves, among other ichnofossils, two deinonychosaurian ichnotaxa: *Velociraptorichnus*, foot length of 10 cm, and the larger *Dromaeopodus*, foot length up to 28.5 cm. Both ichnotaxa are functionally didactyl with only a partial imprint of the second digit, confirming that deinonychosaurs held their "killing claw" off the ground as had previously been supposed. The *Dromaeopodus* likely belong to a large dromaeosaur, as large troodontids are unknown before the terminal Cretaceous (Campanian-Maastrichtian) and even then are not known to have reached sizes large enough to have made prints as large as *Dromaeopodus*, while dromaeosaurs in the size range of *Dromaeopodus* are indeed known from the Early Cretaceous of North America as well as from the early Late Cretaceous of Mongolia (Li, 2007).

Of all the trackways preserved at the site, Trackways 1-6 are perhaps the most relevant for shedding light on dromaeosaur behavior. These trackways occur together on a single bedding plane, and are all closely spaced, nonoverlapping, and indicate an identical travel direction. Footprint size of the six trackways is mostly uniform, and the spacing between trackways is regular and less than a single stride length. All of this suggests that these six individual dromaeosaurs were moving as a coordinated group (Li, 2007). Whether this represents the norm, or an occasional event is impossible to say from this single snapshot in time. But it does strongly suggest that at least some deinonychosaurs were indeed social animals that at least occasionally engaged in group behavior, perhaps including coordinated group hunting behavior.

Surprisingly, cooperative hunting in diapsids is not just limited to birds. While Brinkman and Roach described crocodiles and monitor lizards as solitary hunters which frequently converge on a single kill (Roach, 2007), recent studies show that crocodilians actually display intelligent behavior not traditionally associated with reptiles. For instance, some crocodilians have been observed setting simple traps. During nesting season for birds, American Alligators (*Alligator mississippiensis*) and Mugger Crocodiles (*Crocodylus palustris*) are known to position twigs over their heads so as to lure and catch birds in search of nesting materials (Dinets, 2013). And crocodilians, while generally solitary, have also been observed to occasionally engage in

coordinated hunting efforts with their conspecifics (Dinets, 2014). The presence of intelligent behavior and especially cooperative hunting in crocodilians, which have much smaller brains (Hopson, 1980) and much smaller cerebral proportions (Larsson, 2001) than deinonychosaurs, may suggest that at least occasional cooperative hunting in deinonychosaurs is plausible.

However, it is doubtful that deinonychosaurs were engaging in pack behavior comparable to that of wolves and lions, if they were cooperatively hunting at all. Besides the lack of precedent for such permanent cooperative units among diapsids, recent isotope evidence from fossil *Deinonychus* teeth suggests that those units likely did not exist in that species (Frederickson, 2020).

Some modern species, including crocodiles and varanid lizards, are known to alter their diet as they develop and mature. For instance, a crocodile hatchling preys on different animals than juvenile crocodiles, and juveniles eat different prey than the adults. This is typical of asocial species or species which otherwise do not provide food for their offspring (Werener and Gilliam, 1984) (Wallace and Leslie, 2008) (Frederickson, 2020). Social species, or those that otherwise provide long-term care for their offspring, do not show such ontogenetic change in their diets. In these species, wolves being an example, the young generally eat what their parents provide them, so between immaturity and maturity their diets are fairly consistent (Bryan, 2006) (Frederickson, 2020). Frederickson, et al. used stable isotope analysis on the teeth of *D. antirrhopus*, focusing on ratios of carbon-13 and oxygen-18, which give indication of the general type of food/trophic level the dinosaurs were eating. Adult *Deinonychus* were found to have eaten mostly larger prey. In fact, the isotopic analysis was consistent with frequent *Deinonychus* predation upon *Tenontosaurus*, teeth of which were also analyzed, thus providing more compelling evidence that *Deinonychus* frequently preyed upon this species. However, the analysis also revealed that like modern large carnivores, they weren't above eating smaller prey as well. Young *Deinonychus*, however, were found to have eaten smaller and trophically-higher prey than the adults (Frederickson, 2020). This heavily suggests that young *Deinonychus* were not cared for by the adults, or at least that parental care had concluded well before the offspring were large enough to hunt the same prey as the adults. This could suggest a Komodo Dragon style behavioral paradigm as suggested by Roach and Brinkman (Frederickson, 2020). However other analogues are also possible. A problem with Komodo Dragons as an analogue for dromaeosaur behavior is that Komodo Dragons are not gregarious, with most intraspecific interactions between individuals being hostile. Yet there is evidence that theropods were at least occasionally gregarious, and varanid-style behavior, which frequently involves the cannibalism of juveniles by the adults resulting in infrequent associations between different age groups, is inconsistent with the frequency of juvenile theropods found in association with adults (Currie, 2010)(Frederickson, 2020). While these associations could be purely circumstantial, for instance, predator traps could explain some of the associations, it may suggest that the juveniles were relatively comfortable around adults, whether or not the adults were providing care for them. This, plus the isotopic evidence could be consistent with modern birds of prey, in which post fledgling behavior can vary from complete asociality to gregariousness, varying even within the same species. It could also be consistent with the behavior of some ratites where parental care is given, but the young are precocious and maintain a level of dietary independence. Alternatively, it could be the case that *Deinonychus* did provide parental care, but when raising young, the big game hunting abilities of the parents were somewhat impaired, and thus during the parental care stage, parents and offspring alike consumed smaller prey (Frederickson, 2020).

All things considered, pack hunting in deinonychosaurs is very unlikely, and it appears to be inconsistent with the findings of Frederickson, et al, which suggest that juvenile *Deinonychus* were probably mostly, if not completely independent from the adults. However, the relationship between juveniles and adults was likely not an agonistic one, in contrast to Komodo Dragons. While the adults likely provided very little post-hatching parental care to their offspring, there was also probably a degree of social tolerance for other individuals and age groups, at least comparable to what is seen in crocodilians (Frederickson, 2020).

Evolutionary Trends in Brain Structure

Related to the question of how deinonychosaurs behaved is the question of how intelligent they were and how similar their brain structure was to their extant relatives. Intelligence in non-human animals can be difficult to quantify, but one method that is frequently used, is encephalization quotient. Encephalization quotient, or "EQ", is the ratio of brain size to overall body size, and generally, an animal with a higher EQ is interpreted as being more intelligent, though very large animals are problematic because while some of them don't seem to be any less intelligent than their smaller counterparts, they have much lower EQs due to their much larger overall body mass (Hopson, 1980).

For extinct animals, the size of the brain is estimated based on the endocast, taken from inside the braincase, if it is preserved. In a study by J.A. Hopson, EQs of several dinosaurs were calculated relative to crocodiles based on the endocasts of several different genera. Among them was the troodontid *Stenonychosaurus*. *Stenonychosaurus* was found to possess an EQ of 5.8, far beyond the EQ's of other dinosaurs, and within the range of modern birds, and Hopson notes that it is only a minimum value. For comparison, modern crocodiles, the standard on which these calculations were based, were assigned an EQ of 1. For comparison with other dinosaurs, see the chart below (Hopson, 1980).
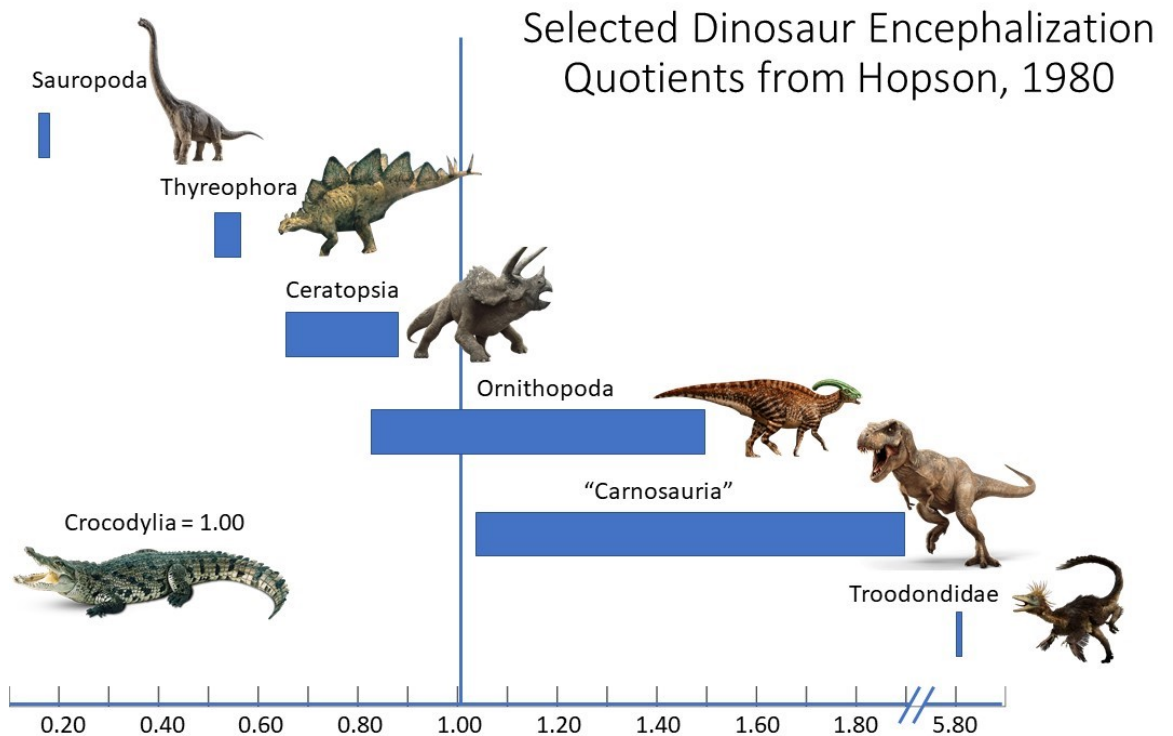
Figure 2. Modified from Hopson, 1980. Chart of dinosaur encephalization quotients calculated by Hopson, 1980. Note the break between 1.90 and 5.80. Ankylosauria and Stegosauria have been combined as Thyreophora in this modified version. "Carnosauria" is in quotations because the true Carnosauria no longer includes the Tyrannosauria, which was included within Carnosauria when these EQs were calculated.

In addition to raw EQ, Hopson corrected the scores to account for body size. While the raw EQ scores put many dinosaurs below the reptilian standard, the corrected scores place them well within the normal reptilian range. In both the cases of raw EQ and corrected EQ, theropods generally seemed to score the highest, with "carnosaurs", at the time of this study, thought to include the tyrannosaurs, ranging from roughly the same relative brain size as crocodilians to almost twice the relative brain size of crocodilians, and with troodontids possessing by far the largest relative brain size (Hopson, 1980).

Of the deinonychosaurs, *Stenonychosaurus* was the only one for which EQ was calculated. However, Hopson also notes that a related troodontid, *Saurornithoides*, and the dromaeosaur, *Dromaeosaurus*, have been observed to have large endocasts like *Stenonychosaurus* (Hopson, 1980). It is therefore likely that deinonychosaurs all possessed relatively high EQs, within the range of modern birds.

Based on relative brain size alone, deinonychosaurs were likely among the most intelligent of dinosaurs, though, relative brain size alone is certainly not the only factor determining intelligence (Hopson, 1980). Additionally, brain to body size ratios based on endocasts may be inaccurate because in many reptiles, the brain does not completely fill the endocranial space, with some filling only 50% (Larsson, 2001). However, others, including birds (Hopson, 1980), have brains that fill their endocranial space more completely (Larsson, 2001). Body mass can also be difficult to calculate with surety and accuracy. In the absence of reliable

brain size estimates and body mass estimates, an alternate method, proposed by Hans Larsson, can be used to compare the brains of extinct animals, which is to compare the cerebral volume to the total endocast volume. The cerebrum is primarily involved with sensory integration and nervous control, and an enlarged forebrain is associated with increased intelligence in birds and mammals. According to Larsson, while cerebrum volume to endocast volume comparisons are still not 100% foolproof, it is a more reliable method than calculating EQ (Larsson, 2001).

Larsson used cerebrum to endocast volume comparisons to calculate the similarity of extinct species to the cerebral proportions of modern birds and reptiles. The taxa used in the study were the crocodylomorph *Sebecus*, the carnosaurs *Allosaurus* and *Carcharodontosaurus*, the coelurosaurs *Tyrannosaurus* and *Troodon*, the basal avialan *Archaeopteryx*, and two species of *Numenius*, an extant bird genus. *Sebecus*, a crocodylomorph, unsurprisingly had very reptilian brain proportions. *Allosaurus* and *Carcharodontosaurus* both had marginally higher cerebral proportions, though still within the 95% confidence limits of the non-avian reptile regression. *Tyrannosaurus* cerebral proportions were found to be 10.71% toward the bird regression, lying just outside the 95% confidence limit of the non-avian reptile regression. There were two values calculated for *Troodon*, suggesting that its cerebral proportions were between 31.54% and 63.06% toward the modern avian condition. Larsson notes that the second, higher, value may be the more accurate, as it is consistent with a previous study on the endocast of *Troodon* by Currie and Zhao in 1993. *Archaeopteryx*, a basal Avialan, was found to be 78.17% toward the modern avian condition. Thus, a phylogenetic pattern becomes apparent. Quasi-avian cerebral proportions in dinosaurs seem to originate in the basal coelurosaurs (including tyrannosaurs) and then become progressively more bird-like as one follows coelurosaur evolution toward the Aves. For reference, a table of Larsson's calculations are included below (Larsson, 2001).

Table 1. Data Calculated by Larsson, 2001 for Fossil Endocrania

Taxon	Total Endocranium Mass (g)	Mass of Cerebrum (g)	Least squares residuals % towards the avian regression from the nonavian reptile regression
Sebecus	31.1	7.41	-9.45
Allosaurus	169.0	46.73	2.61
Carcharodontosaurus	224.4	53.67	-2.46
Tyrannosaurus	338.6	111.84	10.71
Troodon (Lower)	45.0	19.49	31.54
Troodon (Upper)	45.0	26.53	63.06
Archaeopteryx	1.12	0.51	78.17
Numenius gypsorum	3.54	1.67	63.08
Numenius tahitiensis	5.01	2.97	101.07

Source: Table 3.1 in Larsson, 2001

Troodontids are once again found to have some of the most advanced brains among nonavian dinosaurs (Larsson, 2001). Assuming the monophyly of the Deinonychosauria, the dromaeosaurs likely had roughly the same cerebral proportions as *Troodon*, seeing as all deinonychosaurs are the same phylogenetic distance from modern birds (Fowler, 2011) (Turner, 2012). These elevated cerebral proportions in deinonychosaurs could suggest higher intelligence, or at least behavior and brain function more akin to birds than to crocodiles and other reptiles.

Birds of Prey as a Potential Model for Deinonychosaur Behavior

When seeking a modern analogue for an extinct animal, one should look to the living animals that are phylogenetically closest to the extinct creature in question, as well as looking to animals which occupy similar ecological niches to the extinct animal. The latter principle has traditionally been applied with dromaeosaurs, with paleontologists inferring behavior based on similarly sized modern carnivores. However, these have generally been mammalian predators such as wolves and lions, which are not at all closely related to dinosaurs. Roach and Brinkman suggested varanids as a better analogue (Roach, 2008). They too occupy similar niches, and are indeed closer related to dinosaurs than mammals, but they may not be the best analogue either. The closest living relatives of the non-avian dinosaurs are the birds, or avian dinosaurs. Birds are particularly related to deinonychosaurs, and by virtue of phylogenetic closeness, may be the best analogues for deinonychosaurs such as *Deinonychus*, *Troodon*, and *Velociraptor*.

This principle of looking to the deinonychosaurs' closest relatives can be paired with the data from Larsson's analysis of cerebral proportions in various dinosaurs. Not only are dinosaurs closer to modern birds than to anything else, but those dinosaurs with a more avian brain structure, i.e. the coelurosaurs, could reasonably be expected to have more bird-like behavior, whereas dinosaurs with more crocodilian brain structure might be reasonably assumed to have behavior slightly more similar to the dinosaurs' second closest extant relatives, the crocodilians. By both phylogenetic closeness and brain structure, the best analogues for deinonychosaurs are likely the birds.

Among the birds, birds of prey, including accipitrids (eagles and hawks), owls, falcons, and seriemas, are predators like their prehistoric cousins, the deinonychosaurs. Except for behavioral and hunting modifications due to flying, modern birds of prey may be the best proxy available for deinonychosaur behavior. Structural similarities between birds of prey and deinonychosaurs may lend support to this hypothesis.

Dromaeosaurs may have frequently hunted and fed in a similar manner to modern birds of prey, evidenced by their feet and claws. There has long been debate as to how dromaeosaurs used their "killing claws". Ostrom suggested that they could use them to slash at and disembowel prey. However, the extant South American birds known as seriemas (*Cariama cristata* and *Chunga burmeisteri*) have a claw on the second digit of their feet remarkably similar to those of deinonychosaurs, also located on the second digit of the foot, and they use this claw to help tear apart prey (Reford, 1986), but in a way that is different from the way Ostrom described. They do not tear apart prey by slashing. Rather, they use their "killing claw" to pin down or manipulate a prey item, and the prey is dismembered by combination of the mouth and claw, the claw primarily serving to hold down the item (Curtice, 2021). Deinonychosaurs may have used their claws similarly. A study published in 2011 by Fowler notes that the foot morphology of

Deinonychus is most similar to accipitrids and would have been better for grasping and pinning rather than tearing at large prey. Fowler argues that dromaeosaurs would have most likely used their claws to take prey in a manner similar to that of hawks and eagles, grasping and pinning smaller prey while using their wing-like arms to flap and maintain balance. This is would also be consistent with Seriema claw use. However, it is also clear that dromaeosaurs did take larger prey, as evidenced by the frequent association of *Deinonychus* with *Tenontosaurus*, though some modern birds of prey such as Golden Eagles have also been known to prey on animals larger than themselves, including deer and sheep, so similar behavior in dromaeosaurs does not seem too outlandish (Fowler, 2011).

Figure 3. Seriema Claw Use. Left and top are close-up shots displaying the deinonychosaur-like "killing claw" of the Red Legged Seriema (*Cariama cristata*). The bottom image shows how the seriema uses its "killing claw" to pin down an object which is then torn at by the mouth. In this case, prey is being simulated by a keychain. Photo credit: Dr. Brian Curtice, 2021. Photographed at Wildlife World Zoo, Aquarium & Safari Park, Litchfield Park, AZ, USA.

In fact, looking to eagles as a proxy for deinonychosaur behavior could shed light on just how *Deinonychus* was able to frequently tackle large prey like *Tenontosaurus*. As previously

stated, pack-hunting behavior in deinonychosaurs seems unlikely given the available evidence and given that such behavior is extraordinarily rare in diapsids. Like crocodilians and eagles, they may have occasionally hunted cooperatively, though this would likely not have been the norm. The answer to how *Deinonychus* and perhaps other deinonychosaurs routinely brought down such large prey, presumably single-handedly or as mated pairs, may lie in the hunting behavior of Golden Eagles. When Golden Eagles hunt ungulates such as deer, they use what is called the "sustained grip attack". They fly low over their quarry and land on its back or neck and use their powerful feet to grip the animal. The talons and grip force themselves may do extensive damage, or the eagle may just hold on, using its wings for balance, and wait for the animal to collapse from exhaustion and/or shock (Watson, 2011). *Deinonychus*, with its eagle-like foot bones and enlarged killing claws, may have used a similar strategy to the sustained grip attack to bring down large prey, albeit a flightless version of the attack.

In addition to hunting behavior, which may have been similar to the hunting behavior of extant birds of prey, other aspects of deinonychosaur behavior may also have mirrored birds of prey. For one, most bird species tend to be gregarious, or at least tolerant of conspecifics, even among many birds which are more territorial (Frederickson, 2020). For example, Golden Eagle parents are quite tolerant of their offspring remaining in their territory even after parental care has concluded (O'Toole, 1999). It is suggested that many theropods may have had similar behavior (Frederickson, 2020). It is important to note that there is also a trend in most predatory birds toward monogamy, and they often mate for life. Pair bonds, often permanent, are seen in accipitrids (Watson, 2011) (Mannan, 1991), owls (Konig, 2009), seriemas (Redford, 1986) (Silva, 2016), and falcons (Hector, 2010). Some of these groups are not closely related, yet their behavior is remarkably similar. Given that deinonychosaurs are very closely related to birds and operated in similar ecological niches to extant birds of prey, albeit on the ground, it may be that long-term monogamy was the norm for deinonychosaurs as well. Like the accipitrids, some species may have also hunted cooperatively as mated pairs. And on occasion, like Golden Eagles or crocodilians, individuals/pairs may have converged to hunt larger prey or join in on a kill, though that probably would have been more of an occasional occurrence, and if deinonychosaurs had behavior similar to eagles, then conflicts between pairs/individuals over a kill might have also taken place since eagles tend to be territorial (San Diego Zoo, 2011) (Watson, 2011).

It is thought that deinonychosaurs directly incubated their eggs in a similar manner to modern flightless birds. One example of this hypothesized brooding behavior in the fossil record comes from a fossil *Deinonychus* eggshell found close to the gastralia of a *Deinonychus*, which could indicate the eggs were being incubated at the time the *Deinonychus* individual died (Grellet-Tinner, 2006). Oviraptorids, closely related to the deinonychosaurs, are also thought to have incubated their nests directly, as are troodontids. Additionally, it has been proposed that oviraptorids and troodontids, and by extension perhaps all deinonychosaurs, practiced male predominant incubation like modern ratites, which include the modern emu, ostrich, kiwi, rhea, cassowary, and tinamou, and that ratites may be the best proxy for deinonychosaur behavior. The evidence for male brooding behavior is the apparent lack of medullary bone tissue in the brooding oviraptorids and troodontids, as well as the large clutch sizes, large clutch sizes tending to correlate with male brooding in modern birds. The large clutch sizes are also thought to potentially represent communal nests, similar to those of polygynous ostriches (Varricchio, 2008).

Troodontid Eggs at Museum of the Rockies, Bozeman, MT, USA. Note the large clutch size. Photo Credit: James St. John

While male brooding seems likely to have been the case in deinonychosaurs, their exact mating and social behaviors may not have been as ostrich-like. For one, most ratites are predominately herbivorous-omnivorous (Bruning, 2003) and would therefore be expected to have different behavior than deinonychosaurs which were predators, though some troodontids may have been omnivorous (Holtz, 1998). Furthermore, though they all practice predominantly male incubation, the specific patterns of ratite social behavior vary from species to species.

Ostriches (*Struthio*) are polygynous, with a male mating with a harem of females (Bertram, 1992). The females incubate the communal nest during the day, and the males incubate at night (Nell, 2003). Both the male and the females participate in rearing their offspring (Davies and Bertram, 2003).

Emus (*Dromaius novaehollandiae*) tend to be sequentially polyandrous when breeding and mixed parentage is common, with brood parasitism also occurring. Females lay a clutch of eggs in a male's nest, which he incubates, and then the female will move on and mate with another male (Taylor, 2000) (Davies, 1976). The female lays a large clutch of eggs, up to 15 (Eastman, 1969) (Davies, 2003), indicating that large clutch size does not necessarily indicate a communal nest. Emus also occasionally practice short term monogamy where the female stays with the male to help him incubate the nest, switching brooding duty to allow the male to eat and drink, which otherwise wouldn't happen (Eastman, 1969) (Davies, 1976). Once hatched, the pair splits up and the male guards the precocious chicks for up to seven months (Davies, 2002).

Rheas (*Rhea*) are promiscuous, with the males mating with multiple females which lay their eggs in the males' nests, and the females then moving on to mate with additional males. Outside of breeding, rheas are social and tend to form flocks of up to 100 individuals (Davies, 2003).

Most tinamous (Tinamidae) also practice simultaneous male and female polygamy in which the males incubate nests with eggs from multiple females, similar to the breeding style of the rhea (Davies, 2003). However, two species, the ornate tinamou (*Nothoprocta ornate*) and the spotted nothura (*Nothura maculosa*), are known to practice monogamy. Outside of mating, the tinamous range from social and flock-forming to solitary, and the level of gregariousness can also vary by the season (Cabot, 1992).

Cassowaries (*Casuarius*) practice sequential polyandry and male incubation, similar to the emu to which it is closely related. However, unlike other ratites, including the emu, cassowaries are highly solitary (Davies 2003).

Kiwis (*Apteryx*) practice long term monogamy, with males still as the primary egg incubators, though the females may assist in that task so that the males can find food. Outside of mating, the kiwis stay in these pairs permanently and mated pairs are territorial. Young Kiwis are super-precocious and receive little to no parental care (Davies, 2003) (McGregor, 2015).

While all these birds practice predominant male incubation, their mating and social structures are highly different from each other, as well as the length of parental care given to offspring. There does not seem to be a standard pattern of behavior that accompanies male-predominant incubation. While it was likely the male deinonychosaurs which took the lead role in nest incubation, accipitrid-style monogamy and male-predominant incubation are not necessarily mutually exclusive and a combination of these two cannot be ruled out for the likes of deinonychosaurs. This is the case for the kiwi, which practices long-term monogamy. The kiwi is also more carnivorous than other ratites, getting the majority of their diet from invertebrates and small vertebrates (Bruning, 2003) (Davies, 2003) (McGregor, 2015), which could further demonstrate a possible correlation in avian carnivory and long-term monogamy. It should also be noted that in terms of physiology, the kiwi may be the best modern analogue for deinonychosaurs. Deinonychosaurs and some early Aves were warm blooded, feathered, and active, but bone growth rates suggest a lower metabolism than most modern birds. The kiwi shares many features with these extinct animals including, bone structure, overall anatomy, feather type, and the narrow nasal passage anatomy of the deinonychosaurs which are often cited as a key metabolic indicator. Kiwis are warm blooded and highly active but have a lower resting metabolic rate than other birds. Therefore, the kiwi may be an excellent proxy for deinonychosaurs and early aves (Paul, 2002). It is possible that deinonychosaur behavior was similar as well. Additionally, as previously stated, Kiwi chicks are super-precocious and receive very little parental care post-hatching (Davies, 2003), which is consistent with the supposed super-precociality of *Deinonychus* (Frederickson, 2020).

Kiwi-like behavior in deinonychosaurs would be consistent with the evidence for male brooding behavior as well as the accipitrid-like behavior discussed previously. Both kiwis and accipitrids are carnivorous, monogamous, and territorial, and based on the current evidence, it is possible that the true behavior of deinonychosaurs was similar to that of kiwis and eagles. The one thing that may suggest otherwise is clutch size, mentioned by Varracchio et al. There is a correlation with parental investment and clutch size, and both eagles and kiwis have very small

clutch sizes, with eagle clutch sizes ranging from one to four, with two being the most common (Watson, 2010) and kiwis generally only having a clutch size of one (Davies, 2003). This contrasts with what is known from the nests of troodontids which closer resemble those of the ostrich or emu. Therefore, while considering all the other evidence discussed up to this point, eagle-kiwi style monogamy and territoriality may still be the more likely scenario, emu or ostrich-like mating/social behavior, or a mix of eagle-like and ostrich-like behavior, also cannot be ruled out.

Deinonychosaur behavior likely also varied by species, similar to the interspecific and intraspecific behavioral variations observed in modern bird groups, or any animal group for that matter. At the very least, dromaeosaurs and troodontids may have had somewhat different behavior from each other as indicated by potential dietary differences. Based on tooth wear and bite mechanics, dromaeosaurs seemed to include more bone in their diet and were more likely to consume larger prey that could put up more of a struggle, whereas troodontids seemed have taken smaller and softer prey and incorporated less bone in their diet, probably favoring invertebrates, bite-sized vertebrates, and carrion (Torrices, 2018). Some troodontids may have even been omnivorous (Holtz, 1998). The more robust feeding preferences of dromaeosaurs, of which *Deinonychus*' apparent preference for *Tenontosaurus* is an excellent example, could have resulted in significant behavioral differences. Dromaeosaurs such as *Deinonychus* and *Velociraptor*, may have utilized more eagle-like behavior, and occasionally may have even hunted cooperatively, while perhaps the more opportunistic troodontids may have behaved differently to some degree. It is also possible, and indeed likely, that there were behavioral differences between species within the Troodontidae and Dromaeosauridae to accommodate their varying sizes, prey preferences, and environments.

None of this is conclusive, of course. It is impossible to infer the behavior of an extinct animal with 100% accuracy, and the fossil record may yet have much to reveal on the subject of dinosaur behavior. In the absence of hard fossil evidence however, it may be useful to make inferences about the hunting, breeding, and social behavior of deinonychosaurs based on a kiwi-accipitrid behavioral model. The evidence available at the current time is consistent with such a model, and it is likely a more useful model than either the wolf-style pack hunting hypothesis or the varanid-style behavior hypothesis. Birds are the closest living relatives of the deinonychosaurs and are also the animals most similar to them in brain structure (Larsson, 2001), making birds of prey arguably the best behavioral analogues for deinonychosaurs.
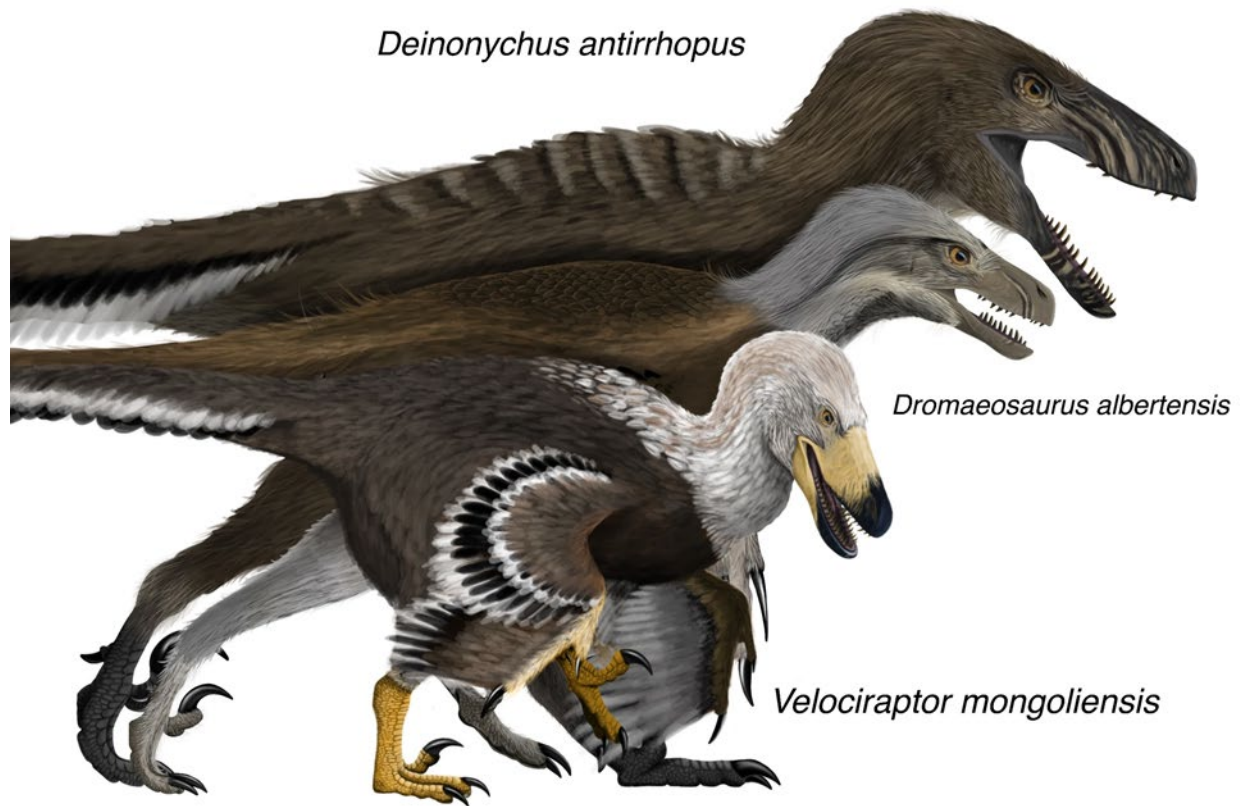
Deinonychus antirrhopus

Dromaeosaurus albertensis

Velociraptor mongoliensis

Photo Credit: fossilcrates.com

Dinosaurs and the Possible Origin of Avian Monogamy

Avian monogamy has been discussed and put forward as a possible or even likely aspect of deinonychosaur behavior. But this raises the question of why monogamy might have been advantageous to them, and when and why it may have originated in the avian lineage.

An overwhelming majority, roughly 90%, of modern birds practice some form of monogamy (Lack, 1968). However, the permanence and fidelity of avian monogamous pairing varies by species, with many pairs only lasting one breeding season and many species practicing only social monogamy but being genetically promiscuous (Black, 1996). Some, notably the kiwis (Davies, 2003), accipitrids (Watson, 2011) (Mannan, 1991), owls (Konig, 2009), and falcons (Hector, 2010), practice long term monogamy and generally mate for life, or until their mate dies. Other birds that mate for life include, but are not limited to condors (Tait, 2006), puffins (Creelman, 1991), hornbills (Stanback, 2002), and macaws (Alderton, 2003). On the other monogamy extreme, some species, such as the Mandarin Duck (*Aix galericulata*), practice only minimal monogamous behavior; the male stays to protect the female while nesting, but leaves right before the eggs hatch (Madge, 1987). This may not even constitute true monogamy

since monogamy generally means the pair stays together for at least a breeding season and cooperates in rearing offspring (Lack, 1968) (Kleiman, 1977).

There are many theories as to why monogamy evolves in various groups of animals, many theories being specific to certain groups, and while the general advantages of monogamy can be easily recognized, the exact reason monogamy evolves, as opposed to other mating systems which are also proven to be highly successful, is more difficult to ascertain. It may be that there isn't one solve-all answer. Considering the highly diverse traits and unique evolutionary backgrounds of the animals in question, monogamy may have evolved in different groups for different reasons.

One reason monogamy may have evolved in the avian lineage is the advantage of biparental care of offspring. However, while it is true that many monogamous birds do practice post-hatching biparental care, it does not seem to be universal among monogamous birds. Some birds, namely kiwis, mate for life, yet provide almost no post-hatching parental care at all (Davies, 2003) (McGregor, 2015). There is also a minority of birds which either aren't monogamous, or, like the Mandarin Duck, do form short-term stable pairs but split up just before the eggs hatch (Madge, 1987). Additionally, the practice of genetic infidelity and nest parasitism, present in many monogamous birds (Lack, 1968), suggests that social monogamy may be more important to many birds than genetic monogamy, adding an additional layer to the monogamy question. While post-hatching biparental care is certainly an advantage of monogamy, and one which many birds practice, it may not be the advantage that drove the evolution of avian monogamy in the first place.

One possibility could be that monogamy evolved as a response to the dinosaurian/avian combination of being endothermic and oviparous. This could also explain why monogamy is practiced in only 3-9% of mammals (Kleiman, 1977) (Lucas, 2013), which are endothermic and, with the exception of monotremes, viviparous. Birds, like mammals, are endotherms, and as endotherms, require a higher energy intake to survive. Ectotherms, such as crocodiles, require far less energy to function. For instance, brooding female Nile Crocodiles are always found with empty stomachs and can go several months without eating (Guggisberg, 1972). A bird cannot do this do its higher metabolism. A Golden Eagle, for example, can only go about a week without food (Brown, 1986). This may create a challenge for avian nest care. Like crocodilians, birds guard and protect their nests/eggs. Birds take this even further than crocodilians do, however, and provide direct incubation of their eggs using their own body heat. This excellent nest care may come at a cost. It ties the bird to its nest, limiting its ability to acquire food. Depending on the species of bird and its diet, this disadvantage may be more or less pronounced. In herbivorous or omnivorous birds, food may be readily available near the nest. But in other species, especially birds of prey such as eagles and kiwis, guarding and incubating a nest may preclude the option of hunting, which is a more involved process that may require a lot of distance travelled. However, these birds avoid this problem by having a permanent mate. While nesting, these birds switch off nest duty so the other can find food, or the incubating individual may have food brought to them by their mate (Gordon, 1955) (McGregor, 2015). Hornbills are another example of monogamous birds, and while nesting, the female is barricaded into her nesting hole. This protects the female and her offspring from most threats, including competition from other hornbills, but completely prevents her from leaving for any reason. But she does not starve, because the male brings her food (Stanback, 2002) (Kalina, 1988). Having a mate to share in nest protection/incubation duty or providing food would be a highly advantageous behavior for an animal that must tend to its

eggs but which also has high energy requirements. Even in some non-monogamous species, such as the Mandarin Duck, the pair stays together during nest incubation (Madge, 1987), which could be a response to the demands of being endothermic and oviparous. In emus, which generally only practice mono-parental nest care, the brooding parent survives off fat reserves and may lose up to a third of their body weight (Taylor, 2000). However, those few emus that do stay as pairs during nesting practice the same "switching off" strategy which allows each parent to find food while the other incubates (Eastman, 1969), thus greatly reducing the proven cost of nest care. And while ostriches are not monogamous, they do form polygynous family groups in which the male and his females all participate in nest care (Nell, 2003), thus solving the same problem monogamy does, but with a different solution.

Mammals are also endotherms, and therefore have high energy requirements, but unlike birds, are viviparous, carrying their unborn offspring inside them rather than laying eggs. This means that mammal mothers can still hunt or forage without needing to worry about guarding a nest full of eggs. Consequently, perhaps, monogamy is less common in mammals. In the minority of mammals that do practice monogamy, the behavior may have evolved due to other evolutionary drivers. And reptiles usually lay eggs, but either do not practice any nest guarding, or if they do, as is the case of crocodilians, they are not under the same energy constraints as their endothermic avian cousins. So, birds have a unique challenge when it comes to reproduction, and it may be nest care which led to the evolution of avian monogamy. Then from the behavior's inception it has been modified to suit the needs of various species, with many also emphasizing post-hatching bi-parental care, some adopting long-term monogamy or "mating for life", some adopting short-term monogamy, some only practicing social monogamy, and a minority experimenting with other, non-monogamous lifestyles.

The reason for monogamy evolving as the avian norm instead of ostrich-style polygyny may be in part due to distribution. Both monogamous pairs and polygynous groups solve the problem of prolonged nest care and endothermy. But monogamy, especially mating for life, is thought to be more common in animals with a wider distribution, where frequent gatherings, and therefore potential mates might be less common. In other words, for some animals with extended individual ranges and less likelihood of socializing with the opposite sex, it may be more beneficial for an individual to pair for life when it finds a mate instead of leaving and risking not finding a new mate. Resource limitations and territoriality may be driving factors in this dispersion (Kleiman, 1977) (Sundin, 2009) (Schacht, 2016) (Kokko, 2006). Of course, many modern birds are highly social, yet are still socially monogamous. It is possible then that the ancestors of modern birds may have been more thinly distributed/territorial, and since modern organisms are largely a product of their evolutionary heritage, monogamy was passed on to most modern birds even if the specific drivers that favored monogamy over polygyny are no longer present in many modern species.

The origin of avian monogamy may very well lie within the birds' dinosaur ancestors. Dinosaurs laid eggs like modern birds (Varricchio, 2002) and most, if not all, species were probably endothermic, perhaps having similar metabolic rates to modern kiwis (Paul, 2002), with many species, including theropods and ornithischians confirmed to have feathers, suggesting that the common ancestor of all dinosaurs was also feathered and therefore endothermic (Godefroit, 2014). Dinosaurs known to lack feathers, such as ankylosaurs, may have still been endotherms, but secondarily lost feathers (Benton, 2019). At least some theropods also seem to have directly incubated their nests, like modern birds (Varricchio, 2002) (Sato, 2005) (Amiot, 2017) (Grellet-

Tinner, 2006) (Varricchio, 2008). Regardless of whether they directly incubated their eggs or used rotting vegetation to incubate them (Dodson, 1994), by phylogenetic bracketing, it can be inferred that most dinosaurs likely practiced nest guarding, since their basal relatives, the crocodilians, do, and their descendants, birds, do as well. For some, like hadrosaurs, which appear to have been colonial nesters (Palmer, 1999), leaving their nests to find food may not have been a major issue since they ate plants which would have been readily available nearby and since there would have been plenty of other parents around the nesting colony that would drive off carnivores or egg thieves. But for those dinosaurs that didn't live in herds or nest in colonies, especially those that were carnivorous, i.e. the theropods, they would have experienced the same conundrum faced by modern birds: protect the nest and risk starvation, or go hunting and risk losing the eggs due to predation or some other form of disruption. This problem would be compounded for those dinosaurs which practiced direct incubation, since prolonged absence of the parent would result in the eggs dying from lack of thermal control. The need to protect their nest plus the need to hunt for food, may have driven the carnivorous theropods toward forming stable pairs or family groups. And because they were predatory, and predators, including avian predators, tend to be more territorial and dispersed than non-predators, eagles and kiwis being avian examples (Davies, 2003) (McGregor, 2015) (San Diego Zoo, 2011) (Watson, 2011), monogamy, and perhaps even mating for life, may have been highly favored in the theropods and subsequently in the avian lineage, creating the evolutionary foundation for avian monogamous behavior.

Currently, territoriality in extinct dinosaurs can only be inferred based on modern observations, and while nest guarding can easily be inferred by phylogenetic bracketing, the degree and type of nest care can currently only be confirmed from a few species. But assuming that both nest guarding and territoriality was present in all or most carnivorous dinosaurs, then it is possible that avian monogamy may have a dinosaurian origin going all the way back to the earliest dinosaurian carnivores, or perhaps even before.

Conclusion

Among theropods, deinonychosaurs are the closest sister group to the Avialae, which includes modern birds, and deinonychosaur behavior was likely very similar to extant birds of prey or extant ratites. This means both the popular image of wolf-like pack hunters as well as the rival hypothesis of deinonychosaurs as having varanid-like behavior, may very well be incorrect or incomplete, with their true behavior likely being somewhere in the middle and distinctly birdlike. They may have formed stable pairs. They may have mated for life. They may have even hunted in these pairs, thus keeping a small part of the pack hunting hypothesis alive. And carnivorous dinosaurs themselves may have been the original pioneers of avian-style monogamous behavior, owing to the dinosaurs' unique blend of endothermic metabolism and oviparous reproduction.

Hopefully more fossil evidence for behavioral traits in dinosaurs will surface in the future. Certainly, the discovery of additional fossil nests or direct evidence of adult-offspring interaction in deinonychosaurs would shed valuable light on the topic. But for now, while we are largely confined to the realm of inference, a monogamous eagle-kiwi model for deinonychosaur behavior may be the most likely behavioral model for understanding the deinonychosaurs and it is consistent with the current available evidence from the fossil record and may help explain why the avian lineage evolved monogamous behavior in the first place.

Acheroraptor temertyorum. Art Credit:

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