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Pain in dinosaurs: what is the evidence?

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Abstract

How far back can we trace behaviour associated with pain? Behaviour is not preserved in the paleontological record so, for dinosaurs, we are restricted to what we can deduce from fossilised bones and tracks. This review is a thought experiment using circumstantial evidence from dinosaur fossils and from the behaviour of their extant relatives to describe probable responses of dinosaurs to serious injuries.

Searches yielded 196 papers and chapters with: reports of healed serious injuries, and limping gait and injured feet in trackways; information about physiology and behaviour relevant to healing; evidence of evolutionary connections with birds and

crocodilians, and their behaviour; and information about relevant aspects of evolution.

Clearly, many dinosaurs survived injuries that would have seriously hampered mobility, impairing hunting or escape from predators, and affecting social interactions. Recovery from severe injuries implies pain-mediated responses. Rates of healing seem faster than for other reptiles, possibility aided by warm-bloodedness. Nesting was often communal, raising the possibility of parental and group protection for injured young. The existence of family groups, packs, or herds raises the possibility of protection or feeding from pack kills. This is the first study of possible pain behaviour and responses to injury in dinosaurs.

Keywords

dinosaur; pain; pain behaviour; healed injury; fossil record

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Introduction

Nociception and related behaviours are found throughout the animal world, from Protozoa to Chordata. These rely on evolved and highly-conserved systems: voltage-gated ion channels are found from prokaryotes onwards (Moran 2015); transient receptor potential ion channels from choanoflagellates onwards; nervous systems in Cnidaria (jellyfish) and more complex groups (Nilius 2011); acid-sensing ion channels in echinoderms, tunicates and chordates (Lynagh 2018). Extinct species, such as dinosaurs, shared this evolutionary heritage. Some deny that vertebrates in general, other than those with a cerebral cortex, can feel pain (Rose 2014), while others describe nociception among fish (Sneddon 2003), similar pain systems and behaviour among birds (Machin 2013), or responses to analgesia among reptiles (Sladky 2013), including opioid receptors in crocodiles (Posner 2013), in terms indistinguishable from those used with mammals. It is reasonable to postulate nociceptive capacities and behavioural responses to injury among dinosaurs: for

brevity,
we shall refer to these as ‘pain’ and ‘pain behaviour.’ Such behaviour would have included
”reduced foraging and exploratory activity, sparing or guarding the injured area or limb,
and memory for and avoidance of cues associated with the injury” (Williams 2016). In contrast to captive animals, few studies have been undertaken on pain behaviour in nonhuman free-living animals (Williams 2016; Williams this issue) and this review is the first attempt to deduce responses to pain in animals known only from fossil bones and traces.

Terrestrial vertebrates were chosen because the challenge of gravity increases skeletal stresses. Consequent injuries from falls, collisions and conflict would be evident in fossil bones and tracks. Most relevant fossils and traces come from non-avian dinosaurs (henceforth ‘dinosaurs’), the dominant vertebrate group for more than 180 million years (My), during the Mesozoic era (occupying half the time since the emergence of terrestrial

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vertebrates), with few from other tetrapods. Therefore, we consider the evidence of healed injuries, mainly serious fractures, predominantly in dinosaurs, and of tracks displaying prima facie pain behaviour or foot pathologies.

Dinosaurs are phylogenetically bracketed by the other archosaurs, crocodylians and birds (and extinct pterosaurs), all showing differences from mammals in healing of fractures (collated in Senter 2016), while dinosaurs show similarities with birds in fracture healing (Anné 2014b). While systems and behaviours in extinct species cannot easily be ascertained, possible forms of these can be found in extant archosaurs.

Methods

We performed a systematic literature search, using PubMed, EMBASE, MEDLINE, Scopus, Proquest Central, Zoological Record (Web of Science), BASE and Google Scholar from their inception to March 2019. Search terms included: healed or healing non-avian dinosaur bone fractures or injuries, including evidence of pathology or

limping from tracks; the same for fossil archosaurs and other tetrapods; fossil evidence for parental and social behaviour in dinosaurs; evidence for such behaviour in other archosaurs; comparative evidence about metabolism and rates of healing. Reference lists of relevant articles, book chapters, bibliographies and reviews were hand-searched. Major palaeontological and other relevant journals and books were also individually searched.

Results

1 Scope of relevant findings

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Some 11,000 results were obtained and, after reading titles, abstracts and whole papers, 196 articles and chapters were identified: 67 dealt with healed or healing bone pathologies, mainly fractures, serious enough to have hampered normal functioning (all but eight in dinosaurs); eight described dinosaur tracks showing injury or altered gait; 82 covered dinosaur social behaviour potentially relevant to survival from injuries; 34 dealt with the physiology of dinosaurs and their extinct or extant relatives; and 37 with general features of the evolution of pain behaviour and relevant social behaviour (some items covered more than one aspect).

We judged that injuries (including subsequent infections) to limbs, shoulder and pelvic girdles, ribs, necks, backs, tails, and jaws, unless described as minor, would impair movement for a significant time, including for predation or escape, breathing, and feeding, but that other injuries would be less likely to cause debility. Fractures to neighbouring vertebrae, ribs or phalanges were treated as single injuries. Severe injuries are rare in the fossil record, with only two identified from before the age of dinosaurs (245-66 Mya) (Bishop 2015; Rothschild 2006). However, there may be under-reporting of pathology (Senter 2016) in describing fossil species.

2 Prevalence of healed or healing injuries in the fossil record

We identified 209 relevant injuries in dinosaurs, 106 (51%) in carnivores (Theropoda) and 103 (49%) in herbivores (Ornithischia and Sauropodomorpha) (Table 1). These were reported in a wide range of species (e.g. Rothschild 1992, 1999; Hanna 2002; Rothschild 2009; Rega 2001, Tanke 2015). Only nine injuries were described in terrestrial non-dinosaurs between emergence on land and the extinction of the dinosaurs.

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Serious injuries to dinosaurs affected some 30 genera, 15 carnivorous (Theropoda) and 15 herbivorous (Ornithischia 12; Sauropodomorpha 3): several individuals had more than one injury. Some fossils could only be linked to a family (e.g. Hadrosauridae), order or sub-order (e.g. Theropoda); others are identified as species.

The number of dinosaur species so far identified is at least 1124 (Starrfelt 2016), 46% theropods, 32% ornithischians, and 22% sauropodomorphs. Assuming each genus to be represented by at least one species, fossil evidence of serious healed or healing injuries has been found in upwards of 3% of species so far. There is a slight preponderance of injuries to carnivores, despite being a minority of species.

The frequency of serious injuries is in general impossible to estimate, with the exception of Tanke and Currie (1996a, 1998), who provide evidence of fibular fractures in 10-15% of Albertan tyrannosaurids. Tanke (quoted in Rothschild 2006) found between 0.025 and 1% of herbivore bones studied to have healed fractures, though not all would have been debilitating. Hadrosaurs (herbivores) show many healed injuries (Tanke 2011); a study of theropods found about a quarter to have forelimb and foot fractures (Rothschild 2006). Carnivores seem particularly vulnerable: a study of 31 T. rex skeletons found about 0.8 serious injuries per animal (Rothschild 2009), while in 12,000 Allosaurus bones there was about one fracture per animal (Rega 2001; Brochu 2003). Some individual theropods have been found with large numbers of injuries: these include the Tyrannosaurus rex

"Sue"

(Larson 2001), *Allosauri fragilis* 'Big Al' (Hanna 2002) and 'Big Al 2' (Foth 2015), and *Dilophosaurus wetherilli* (Senter 2016).

3 Types, causes and effects of injuries

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About 25% of injuries were to the upper limbs and shoulder girdle, 38% to the lower limbs and pelvic girdle, and the rest to the head, body and tail. Injuries may have been caused by predation attempts, fights, and falls, whether accidental or linked to conflict. Stress fractures can be caused by repeated sudden forceful movements, such as leaping to escape attack or grappling with powerful prey (Rothschild 1988, 2005).

Forelimb, shoulder and torso injuries were probably caused by falls and fights: these might have interfered with locomotion (for quadrupeds), feeding, predation, or resistance to predation. Hindlimb injuries perhaps arose from falls and predation: these would have hindered locomotion, and predation by carnivores using hindlimb claws for attack. Some foot and other injuries were stress fractures perhaps caused by dominance behaviours or by sudden movements in flight from predators (Rothschild 1988). Injuries to head, neck, back and tail may have been painful but not necessarily debilitating: these might have hindered feeding and locomotion, particularly at higher speeds. Injuries in sub-adult theropods, such as head- or face-biting wounds, may have been the result of fights with conspecifics (Tanke 1998). Carnivores' injuries were probably caused by falls when pursuing prey, struggles with prey or fights with conspecifics. The possibility of injuries during play among young dinosaurs must not be ruled out: Rothschild (2015) infers *T. rex* play from tooth-marked bones, roughly ball-shaped, which would not have made up part of a meal. This is consistent with evidence of play in reptiles, including crocodylians (Dinets 2015), and birds (Emery 2015). Injuries to prey, often to head, neck, back and tail, are

more likely to have been fatal, either immediately or later from infections. Falls and struggles are more likely to have caused debilitating injuries to legs, shoulders, hips and ribs, interfering with predation, escape from predators, feeding, breathing, and keeping up with social groups.

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In general, injuries to the upper body would have impaired predation, defence against predation or feeding. Injuries to the lower body, and, for quadrupeds, to the upper body as well, would have affected locomotion. Midline injuries, from the head (including skull and jaw) to the tail, would have had various effects, from impairing feeding to impeding free movement. Rib injuries might have had impacts on breathing, affecting ability for vigorous movement.

A Lower limbs and pelvic girdle

Survival of injuries to weight-bearing bones would have been more difficult for obligatory bipeds. Healed injuries to weight-bearing bones are rare. Tibial pathologies included two infections probably resulting from injury, one with growth delay which would have caused limping (Tanke 2002, 2015). Fractured fibulae were about 7% of serious injuries (e.g. Hedrick 2016; Larson 2000), rising to 13% in the tyrannosaurid *Albertosaurus* (Tanke 1996a; Rothschild 2005). Two remodelled tibiae, consistent with extra weight demands imposed by fibular fractures, have been reported in the elephant-sized herbivore

Maiasaura peeblesorum (Cubo 2015). Pes (hind foot) injuries are more common, many being fractures (including stress fractures) of foot bones (e.g. Hanna 2002; Anné 2014a). Some bones show likely post-injury infections, including a probably painful abscess (Vittore 2013), and deformed or missing toes are detected in trackways (Ishigaki 2010; McCrea 2015) (see Fig. 1). Surprisingly, there are several fractures of pelvic bones (ischial, pubic), mainly in herbivores (Tanke 2015; Longrich 2009), one

well-healed

bilateral ischial fracture being “the most severe non-fatal bone injury in a hadrosaur”

observed by Tanke (Tanke 1996b).

B Upper limbs and shoulder girdle

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Fractures of arm bones were fairly common, the radius being most frequently affected

(Table 1). Fractures of the humerus and ulna were less frequent: there was a healed but

deformed humerus; one ulna and radius pair had been broken at the same time and healed fused (Tanke 2011, 2015); one nesting theropod had a well-healed ulna in an arm

used for predation (see Fig 2: Clark 1999); and there was a septic arthritic elbow joint,

possibly post-injury, involving ulna and radius (Anné 2016). A healed fracture of the radius

in a hadrosaur shows thickening due to callus and a slight bending (Sawyer 1987). As

these animals could operate bipedally, the injury might not have hindered locomotion but

could have impaired feeding (e.g. reaching out to browse on leaves), and defence: Tanke

(2011) observes that many hadrosaur fractures had not completely healed by time of

death. Manus (hand) injuries were fairly common, including stress fractures in quadrupeds

(e.g. Rothschild 1988). One individual theropod had gout in two metacarpal joints

(Rothschild 1997). Sometimes two or more bones in the same hand were injured.

Only

one herbivore suffered a broken scapula compared with seven carnivores (and one with a

tendon avulsion) (e.g. Anné 2014a; Evans 2003; Foth 2015; Hanna 2002).

C Head, body and tail

There were many rib fractures, several multiple, some 30% of all injuries considered here:

these were of similar frequency in herbivores and carnivores (e.g. Anné 2015;) (Table 1).

There were a few examples of damage to neck and back vertebrae (including a broken

neck: Tanke 2017), and three of damage to skulls, including one with a massive fracture

and another with a serious bite at the back (Manchester nd). There were five

serious

injuries to carnivore jaws, one extensive predator bite injury and one bilateral fracture to herbivore jaws (Tanke 2015). Apparently less severe healed facial bite injuries seem fairly common in some theropods and may indicate their aggressive tendencies (Tanke 1998).

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There were four examples of extensive damage to tails, probably impeding mobility, including two of half the tail having been lost (e.g. Gonzalez 2017).

5 Individual examples

The most complete *T. rex* so far found, 'Sue', had a damaged scapula, humerus, and three healed ribs (probably from struggling with prey), a deformed fibula (from post-injury infection), and two fused tail vertebrae (Larson 2001). She survived this series of potentially debilitating injuries, living for 28 years.

A record number of healed forearm pathologies has been found in an individual *D. wetherilli*, a theropod from the early Jurassic (193 My ago) (Senter 2016). These include fractures in scapula and radius, possibly caused by collision with a hard surface or fighting. There are abscesses in forearm and hand, probably due to infection following puncture wounds. The animal had survived despite inability to hunt for perhaps several weeks, though scavenging was a possibility.

The case of the Oviraptor (Norell 1995; Clark 1999) (Fig. 2) is informative. This probable female was apparently incubating a nest of eggs at time of death. Closer examination of the skeleton shows a well-healed ulna with callus: the animal survived an injury which would have hindered hunting for several weeks to lay and start to incubate a sizeable clutch of eggs.

6 Pain and recovery-related responses and behaviour

Wall describes the recovering injured animal as "solitary inert...with marked changes of its eating, escape, and social behaviour" (cited in Williams 2016), but it must eat,

drink,
protect itself, and maintain social contact, so its resources must be shared
between

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healing and survival activities (Williams 2016, this issue): support from
conspecifics,
parents or group-mates, could be vital. With one exception, the behaviour of
injured
dinosaurs must remain largely conjectural.

A Healing

The ability to survive serious injuries such as fractures is linked to rate of
healing, itself a
function of metabolic rate. For dinosaurs, this is thought to have been
intermediate
between that of cold-blooded (ectothermic) non-archosaur reptiles and
warm-blooded
(endothermic) birds (Straight 2009). Furthermore, analysing ratios of oxygen
isotopes in
phosphate ions, preserved during fossilisation, in the early callus of a
fractured neural
spine, Straight et al. (2009) deduce a warming of 2.6°C in the area of the
injury. They
describe the process of callus replacement as intermediate between modern
reptiles and
birds.

Penetrating injuries carry a risk of infection. Extant archosaurs bracketing
dinosaurs
(crocodilians and birds) have effective immune systems (Finger 2012; Sharma
1991), so it
is safe to assume that dinosaurs did, too. Evidence of localised infections
attributed to
injury has been found in, for example, the fibula of *T. rex* "Sue" (Larson 2001).

B Limping and guarding

Injuries to limbs involved in locomotion result in initial withdrawal and later
sparing of
affected parts while they heal. Such responses might be detectable in dinosaur
trackways
as altered gaits; also, deformed footprints may offer evidence of relevant
injuries.

Limping is a common response to limb pain (antalgic) or to imperfect healing of

an injury.

In antalgic limping, the painful limb is spared, resulting in a systematic difference in left and

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right pace lengths (see Fig. 1, Trackway C). This is shown by comparison of pace length in trackways of four or more paces (Dantas 1994). About 1% of dinosaur trackways show limping (Lockley 1994; McCrea 2015), with some providing evidence of foot injuries (McCrea 2015). Ishigaki et al. (2010) describe two tracks of limping tridactyl dinosaurs, one with an apparent injury to a toe (shortened and not able to spread as much as the others) (Fig. 1). In published examples, the shorter pace is between 73 and 88% of the longer (Dantas 1994; Lockley 1994; McCrea 2015).

When other parts of the locomotor system are affected, it will not normally be evident from tracks, though placement of the foot may be suggestive. Lockley et al. (1994) report the track of an individual in a herd of quadrupedal ornithopods. From the different placement of the front foot, and a twisting in of the hind foot, they deduce an injury to left forelimb, probably healed with deformity since the animal was keeping up with the herd. Xing et al. (2016) report a tripedal trackway of a quadrupedal sauropod with single front footprints in the middle: the animal seemed unable to use the other foreleg, presumably because of pain or loss of limb. Some footprints show injuries that could explain altered gaits: a photogrammetric examination of the trackway of a limping ornithopod reveals a biomechanical injury to the pad of the middle toe on the left hind foot, said to explain the 8% difference in pace length (Razzolini 2016).

C Other individual protective behaviours

Communication by facial expression or vocalisation cannot be detected in dinosaurs: no sign of vocal apparatus, such as larynx or syrinx, has so far been found in fossils.

However, distress calls, found in crocodylians and birds, and of ancient origin (Senter 2008), are possible dinosaur responses (Brazaitis 2011): these might inform parents of

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predator attack and elicit protective behaviour (Chabert 2015). Modern young crocodylians show many head, limb and tail injuries related to predation (Sawyer 1987) and survival is doubtless enhanced by adults' response to distress calls.

Sheltering while recovering is protective: fossil dinosaurs found in burrows indicate that smaller ones may have sheltered in these (Varricchio 2007) (some dinosaurs showed adaptations for burrowing (Huh 2010)); caves may have been used by larger species.

D Protective and supportive behaviour by conspecifics

Direct evidence of supportive behaviour toward injured dinosaurs is unlikely to be found but fossil evidence suggestive of parental and social behaviour exists. Parental behaviour has evolved many times throughout evolution and has a clear gene survival advantage. It requires the neural architecture to recognise one's young, detect a need state, and initiate protective behaviour. All of these are found in tetrapods and, in particular, in the surviving archosaur groups bracketing the dinosaurs. Physiological similarities between extant archosaurs are consistent with ancient origins for such behaviour (Brazaitis 2011).

Dinosaur brains seem capable of supporting a range of complex behaviours, particularly if the density of neurons was similar to that in birds' brains. These have recently been found to contain many more neurons than previously realised, comparable to many primates (Olkowicz 2016). Notably, a fossilised Iguanodon brain shows a quite well-developed forebrain, associated with behavioural complexity (Brasier 2016).

Proximity of adults able to protect injured young is a necessity: the nesting behaviour of

some dinosaurs is compatible with this (Clark 1999; Varricchio 2015). Some buried eggs in supervised mounds, as do crocodylians and some birds. Others incubated their eggs,

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evidence of which is provided by adults buried and fossilised on nests (see Fig. 2) (Clark 1999). Nesting sites (whether mounds or open nests) were often communal, as in some other fossil and living archosaurs (Avanzini 2007; Horner 1982). In others, several individuals laid eggs in one nest, as do modern ostriches in which, also, one adult, male or female, guards the eggs of several (Varricchio 2008a). Evidence of communal nesting with post-hatchlings present in pterosaurs also points towards some post-hatching care, as does immature bone mineralisation in advanced embryos (Wang 2017).

Trackways of herds or packs provide evidence of social behaviour with a protective element (such as younger individuals travelling close to a larger adult (Diedrich 2011)). Currie (2010) describes a bonebed of at least 12 *Albertosauri* (theropods), concluding that some form of gregarious behaviour was likely, though its nature could not be determined: he also collates 41 examples of bonebeds or trackways with from 2 to over 1000 individual theropods. Older injured dinosaurs, too, may have been protected by family, herd or pack groupings. Hamilton describes how herding behaviour can advantage individuals, even without active protection (1971): there are reports of herds of post-nestling juveniles possibly exemplifying this (e.g. Varricchio 2008b; Zhao 2007). Reports of several young with an adult non-parent, in one case in a burrow, may reflect a protective relationship as in a crèche (Meng 2004; Varricchio 2007). A similar report of a group of synapsids (ancestral to mammals) shows that such behaviour pre-dates archosaurs by some 40 My (Botha-Brink 2007). Another report of such a family group in a diapsid, the group ancestral to dinosaurs and modern reptiles, suggests parental care to be the ancestral condition in

archosaurs, supported by the almost universal occurrence of parental care in modern amniotes (Lu 2015). Whether dinosaur parents were able to respond protectively to alarm or pain cries from young cannot be known but young extant crocodylians do benefit from such protection (Brazaitis 2011; Chabert 2015; Sawyer 1987).

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Hunting ability would be affected by injury, one example being that of the oviraptor with the fractured ulna in an arm used for slashing (Clark 1999) but it is possible that recovering animals could travel with family groups or packs and share kills, as in some modern predators. Parallel trackways have been found which suggest this (e.g. Li 2008). The T. rex 'Sue' was found in a possible family group (Erickson 1999).

Protection of the young is found among most living archosaurs, and other reptiles, such as some turtles and snakes (Ferrara 2013, 2014), including responses to alarm calls. Furthermore, it has been shown that maternal care can evolve easily in a modern lizard species subject to increased egg predation (Pike 2016).

Discussion and conclusions

In reports of dinosaur fossils, over 200 descriptions of healed injuries serious enough to imperil normal life were found. There were far fewer reports of dinosaur trackways that provide evidence of pathologies affecting normal movement. The important lesson is that dinosaurs were able to recover from injuries that would likely have impaired their ability to forage, predate or avoid predation. Many serious injuries would have led to the death of victims in the short term but some survived, even after several serious injuries over a lifetime, with the curtailment of normal activities that these imply. This mirrors findings in mammals of survival from quite serious injuries (Williams, this issue): Chapman (1969) give the example of road-killed deer, a herd animal, where nearly half had healed fractures (even of the pelvis) and one pregnant hind had suffered loss of a forelimb. What

circumstances aided survival until recovery? Since most behaviour cannot fossilise, this question requires a thought experiment.

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Undoubtedly, dinosaurs possessed the highly-conserved pain systems found in vertebrates which foster protective behaviour while fractures mend. Evidence of localised warming and suggestions of warm-bloodedness produced faster healing than for ectothermic vertebrates. The vertebrate immune system, also highly conserved, would have helped to fight infection in injured dinosaurs. All these divert energy from other activity, but animals could not shelter for long without needing to find food or water, and larger dinosaurs could not hide so easily. However, water demand may have been less than for mammals of comparable size since dinosaurs, like birds, crocodilians and other reptiles, are likely to have eliminated nitrogenous waste as semi-solid uric acid. Need for food is reduced in animals that can hide and conserve resources. Another factor is endo- or ectothermy: endotherms generally require more energy to replace lost heat (though less so for larger individuals) while ectotherms (cold-blooded) can often survive long periods without food. However, wounds heal faster with higher body temperatures, which seems to have been the case with dinosaurs (Straight 2009). An ability to lower metabolic rate, combined with local heating of wounds, may have allowed dinosaurs to recover quickly while conserving resources.

Social groups may well have provided some protection against predation, and more active support for dependent young. Active but wounded herbivores are preferentially predated but can gain some passive protection from herding with conspecifics or other herbivores (Hamilton 1971). There may even be active protection, if herds tend to be family groups (Hamilton 1971). However, herds sometimes expel wounded members "lest beasts of prey...should be tempted to follow the troop" (Darwin 2004). Wounded carnivores living in packs, probably closely related, may have shared others' kills while recovering

from injury,
as happens with some extant canid species.

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There are several limitations to this review. Most important is the incompleteness of the fossil record and, in particular, the paucity or indirectness of evidence of behaviour. It is likely that pathology in dinosaur fossils is under-reported (Senter 2016; Norell 1995/Clark 1999). Many pathological bones may not be described in peer-reviewed or indexed journals although documented in museum records or house journals (see Tanke 2002 for examples), but the search could not feasibly extend to these. Even when healed injury or pathology is clear, the extent of pain and interference with normal activity cannot be ascertained. Last, extrapolation from living relatives of the dinosaurs, birds and crocodylians, is hampered by the comparative rarity of studies of pain in either.

Nevertheless, to our knowledge, this is the first time that pain in dinosaurs has been reviewed in the literature, and we hope it encourages others to consider pain in the health and social lives of dinosaurs and other extinct species.

Authors' contributions

Both designed the article concept. LH searched for the data and collated the findings. LH wrote the first draft of the manuscript; AW drafted the discussion; both authors contributed to its final form.

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Conflicts of interest

None.

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Captions

Table 1: Sites and numbers of severe injuries : n (%). C = carnivore; H = herbivore

Figure 1: Trackways showing limping gait. Ratio of longer to shorter alternating steps is

1.25:1 in both tracks. Trackway C shows deformity of right foot (Ishigaki 2010).

By kind permission of Martin G Lockley.

Figure 2: (a) Oviraptor on nest, with healed ulnar fracture (Clark 1999).

(b) Detail showing callus on ulna.

By kind permission of Mark A Norell.

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Table 1 Sites and numbers of debilitating injuries : n (%). C = carnivore; H = herbivore

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C
or
H
Arm Hand Shoulder
Upper
limb
total
Leg Feet Hip Lower
limb
total
Vert/
tail
Rib Jaw/
head
Head
to tail
total
Total
C 9 7 8 24 (23) 9 28 1 38 (36) 4 34 6 44
(42)
106
(100)
H 14 9 1 24 (23) 11 19 7 37 (36) 10 28 4 42
(41)
103
(100)
All 23 16 9 48 (23) 20 47 8 75 (36) 14 62 10 86
(41)
209
(100)

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Table 1 Sites and numbers of debilitating injuries : n (%). C = carnivore; H = herbivore

C
or
H
Arm Hand Shoulder
Upper
limb
total
Leg Feet Hip Lower
limb
total
Vert/
tail
Rib Jaw/

head
Head
to tail
total
Total
C 9 7 8 24 (23) 9 28 1 38 (36) 4 34 6 44
(42)
106
(100)
H 14 9 1 24 (23) 11 19 7 37 (36) 10 28 4 42
(41)
103
(100)
All 23 16 9 48 (23) 20 47 8 75 (36) 14 62 10 86
(41)
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(100)

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Figure 1 Trackways showing limping gait. Ratio of longer to shorter alternating steps is

1.25:1 in both tracks. Trackway C shows deformity of right foot (Ishigaki 2010).

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Figure 2 (a) Oviraptor on nest, with healed ulnar fracture (Clark 1999).

(b) Detail showing callus on ulna.

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(a)

(b)

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