

# Dinosaur nest ecology and predation during the Late Cretaceous: was there a relationship between upper Cretaceous extinction and nesting behavior?

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## ABSTRACT

Many hypotheses have been advanced to explain the K/Pg extinctions, yet none closely examines the likely interactions between dinosaurs and contemporary taxa within their communities. The diversity of predators of dinosaur nests and hatchlings increased toward the end of the Cretaceous. In addition to large snakes having been found fossilized in the act of foraging in dinosaur nests, mammals and birds had also evolved new forms potentially capable of exploiting this resource. The constraints on mammal size and niche diversity lessened prior to the K/Pg boundary. Using comparisons of predator/prey size ratios between extant species and known fossils, we demonstrate that mammalian and avian clades had members large enough to prey on dinosaur eggs and hatchlings. We argue that the reproductive strategy of obligatory nest defense was likely practiced by most non-avian dinosaur species. This strategy was highly susceptible to the increasing numbers of mammalian, avian, and reptilian predators, which rendered this strategy obsolete. Continued selection against large oviparous species in the Cenozoic has limited this life-history strategy to habitats that provide concealment – primarily grasslands, a habitat that did not exist until the Miocene. We urge the evaluation of multiple, perhaps synergistic, hypotheses when considering extinction events of this magnitude.

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## Introduction

Several hypotheses seek to explain the patterns of survival and extinction observed in the fossil record at the Cretaceous/Paleogene (K/Pg) boundary (Alvarez et al. 1980; Officer & Drake 1983; Archibald 1996; Robertson et al. 2004; Schoene et al. 2015). Most explanations invoke environmental deterioration selecting against dinosaurs because they were large and required greater quantities of food than those taxa that survived (e.g. Alvarez et al. 1980, 1984). While we recognize the validity of this approach, we have identified a correlation between the reproductive strategies practiced by extant species and those in extinct communities. With the exception of crocodylians (discussed below), all extant large oviparous species rely primarily on the strategy of concealment of their eggs or the positioning of nests remote from most predators. We suggest this was also true for species throughout the Cenozoic. We argue that because the majority of Late Cretaceous non-avian dinosaurs were large – approximately 80% exceeded 30 kg (Benson et al. 2014, Figure 1) – and unable to fly, they could not employ these strategies and were, instead, primarily obligate nest defenders.

We argue that the evolution during the Cretaceous of morphological and behavioral innovations in birds (Mayr 2016) resulted in reduced predation at the nest (Tanaka et al. 2015), a trend that enhanced their survival relative to non-avian species. Non-avian dinosaur extinction was immediately preceded by the appearance of diversified mammalian, avian, and snake

species (Table 1; Wilson et al. 2010, 2012, 2016; Longrich et al. 2011; Donohue et al. 2013; Wilson 2013; Newham et al. 2014; Grossnickle & Newham 2016; Tarver et al. 2016) whose descendants were among the selective pressures against large size in oviparous species throughout the Cenozoic. The existence of this new predatory guild establishes an inference of potential causality for some K/Pg extinctions. Although nest predation has been previously invoked as a cause of dinosaur extinction (see Benton 1990 and references therein), we consider the specific roles of habitat type, and nest attendance and defense in contributing to the decline of this clade. We structure our thesis with the following three predictions: (i) mammalian, avian, and snake predators evolved novel morphologies and size classes capable of exploiting dinosaur eggs and hatchlings; (ii) the strategy of obligate nest defense was ineffective against these new predator guilds who exploited the fact that most dinosaurs and their nests were difficult to conceal; (iii) extant predatory guilds limit the evolution of large terrestrial oviparous species.

## Pre-K/Pg radiations of new mammalian, avian, and snake species increased the predation rate on dinosaur nests and contributed to their extinction

### Mammals

Non-avian dinosaurs coexisted with mammals prior to the K/Pg (Carroll 1997). Mammals evolved morphologies and size classes

**Table 1.** Mass and size estimates of representative mammalian species of the Late Cretaceous, with comments on their likely ecological roles.

Species	Size (mass estimate, g; or skull length,cm)	Comments (modern analogues are based on similarity of mass and size only)	Geographical Range	Temporal Range	References
Eutherians <i>Altacreadodus magnus</i>	565 g	Paleocene 'Creodonta' and possible ancestor to Carnivora. Similar to a small mink (550–800 g)	Alberta, Wyoming	Latest Cretaceous	Fox 2015; size estimate from Wilson (2013)
Metatherians <i>Nanocuris improvida</i>	523 g	Carnivorous lifestyle. Almost twice as massive as a stoat (300 g)	Saskatchewan, Wyoming	Latest Cretaceous	Wilson (2013), Wilson and Riedel (2010)
<i>Didelphodon vorax</i>	5200 g	Predatory lifestyle. Molars for crushing bone or shellfish. Size of a tayra ( <i>Eira</i> ).	Alberta, Wyoming	Latest Cretaceous	Wilson et al. (2016)
Multituberculates <i>Bubodens magnus</i>	5250 g	Size of Alpine marmot (3000–8000 g)	South Dakota	Late Cretaceous	Wilson (1987)
<i>Yubaartar zhongyuanensis</i>	7 cm	Shows affinities with Taeniolabidoideans indicating faunal exchange between China and America just prior to K/Pg. Size of black-footed ferret.	Henan Province, China	Latest Cretaceous	Xu et al. (2015)
<i>Vintana sertichi</i>	9000 g	Size of badger. Affinities to multituberculates.	Madagascar	Late Cretaceous	Krause et al. (2014)

capable of greater impact on dinosaur populations towards the K/Pg. Studies of Late Cretaceous mammals (Table 1; Wilson et al. 2012, 2016; Wilson 2013; Newham et al. 2014) have found they were larger and more ecologically diverse than suggested by previous work (*cf.* Alroy 1999). The dentition (to include omnivory, carnivory, herbivory) and body mass of mammals had both diversified through the Late Cretaceous. Wilson et al. (2012) found that these radiations, particularly among multituberculate mammals, track angiosperm increases in abundance, diversity, and leaf-vein density (i.e. water-transport efficiency) through the Campanian and Maastrichtian. They suggested that floral diversity led to extensive niche partitioning, providing opportunities for establishment of mammals into new niches formed during and after the Cretaceous Terrestrial Revolution (*sensu* Meredith et al. 2011). Using data from 'exemplar' faunas, Wilson (2013) reported a ~55% increase in species and a ~44% increase in the number of mammalian families from the Judith River (~78 mya) to the upper Hell Creek (~67 mya) formations. In addition to increased dietary, body mass, species and family diversity in the Late Cretaceous, Donohue et al. (2013, Table 1) noted that the mammal species from Black Butte Station, Wyoming (representing the latest Cretaceous Lance Formation), is the most abundant and diverse assemblage known from the central and southern parts of the Western Interior of the United States. Lastly, whereas the extinction of non-avian dinosaurs undoubtedly allowed ecological release for mammalian species after the K/Pg (Alroy 1999), current research indicates that origination of placental orders occurred before the K/Pg (e.g. Tarver et al. 2016). Indeed, Grossnickle and Newham (2016) reported that eutherians, metatherians and multituberculates all experienced radiations in both North America and Eurasia just prior

to the boundary. These taxa might well have influenced regional ecologies before the K/Pg extinction event.

Could these animals prey on dinosaur eggs and hatchlings? Available data show that, in comparison with prey-offspring/predator ratios common in modern communities, Late Cretaceous mammals were well above the size needed for this capacity (Table 2). In particular, Wilson et al. (2016, p. 4) analyzed a near complete *Didelphodon vorax* skull from the latest Cretaceous Hell Creek formation. At an estimated 5.2 kg., and with a relative bite force greater than 'all other measured extant and fossil mammals' its dentition supports it being 'a powerful predator-scavenger' and whose estimated maximum prey size would include 'small and juvenile dinosaurs.' Indeed, predators of the egg and hatchling stages of large dinosaurs need not be larger than nest predators of large extant birds (e.g. ostrich, emu, rhea). In birds, egg and hatchling size generally decrease as a proportion of adult size (Rahn et al. 1975) and this disparity seems further exaggerated in non-avian dinosaurs (Varricchio & Jackson 2004; Werner & Griebeler 2013). Finally, a mammal's gape is often irrelevant to its ability to prey on nests of much larger animals because a variety of prey-handling techniques can be used to access eggs and hatchlings (Table 3). For example, eggs may be rolled onto a stone or knocked together as is assumed for both black-backed jackals (Bertram 1992) and hairy armadillos (*Chaetophractus vellosus*; Reborada, personal communication) preying on ostrich (*Struthio camelus*) and rhea (*Rhea americana*) eggs, respectively. The integrity of these egg shells gives no protection against such strategies. The rhea case is especially informative because the eggs are opened underground by hairy armadillos (Fernandez & Reborada 1998); we suggest these predators provide a model for fossorial species accessing dinosaur clutches covered in sediment.

**Table 2.** Nest predation events featuring a predator taxon of similar or smaller body mass (kg) than its prey (eggs or hatchlings). Hypothetical dinosaur species are included strictly for purposes of comparison and are not intended to suggest a particular predator-prey relationship involving particular species.

Predator taxon	Prey taxon and lifestage	Predator mass	Prey parent mass	Prey offspring mass	Predator/Prey offspring ratio	Pred./prey parent ratio	References
<i>Osbornictis piscivora</i> (aquatic genet)	<i>Crocodylus niloticus</i> (Nile crocodile) egg	1.5	900	0.09	16.7	0.002	Pooley and Ross (1989)
<i>Rattus norvegicus</i> (Norway rat)	<i>Crocodylus niloticus</i> (Nile crocodile) egg	0.3	900	0.09	3.3	0.0003	Pooley and Ross (1989)
<i>Didelphis virginiana</i> (opossum)	<i>Alligator mississippiensis</i> (American alligator) egg	4	181	0.07	57.1	0.022	Pooley and Ross (1989)
<i>Rattus exulans</i> (Polynesian rat)	<i>Sphenodon punctatus</i> (tuatara) egg	0.08	1.5	0.07	1.1	0.053	Cree et al. (1995)
<i>Neophron percnopterus</i> (Egyptian vulture)	<i>Struthio camelus</i> (ostrich) egg	1.8	86	1.6	1.1	0.02	Ehrlich et al. (1988)
<i>Lithobates catesbeianus</i> (bullfrog)	<i>Alligator mississippiensis</i> (American alligator) hatchling	0.33	181	0.07	4.71	0.002	Wright (1920)
<i>ChaetophRACTUS vellerosus</i> (hairy armadillo)	<i>Rhea americana</i> (rhea) egg	4	25	0.6	6.6	0.16	Fernandez and Reboresda (1998)
<i>Sorex</i> sp. (shrew)	<i>Chelydra serpentina</i> (snapping turtle) egg	0.012	13	0.01	1.2	0.0009	Mitchell and Anderson (1994)
<i>Vulpes vulpes</i> (red fox)	<i>Dromaius novaehollandiae</i> (emu) egg	5	55	0.65	7.7	0.09	Coddington and Cockburn (1995)
<i>Vulpes vulpes</i> (red fox)	<i>Dromaius novaehollandiae</i> (emu) hatchling	5	55	0.5	10	0.09	Coddington and Cockburn (1995)
<i>Caracara plancus</i> (crested caracara)	<i>Rhea americana</i> (rhea) chick	0.9	25	0.55	1.6	0.04	Bruning (1974)
Hypothetical <i>Didephodon vorax</i>	Dinosaur egg/hatchling	5.2	3000	1	5.2	0.002	Wilson et al. (2016)
Hypothetical <i>Bubodens magnus</i>	Dinosaur egg/hatchling	5.25	3000	1	5.25	0.002	Horner and Dobb (1997)
Hypothetical <i>Vintana sertichi</i>	Dinosaur egg/hatchling	9	3000	1	9.0	0.003	Horner and Dobb (1997)

**Table 3.** Modes of predation, and predation-caused mortality estimates affected on eggs and/or hatchlings of three ratite species.

Prey species	Predators	Mode of exploitation	Mortality	Reference
<i>Struthio camelus</i> (ostrich)	<i>Canis mesomelas</i> (jackal)	Knocking eggs together	95% in the first year	Bertram (1992)
	<i>Hyaena hyaena</i> (hyena)	Crushing with jaws		
	<i>Neophron percnopterus</i> (Egyptian vulture)	Crushing eggs with stones		
<i>Rhea americana</i> (rhea)	<i>Polemaetus bellicosus</i> (martial eagle)	Hatchling predation	90% in first four months	Fernandez and Reboresda (1998)
	<i>ChaetophRACTUS vellerosus</i> (hairy armadillo)	Knocking eggs together		
	<i>Caracara plancus</i> (crested caracara)	Hatchling predation		
<i>Dromaius novaehollandiae</i> (emu)	<i>Canis</i> spp. (wild dog)	Unknown	>95% in the first year	Coddington and Cockburn (1995)
	<i>Vulpes</i> spp. (fox)	Unknown		

## Birds

Among the extant diversity of vertebrate predators on eggs and hatchlings of large oviparous species (Tables 2 and 3), several bird species are, themselves, very effective at consuming eggs and juveniles (Bruning 1974; Bertram 1992). We suggest that avian predators posed an increased threat particularly to non-avian dinosaur hatchlings around the K/Pg.

As in the case of mammals, Late Cretaceous birds had also attained diversity in body size with some ornithurines – the clade

leading to crown neoaves – known to reach 1.5–3 kg (Longrich et al. 2011; for comparison, Turkey Vultures [*Cathartes aura*] range from 0.8 to 2.3 kg). The exact timing of this rapid speciation is unknown, but by the latest Cretaceous, ornithurine birds outnumbered enantiornithine species, in North America at least. In Longrich et al.'s (2011) study of three formations from the final 1.5 million years of the Cretaceous, only 3 of the 17 species are enantiornithines. Clearly, bird assemblages were experiencing dramatic changes in the period just before the K/Pg boundary

(but, see Feduccia 1995). We suggest niche expansion accompanied these morphological changes, and, while the large size and shell-thickness of many non-avian dinosaur eggs would have protected offspring, predation on hatchlings would be expected. As modern analogues, skua (*Catharacta lonnbergi*) frequently prey on King Penguin (*Aptenodytes patagonicus*) chicks (Hunter 1991); and Crested Caracara (*Caracara plancus*) inflict heavy predation on rhea chicks after hatching (Fernandez & Reboresda 1998). Non-avian hatchlings would surely have faced similar threats.

Mayr (2016) suggested that diversified offspring predators might have influenced the success of ornithurines over enantiornithines. If offspring predators were indeed involved, we propose that this was possible via at least two mechanisms: direct predation of one group on the other; and/or competitive success of ornithurines attributable to their relative immunity to predation from other species (Tanaka et al. 2015). In any case, the advanced capacity of predation and/or competition of Late Cretaceous birds (as shown by their domination in North American Maastrichtian ecosystems) should be considered when discussing both avian and non-avian extinctions

### Snakes

Multiple snake and non-avian dinosaur egg/hatchling associations have been discovered in the uppermost Cretaceous horizons of India (Wilson et al. 2010). The large size ( $\geq 3.5$  m) and increased jaw mobility of the madtsoiid snake, *Sanajeh indidicus*, allowed a greater diversity of prey items, to include at least hatchlings and possibly sauropod eggs. These adaptations are seen as a progression toward the evolution of wide-gaped macrostomatan snakes (Wilson et al. 2010). Indeed, madtsoiid snakes have now been found in the following Laurasian and Gondwanan Late Cretaceous land masses: Madagascar, Patagonia, Spain, and France (Venczel et al. 2015; and references therein). In another Late Cretaceous madtsoiid snake/dinosaur nest association, *Nidophis insularis* was found fossilized within a hadrosaur nest in the Hateg basin of Romania. Venczel et al. (2015) discuss the likelihood that this species consumed dinosaur eggs or hatchlings. They find that the eggs were too large and that hatchlings were at about the upper limit for consumption. Although hatchling consumption may not have been possible, the snake was likely foraging in the nest for other prey (Venczel et al. 2015). This finding allows the inference that dinosaur nesting sites were an ecosystem within themselves. Where our prediction is concerned, these fossil snakes represent novel predators at and around dinosaur nests, including predation of at least hatchlings. They were members of an increasingly diverse predatory guild.

There is evidence that non-avian dinosaurs had always experienced egg and hatchling predation by mammals (Hu et al. 2005), varanids, and crocodylians, as well as other dinosaurs (Ruxton et al. 2014; and references therein). One could argue that, because they had survived under that predatory regime, non-avian dinosaurs could respond similarly to an increased diversity of birds, mammals, and snakes. However, the large body size of non-avian dinosaurs conferred the disadvantage of relatively long generation times. Therefore, their ability to adapt quickly to sudden changes in their environment was decreased (Hone & Benton

2005). We suggest that additional environmental pressure from a growing guild of offspring predators would cause unsustainable attrition of offspring.

### Non-avian dinosaurs were obligatory nest defenders

We use the term ‘nest attendance’ to include any parental activity at the nest that continues after oviposition until hatching: nest defense (e.g. crocodylians), nest manipulation (e.g. megapodes), and contact incubation (e.g. extant birds excluding megapodes). ‘Nest defense’ can occur without any further care during incubation than the defense of the nest against predators. A minimal form of nest defense is ‘nest guarding’ which might or might not require an agonistic response by a parent (i.e. a potential nest predator can be deterred merely by the presence of a guarding parent; Somaweera et al. 2013). We also distinguish between facultative and obligate nest defense: whereas oviparous species that attend nests are obliged to either defend or abandon their reproductive investment depending on the level of risk perceived by the parent (Montgomerie & Weatherhead 1988; and references therein), we argue that the relative large size and inability to fly of most non-avian dinosaurs biased them towards strategies of defense versus strategies of concealment. For example, Nile Crocodiles (*Crocodylus niloticus*) are obligate defenders that remain in view of potential nest predators (Somaweera et al. 2013), whereas an ostrich is a facultative defender in that it depends on concealment but will defend the nest upon discovery, depending on the predator (Bertram 1992).

### Nest attendance

Despite difficulties associating fossil eggs and juveniles with specific parents (Varricchio & Jackson 2016; Deeming 2006), both oviparity and parental care of nests are supported equally in the fossil record (reviewed in Varricchio 2011). Oviparity is universal in extant crocodylians and birds; and parental care of eggs is universal in crocodylians and in all but one bird species. This suggests that non-avian dinosaurs were oviparous and practiced parental care of eggs (i.e. crocodylians and birds provide an extant phylogenetic bracket that includes extinct archosaurs; Witmer 1995). While we agree with Varricchio (2011) that caution is warranted when making such inclusive statements about behavioral homology, we note the following arguments in favor of nest attendance in non-avian dinosaurs:

Once acquired, parental care strategies are rarely reversed (Moore & Varricchio 2016), i.e. crocodylians guard nests and reversal in derived archosaurs is unlikely.

Deeming (2006) noted that high water vapor conductance values indicated a saturated nest environment demonstrating that most non-avian dinosaurs clutches were buried in a substrate. Unwin and Deeming (2008) suggested some pterosaurs (also archosaurs) eggs were buried in sediment and that this resulted in independence of offspring on parental care. We question the assumption that burial of eggs *ipso facto* means that dinosaur or pterosaur parents abandoned the nest. In crocodylians, nest attendance during incubation is not predicated on the need to tend eggs (i.e. it can have a purely defensive value; Kushlan & Kushlan 1980). If a reversal to nonattendance did occur in

pterosaurs, it is likely attributable to the ability of volant species to either hide nests or fly to remote locations. This could not be the case for larger, cursorial species. Therefore, we suggest that nest defense – nest guarding at a minimum – was a basal trait for all archosaurs. In any case, whereas nest attendance is a testable hypothesis from the fossil record, nest abandonment is not.

While the largest clutch size known for sauropods is < 40 eggs (Sander et al. 2008), Werner and Griebeler (2013) suggested that some sauropods laid multiple clutches totaling over 300 eggs per year. Ruxton et al. (2014) inferred from this that sauropods were unable to both attend their nests and acquire food resources, and proposed the idea that parents could hide multiple clutches across space. However, we find little support for the multiple clutch hypothesis. Janis and Carrano (1992), seeking to establish a link between large size and immunity from extinction, argued that massive offspring production could be an evolutionary strategy to re-establish endangered populations. Grellet-Tinner et al. (2006) observed that the random distribution of nests and the arrangement of eggs within titanosaurid clutches in Patagonia, resembled reproductive traits found in crocodylians and chelonians. They suggested that these sauropods were more like reptiles than birds in their reproductive habit, and that they would likely have multiple clutches. Werner and Griebeler (2011) cite the ‘reptilian’ hypothesis of Grellet-Tinner et al. (2006) in attempting to corroborate Janis and Carrano’s hypothesis. They find no correlation between body mass and clutch size in birds, however, and only two of their 116 avian species (selected for phylogenetic proximity to non-avian dinosaurs) are documented to produce more than one clutch per year (Table S1). Nevertheless, the authors repeat the ‘reptilian’ claim and state that sauropods must have had several clutches while lacking any empirical evidence for multiple clutches. Werner and Griebeler (2013) attempt to corroborate their own paper (Werner & Griebeler 2011) by establishing allometric relations between extinct and extant species. They conclude that sauropods adhere most closely to the reproductive strategies of tortoises. A phylogenetic argument would suggest more reproductive homology among members of the saurischian clade (i.e. sauropods and theropods) than between sauropods and more distant tortoise species. Indeed, even while arguing a more reptilian style, Grellet-Tinner et al. (2006) note an egg shell synapomorphy shared by saurischians (including birds), but absent from other diapsids. Rather than viewing their result with skepticism, however, Werner and Griebeler (2013, p. 9) argue their allometric studies revealed that reproductive traits ‘of dinosaurs that were probably more reptile-like (prosauropods, sauropods) coincided with those of reptiles.’ We agree with Martin et al. (2007) who found that, among extant passerine birds, allometric expectations of life history traits were often contradicted by empirical findings. We suggest that caution is even more advisable when drawing conclusions based on allometric data on extinct species, and contend that the multiple clutch hypothesis has acquired an orthodoxy it does not yet deserve.

Ruxton et al. (2014) proposed that sauropods employed spatial dispersal of small, unguarded nests, suggesting an analogy with some animals that hoard their food in different locations. We view this possibility as unlikely, however, because most sauropods nested in colonies (Chiappe et al. 1998, 2005; Salgado et al. 2007; Grellet-Tinner & Fiorelli 2010; Hechenleitner et al.

2016), and such a congregation of large adults would be easily detected by predators.

Perhaps intrinsic to the idea of multiple unattended clutches, is the idea of predator swamping. We contend that it is unlikely that a colony of dinosaurs could abandon their nests and survive excessive offspring predation by overwhelming or satiating predators. For this strategy to be effective, non-avian dinosaurs would have to limit the intensity of destruction of their offspring by avoiding predation and/or limiting temporal access to their eggs and hatchlings. Reproductive effort by many turtle species benefits from both of these factors and provides a relevant contrast to non-avian dinosaur nesting ecology because, even when discovered, the contents of turtle nests swamp predators (Santos et al. 2016).

Avoiding predation: because turtles are aquatic, they have greater capacity to nest in remote locations. Murray River Turtles (*Emydura macquarii*) can recognize specific predators via olfactory and visual cues (Spencer 2002), and some sea turtles are sensitive to airborne molecules (Endres et al. 2009). Risk of predation is likely one of several parameters that turtles assess before deciding to leave the water to nest. The severity of predation has increased in extant communities: raccoons are supported in near-shore environments often by human activities, probably adding to the reproductive failure of several species (Engeman et al. 2006). In the past, however, the reproductive success of freshwater and sea turtles was likely aided by their ability to perceive and avoid the risk of heavy predation on offspring (Spencer 2002; Endres et al. 2009). Whereas nesting non-avian dinosaurs could likely perceive the risk of predation, compared to an aquatic species, they were less able to avoid it.

Limiting temporal access: many turtles have large clutch sizes and hatchlings that emerge from the nest synchronously (Spencer 2002; Endres et al. 2009; Santos et al. 2016); and many escape predation by reaching the relatively low risk medium of water (Türkecan & Yerli 2007). This avenue of escape was not available to non-avian dinosaurs. Indeed, if dinosaur offspring suffered predation at the nest, they likely encountered these same predators during their first months after hatching. Therefore, relative to turtle species, we suggest that non-avian dinosaurs were less able to avoid predation by isolation from predators, and by reducing the time of vulnerability to predation. Without these ameliorating factors, the strategy of predator satiation was unlikely to be successful.

Unlike placental mammals, oviparous vertebrates cannot protect embryonic offspring by simply running away. However, they have evolved strategies to minimize the risk of nest predation. These strategies include defending the nest, concealing the nest, or nesting in a remote habitat with low predator density. Combinations of all strategies are common among extant species. For example, ostriches (*Struthio camelus*) conceal their nests amid savanna grasses, oviposit in remote sites in the sense that they can tolerate arid conditions in places with relatively fewer predators, and will defend the nest upon discovery, depending upon the predator (Bertram 1992). However, in almost all oviparous species, predator avoidance has been the nesting priority, and the evolutionary success of extant birds has been credited in part to their ability to maximize concealment and remote nesting (Tanaka et al. 2015). We discuss the likelihood that nonavian dinosaurs practiced these strategies.

### Remote nesting

Birds can avoid predation by nesting in remote and/or inaccessible habitats such as on cliffs or islands, or in the upper canopy of trees. In contrast, non-avian dinosaurs could not as easily distance themselves from their predators (Varricchio 2011).

### Concealment

Most nests described from Late Cretaceous strata have been in relatively open habitats: as examples, Venczel et al. (2015) describe a 'well drained, relatively dry and open distal flood-plain area' for the nest of hadrosauroid *Telmatosaurus transylvanicus*; Hechenleitner et al. (2016) note that all titanosaur nests found were colonial; Carpenter (1999) states that non-avian dinosaur nesting sites are found in disturbed flood plains, sand dunes, beaches, and volcanic deposits. Nests from this period indicate oviposition in open scrapes, or nests covered with sediment or mounds of vegetation (Horner 1984; Coombs 1989; Clark et al. 1999; Deeming 2006; Tanaka et al. 2015; Hechenleitner et al. 2016). The following points indicate why the relative large size of non-avian dinosaurs, combined with the behavior of nest preparation and/or attendance, made concealment a nesting strategy that was unavailable to most species of non-avian dinosaurs.

### Size

Fossil evidence indicates that greater than 80% of Late Cretaceous non-avian dinosaurs were large (>30 kg; Benson et al. 2014). In contrast to extant egg layers, the large size of non-avian dinosaurs likely facilitated the detection of an attended nest by potential predators (Pianka 1988; Martin 1995). Even if unattended, a large animal's nest has a greater chance of being discovered on account of greater substrate disturbance, or the presence of olfactory and visual cues. Indeed, relatively small turtle nests are depredated by a range of predators using a variety of such cues to locate nests well after the parent turtle has left (Ehrhart & Witherington 1987; Riley & Litzgus 2014). The following cues could potentially be used by predators to locate a sauropod's nest even if buried in sediment: the sight and sound of a colony (Hechenleitner et al. 2016) engaged in territorial interactions; the smell of feces, urine, and cloacal fluids; the excavations and tracks of previous predators; and the activities of other residents of nests (Venczel et al. 2015; Wilson et al. 2010). Therefore, even though the eggs of large dinosaurs were hidden beneath sediment, the nests themselves were unlikely to be concealed.

In comparison to almost all extant terrestrial oviparous vertebrates of <30 kg in body mass, the large size of non-avian dinosaurs precluded stealth when laying and incubating their eggs. We recognize that several small carnivorous non-avian dinosaurs remained into the latest Cretaceous (Turner et al. 2007; Benson et al. 2014; Larson et al. 2016), and that concealment was a likely strategy for them. However, we argue that no single extinction hypothesis can consider every extinct species. Indeed, other scenarios invoke the extinction of carnivorous species following the disappearance of their herbivorous prey (e.g. Alvarez et al. 1980), and we predict a similar fate for the smaller members of the clade Deinonychosauria.

### Lack of suitable cover

Two biomes used for effective nest concealment by large oviparous species throughout the Holocene are grasslands and wetlands. In contrast to grasses, we argue shrub vegetation by itself is less productive, less dense, and not as effective a microhabitat for nest concealment. We recognize that heterogeneity of a concealment habitat is important and that shrubs contribute to this within grasslands (Fernandez & Reboresda 2002). Ferns might have afforded concealment, especially for hatchlings. They are not as suitable a habitat as grasslands, however: while grass produces consumable seeds and young shoots, fern species are seedless and some are toxic (e.g. bracken Yamada et al. 2007). We suggest that the absence of grasslands in the Mesozoic (Stromberg 2011), the reduction in wetland habitat at the terminal Cretaceous (Thomasson et al. 1986; Archibald 1997, 2014), and the reduction of fern habitat coincident with the rise of flowering plants (Schuettpelz & Pryer 2009) meant that even ostrich-sized non-avian dinosaurs had fewer concealed nest-site choices than Cenozoic taxa.

### Nest defense

We argued above that large non-avian dinosaurs attended their nests. We now discuss the effectiveness of defensive strategies in response to small offspring predation. With the exception of crocodylians, if any nest defense occurs among large extant oviparous species, it is facultative. In other words, individuals position their nests to avoid predator detection and defend it only after discovery. Shine (1988) argued that nest defense should evolve most often in species in which the parent can deter predators – this being true for either large or venomous species. We suggest that, because they were relatively less able to use remote nesting and concealment, the majority of non-avian dinosaurs depended on nest defense.

If dinosaurs actively defended their nests, we question the effectiveness of this strategy in the face of an emerging guild of small predators for at least two reasons: (i) dinosaurs needed to maintain structural integrity of their nests and lacked the capacity to defend them against burrowing animals. As a modern analogy, the hairy armadillo (*Chaetophractus* sp.) burrows beneath the nest of the much larger rhea (*Rhea americana*) parent (Fernandez & Reboresda 1998). While this source of predation causes many nests to fail, rheas have no defensive response to it. (ii) small nocturnal predators have an advantage over large diurnal oviparous species. Ostriches that effectively defend the nest from black-backed jackals (*Canis mesomelas*) in the daylight, apparently abandon the nest under similar attack at night (Bertram 1992). Some non-avian dinosaurs might have been nocturnally active (Schmitz & Motani 2011); however, this interpretation has not been widely accepted (e.g. Hall et al. 2011). While non-avian dinosaurs are presumed to have been primarily diurnal, contemporary mammals and snakes were species whose ancestors were predominantly fossorial (Luo et al. 2007). They had lost many of the adaptations that worked well in daylight (e.g. cone cells, oil droplets, sclerotic rings and fovea) in favor of traits that were adaptive at night (e.g. large cornea, and rod-only retinas). Auditory and olfactory sensitivity can supplement the role of vision among nocturnally-active animals, and mammals are

superior to most other vertebrates in this regard (Streidter 2005; Coleman & Boyer 2012). Vibrissae on the face further enhance a mammal's ability to negotiate their environment at night (Hall et al. 2012). Finally, because dinosaur parents were large relative to their offspring, they almost certainly restricted their movements around the nest at night (i.e. to minimize the risk of crushing the eggs or hatchlings). Such a behavioral imperative would provide an opportunity for small, nocturnal predators such as mammals or snakes to consume nest contents without detection.

Nest defense is practiced by most species of crocodylians (Somaweera et al. 2013). This represents an exception to our claim that dependence on nest defense cannot be a viable strategy amid extant predators. We argue that crocodylians have experienced a relatively reduced frequency of offspring predation because their hatchlings find refuge in water. Factors such as turbidity and submerged aquatic vegetation probably enhance crocodylian reproductive success in wetlands (Somaweera et al. 2013); and the semi-aquatic habitat is a particularly effective refuge from mammalian predation (Pasitschniak-Arts & Messier 1995).

Relative to extant oviparous species, we conclude that non-avian dinosaurs were limited in how they protected their reproductive investment. Our arguments in this section might also be applied to explaining dinosaur size per se: large size confers some advantages, for example predator protection and thermal inertia that minimizes fluctuation in body temperature (Paladino et al. 1990). Over some size threshold, however, we argue that dinosaurs were obliged to defend their nest. This likely placed a premium on defense versus speed, and fueled a predator/prey arms race in that direction. We suggest that the protection of their reproductive investment was a powerful selective force for increased adult size. We contend this factor has been under-appreciated in discussions of dinosaur paleoecology.

### **Nest and hatchling predators have limited the evolution of large terrestrial oviparous species since the K/Pg**

If predation on offspring caused unsustainable losses of non-avian populations before the K/Pg, we would expect similar mechanisms to constrain this body plan in the Cenozoic. We claim predators of eggs and juveniles throughout the Holocene epoch have limited the distribution of large flightless birds (mass > 25 kg, including extant ratites) to grasslands, wetlands, and locations lacking carnivorous fauna (e.g. New Zealand). Specifically, concealment of nesting sites is possible only in these locations, and dependence on nest defense is ineffective amid extant predatory guilds. We examine these predictions for species in Holocene and pre-Holocene habitats separately.

#### **Holocene habitats**

##### **Grasslands**

James and Olson (1983) argued that flightlessness evolved on islands in the absence of predation. We suggest that grasslands, especially in their more arid ranges, are 'islands' of low predator density where large oviparous species can effectively conceal their nests. Bertram (1992) noted that he could not detect an ostrich nest to within 10 m, but that it is sited within a territory of

>2 km<sup>2</sup>. Rheas of South America, also nest in grassy open habitat (Bruning 1974) and are similarly inconspicuous (Darwin 1839).

Ratites might be analogous to non-avian dinosaurs in that, unlike their adult forms, their eggs and juveniles are susceptible to predation by a wide range of species and size classes (Tables 2 and 3). Magige et al. (2009) found that all observed nests failed in the Serengeti ecosystem. Predation accounted for 80% of these failures. Studying ostrich reproductive success in Nairobi National Park, Davies (2002) found a 73% failure rate of nests (mainly attributable to predation) and of those chicks that hatched, 88% were taken by predators. Without the concealment property of grasses, this rate might be higher. Indeed, the chicks of both rhea and emu are known to utilize grasses for concealment when danger threatens (Bruning 1974; Davies 2002). This factor is particularly relevant for large oviparous species because the disparity of adult versus hatchling size necessitates that small oviparous offspring spend a proportionally greater period of their early life-history at risk of predation.

##### **Habitats with relatively low predator density**

The presence of large birds in the Holocene fossil records of Madagascar and New Zealand has been interpreted as resulting primarily from the absence of predation by terrestrial predators (Romer 1964; Quammen 1996; Diamond 1998). The existence of cassowaries (*Casuarius* sp.), the only large species known to nest in rainforests, might also depend on the low diversity of carnivorous mammals in New Guinea and North Eastern Australia (Flannery 1995; Wilson 1992).

#### **Pre-Holocene habitats**

##### **Grasslands**

Grass is an important component of nesting habitat for almost all extant large oviparous species, and we hypothesize that it was also important for species before the Holocene.

**Ratites.** Didactyl ostriches appeared in Africa and Europe in the Miocene and have always existed in open habitats like savannas (Kurotchkin & Lungu 1970). Emus specialized on the open woodlands and grasslands across Australia (Worthy et al. 2014). Rheiformes from the Miocene possess limb proportions similar to their descendants indicative of adaptations for running in open habitats (Tambussi & Degrange 2013). Ratites are also known from the Paleocene of Europe, but the quality of their fossil record is poor (Buffetaut & Angst 2014).

**Dromornithids.** These birds existed in Australia from the Eocene until the Pleistocene, during which time representative species experienced steady increases in body size (up to 500 kg; Murray & Vickers-Rich 2004). This increase was coincident with a progressive increase in the role of grasses in Australian ecosystems (Stromberg 2011). Eggshells of dromornithids and emus are found at the same locations (Miller et al. 1999). This observation is important because, given the role of grasses for the survival of emu offspring (Davies 2002), it indicates that both large birds depended on grass for successful reproduction.

**Phorusrhacids.** The largest and most numerous fossils representing this clade are found in open habitats of South

America dating to the Miocene and Pliocene (Alvarenga & Hofling 2003; Tambussi & Degrange 2013). This record coincides with the evolution of grass-dominated habitats, and the advent of environments in the Miocene having many plant species using C4 photosynthetic processes (Stromberg 2011). Grass was an important aspect of the phorusrhacid niche (Marshall 1994), and was likely a valuable medium for nest concealment.

### Wetlands

**Gastornithids.** While no large flightless birds exploit wetland habitats today, it is likely that some did in the past. Andors (1992) argues that the evolution and extinction of gastornithids is linked to the presence, and then reduction of wetlands in both Europe and North America. Studies of extant endangered wetland species report that high nest failure rates result from contraction of wetland habitat that allows access by mammalian predators (Pasitschniak-Arts & Messier 1995; Picman 1988; Sanchez-Lafuente et al. 1998; Murkin & Caldwell 2000). We suggest this has also been true for species throughout the Cenozoic.

**Aepyornis.** The elephant bird (~500 kg) likely owed its success to the existence of wetland habitat for nesting; wetland contraction is implicated in the extinction of *Aepyornis* (Heuvelmans 2014).

### Habitats with relatively low predator density

**Cassowaries.** Three species are known in New Guinea and one in Australia (Naish & Perron 2016). New Guinea has a much lower diversity of predators compared to Australia (Flannery 1995), and this is likely to have been one of the factors enabling greater speciation within this clade of forest birds.

The issues presented in this section demand consideration of the following evolutionary puzzle: compared to the diversity of non-avian dinosaurs before the K/Pg, there is a very small number of Cenozoic fauna having similar sizes, and practicing similar reproductive strategies. What factors prevented this body plan from re-entering the large animal niche? Sander (2013) proposed that obligatory contact incubation in birds limited the parent size on account of the parents crushing their eggs; furthermore, bipedalism constrained the evolution of larger body sizes because four legs are needed to support masses of that magnitude. We accept these explanations for limiting sauropod-like forms, but note the low diversity of forms that are not limited by these factors. Cenozoic flightless birds are/were successful in grasslands and perhaps wetlands, but they have failed to radiate into a wider array of niches. We propose that, in an environment with heavy predation pressure on inadequately protected offspring, natural selection has favored smaller oviparous species over those having large body sizes.

In summary, we suggest the following: (i) the trait of large terrestrial oviparous species that would be subject to the greatest selective pressure is their mode of reproduction; (ii) predatory guilds are the agent of that selective pressure; and (iii) species practicing similar reproductive strategies as non-avian dinosaurs can do so only in habitats that limit predator access or detection, and that these habitat types were unavailable to non-avian dinosaurs.

## Biogeography and timing of extinctions

A challenge for any hypothesis for the K/Pg extinctions is the global timing of dinosaur extinction. If predation on non-avian dinosaur nest contents was amplified around the K/Pg boundary, we would expect the distribution of novel predators would correlate with the extinctions of local populations. While birds could migrate across water, mammal and snake species would tend to use terrestrial avenues. Recent conclusions about the paleobiogeography of this time suggest that opportunities for nearly global migrations existed.

Laurasian floral and faunal fossils demonstrate biotic exchange between North America and East Asia via Beringia, North America and Eastern Eurasia via Greenland by the DeGeer route, East Eurasia and West Eurasia via the closure of the Turgai Straights, and a connection between Fennoscandia and Western Europe, all coincident with the K/Pg boundary (Brikiatis 2014; and references therein). Immigrant mammal species including archaic ungulates and large taeniolauidoid multituberculates appear in North America immediately after the K/Pg. The source of this invasion is not known, but most researchers propose an Asian connection (e.g. Donohue et al. 2013). A similar body of evidence supports the occurrence of Gondwanan migrations; specifically, African, South American, Antarctic, Australian and possible Madagascar and Indian connections with Europe and North America are also probable during Campanian/Maastrichtian stages (Rabi & Sebök 2014, and references therein).

While proponents of an instantaneous extinction event might demand a more tightly bounded set of data from the fossil record regarding migrations of terrestrial taxa at and around this critical period, this is seldom available. Nevertheless, we note the real possibility of asynchronous extinctions on one hand, and different causes for different continents on the other (e.g. trophic collapse caused by volcanism on the Indian sub-continent – Schoene et al. 2015). Indeed, Archibald (2014) contends that 50% of non-avian species became extinct in the last 10 million years before the K/Pg in North America. This claim supports the idea that a single event did not wipe out this globally distributed, diverse and robust clade. Taken together, the evidence indicates that non-avian dinosaurs were effectively endangered before going extinct.

## Conclusions

A number of factors probably contributed to the extinction phenomena recorded at the Cretaceous-Paleogene boundary, including a bolide strike, orogeny, volcanism, and sea-level recession (Clemens et al. 1981; Alvarez et al. 1980; Archibald 1996; Macleod et al. 1997). We have argued for a causal influence of the species themselves. At present, there is no way of distinguishing which factor had the greatest influence, or whether a complex synergy between these and other factors led to the extinction of non-avian dinosaurs around the boundary. We claim that a pattern exists in these extinctions, however, and that it is partially illuminated by the fossil record and reflected in extant species' diversity, life histories, and behavior. The apparent continuing operation of selection against large-bodied oviparous species leads us to conclude that predation was also a causal factor in the



extinction of this body form at the K/Pg. Observation of current ecological processes can guide the construction of hypotheses about past ecosystems. We advocate a more comprehensive application of this principle.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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