Lesson 6: Attack and Defense

Written by Victoria Arbour, W. Scott Persons, Matthew Vavrek, Philip Currie, and Eva Koppelhus

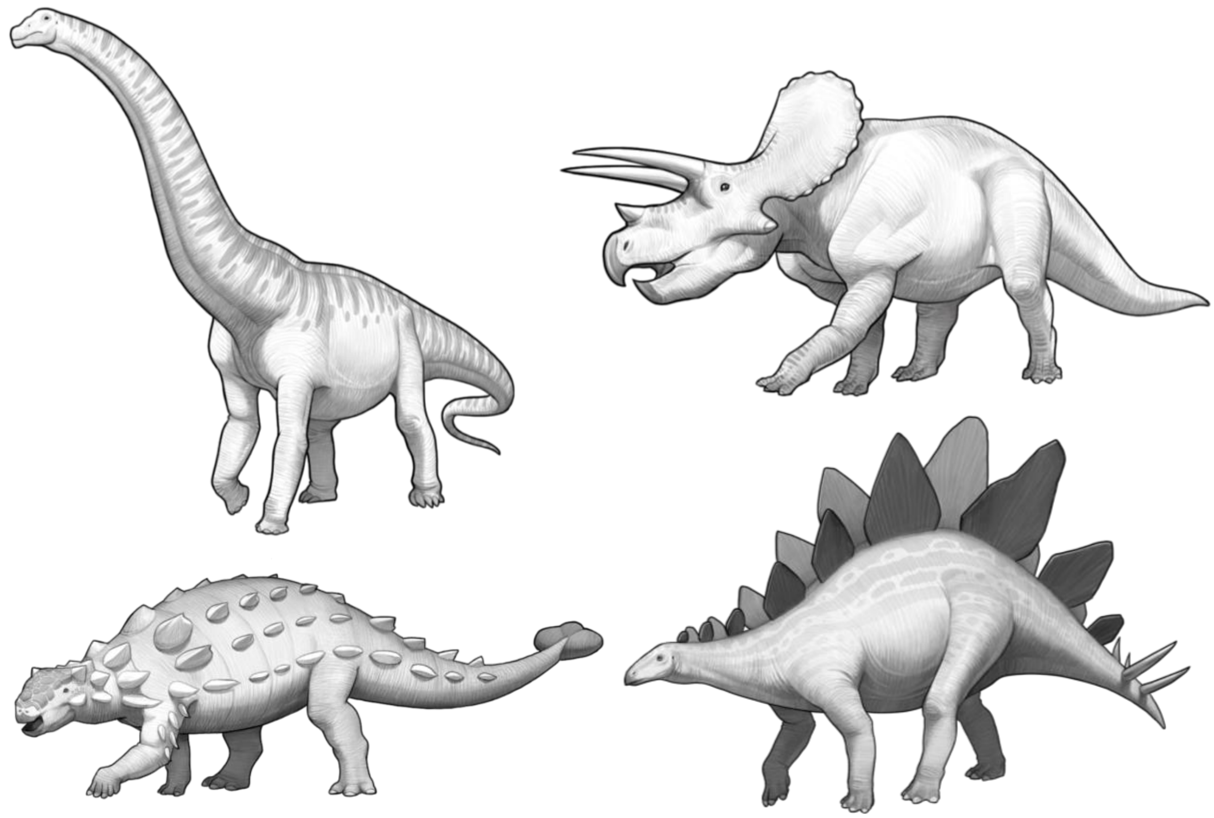
Learning objective for lesson 6: Students will learn about defensive and offensive behaviors and structures

Learning objective 6.1: Identify potential defensive and predatory adaptations in dinosaur skeletons.

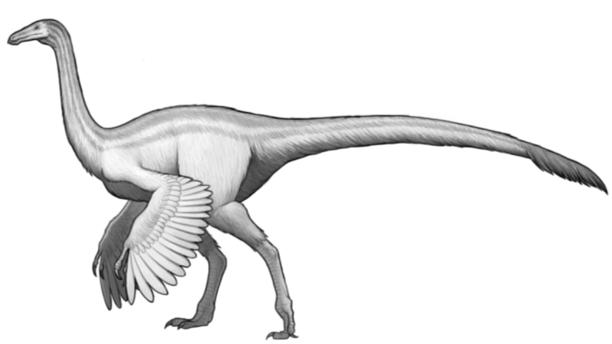
Although dinosaurs were certainly not the insatiable, blood-thirsty monsters that are commonly depicted by Hollywood, there is no doubt that dinosaurs lived with the threat or with the self-sustaining necessity of violence. Herbivorous dinosaurs had to avoid being caught and killed, and carnivorous dinosaurs had to catch and kill prey. The killing tools of carnivorous dinosaurs, like the bone-crushing jaws of tyrannosaurs and the sickle-claws of dromaeosaurs, are among the most impressive in the whole armory of the animal kingdom. Such adaptations in carnivorous dinosaurs were countered by an array of defensive adaptations in herbivorous dinosaurs.

As have been previously described, many ceratopsians evolved long horns, and ankylosaurs and stegosaurs evolved an array of spikes and armor. Having horns or spikes is a common strategy used by modern animals. Horns of buffalo and rhinos or the spiky quills of porcupines make them dangerous prey to attack. Even if predators succeed at killing such prey, they may be seriously injured in the process. Weapons like horns and spikes, beyond their usefulness in defending prey when attacked, are also **deterrents**. They discourage predators from choosing to attack in the first place. Armour, like the shell of a turtle, can also be a deterrent because it makes the animal difficult to eat, and therefore not worth the effort. Large size can be a defense entirely on its own. Giant sauropods may have lacked horns and armor, but their sheer size would have made them formidable prey. Like modern elephants, giant sauropods could have trampled even their largest potential predators, and, although they were not armed with spikes and clubs, sauropods could have dealt severe blows with their massive tails.

Cursorial limbs are another obvious prey defense. Being able to outrun and/or outmaneuver potential predators keeps prey safe and avoids a physical fight altogether. Based on their hind limb proportions, ornithomimids and many small ornithopods are cursorially adapted, and it is likely that these dinosaurs made use of their speed when threatened. However, predators can also make use of speed, and long limbs in a carnivore can be seen as a predatory adaptation.



Top left: *Argentinosaurus*, a sauropod, may have relied on its large size to deter predators. Top right: the horns and frill of *Triceratops* would have made an excellent threat display, and the horns could also have been used as weapons. Bottom left: *Anodontosaurus*, an ankylosaur, was covered in osteoderms and had a tail modified into a club, all of which would have been excellent defenses. Bottom right: The large osteoderm plates of *Stegosaurus* may not have provided much protection, but the spikes at the end of the tail could have been swung at attackers. Art by Joy Ang.



Ornithomimus had proportionately long legs, which would have made it a relatively fast runner. Art by Joy Ang.

Cryptic adaptations allow potential prey to go a step further and avoid even being seen by predators. Crypsis is the ability of an animal to avoid detection, and cryptic adaptations include camouflage color patterns, hiding behaviors, and odor-masking chemicals. Crypsis is difficult to judge from only fossil evidence. Because cryptic adaptations are widespread among modern animals, it is reasonable to assume that cryptic adaptations were also wide spread among dinosaurs. However, relying primarily on crypsis as a predator defense is more common among small animals, which are able to hide more easily behind environmental structures, than among large animals, and it is unlikely that crypsis was the sole predator defense of any large herbivorous dinosaurs. It is difficult to demonstrate that any dinosaur species used cryptic adaptations like camouflage, because colour and colour patterns are not usually preserved in dinosaur fossils, and 'hiding' isn't something that can be fossilized.

Like crypsis, many defenses, including chemical weapons and intimidating displays, are difficult to detect from fossil evidence. Some modern animals use bright colours or false eyes to

The potoo (*Nyctibius grandis*) is one of the most well-comouflaged birds, blending almost seamlessly into the bark of the branches they roost on. Image from ARKive.

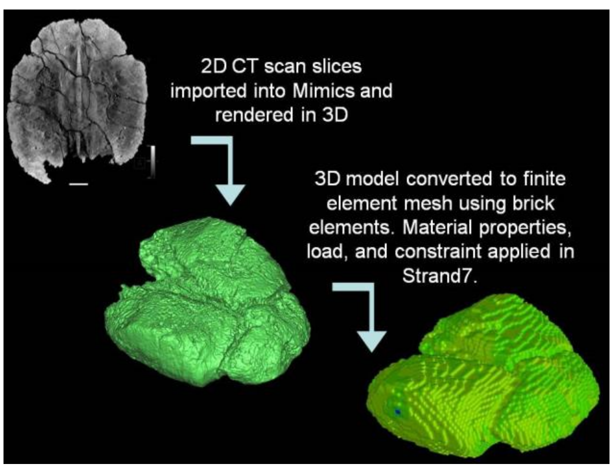
The striped skunk (*Mephitis mephitis*) has dramatic warning colouration and scent glands that release a powerful odour – but neither of these defensive adaptations would be likely to fossilize. Image from ARKive.


The sunbittern (*Eurypyga helias*) has vivid eyespots on its outstretched wings which it uses to scare larger animals away, but again, this threat display would not fossilize and colours rarely fossilize. Image from Stavenn via Wikimedia Commons and used under the CC-BY-SA license.

scare predators away, or to clearly label themselves as toxic or otherwise dangerous. Given the diversity of dinosaurs, it is more likely that some dinosaurs used such defenses than that no dinosaurs did.

Some features of dinosaurs, like horns, spikes, and teeth, are similar to structures observed in modern animals and have a form that make their function appear obvious. However, some features of dinosaurs are novel, without comparable modern analogs, and sometimes appearances may be deceiving.

Finite element analysis is a technique that has been used by paleontologist to help evaluate hypotheses about the functions of many dinosaur adaptations. Finite element analyses are computer simulations that apply set material properties to a digital object and that report data on how stresses are dispersed through the object, when a force is applied at a particular point. A recent finite element analysis carried out by University of Alberta researchers attempted to evaluate the



CT scans of tail clubs were converted into 3D models and tested using finite element analysis. Image by Victoria Arbour.

hypothesis that the tail cubs of ankylosaurs were used as weapons. The reasoning behind this study was that, if ankylosaur tail cubs were used as weapons, it is likely that the tail cubs were able to withstand large impact forces without breaking, whereas, if ankylosaur tail clubs were not used as weapons, it would be very unlikely that the tail cubs were adapted in such a way as to withstand large impact forces. The tail club of the ankylosaur *Euoplocephalus* was digitally scanned, and this digital model was then imported into a finite element analysis program. The digital tail club model was given material properties equivalent to that of bone. To simulate a tail club strike, the force of a *Euoplocephalus* tail swing was estimated and was applied to a point on the outer surface of the digital tail cub model. The results showed that the resulting stresses across the tail club were insufficient to damage to club. Thus, the study concluded that ankylosaur tail clubs were capable of serving as weapons, and this supports the hypothesis that weapons were the function of the tail clubs.

Determining how well a dinosaur could see, hear, and smell is difficult . . . but not impossible. The brain cases of dinosaurs offer some clues, because the sizes of different regions of the brain relate directly to the strength of specific senses. Eye size can be estimated from the size of the orbits, and the inner ear cavity of the skull offers many clues to the strength of a dinosaur's hearing.

Naturally, both predators and prey benefit from keen senses that can alert the one to the presence of the other. However, the sensory needs of predators and prey are not identical. For example, herbivores, who are concerned with avoiding being snuck up on by predators, benefit from a wide field of view. For this reason, herbivores often have eyes positioned on the sides of their heads. This prevents the field of vision of one eye from redundantly overlapping with the field of vision of the other eye and maximizes how much of its surrounding an animal can see at one time.

Conversely, predators benefit from being able to maximize their perception of a single target. Often, but by no means always, predators have eyes that are positioned near each other and that both face forward. This causes the field of vision of both eyes to overlap and grants the predator stereoscopic vision. Stereoscopic vision allows an animal to see the same object with both eyes, and thus to see it from two slightly different angles, which improves the animal's ability to judge depth. Other animals besides predators may benefit from enhanced depth perception, and stereoscopic vision is also common among animals that fly and climb.

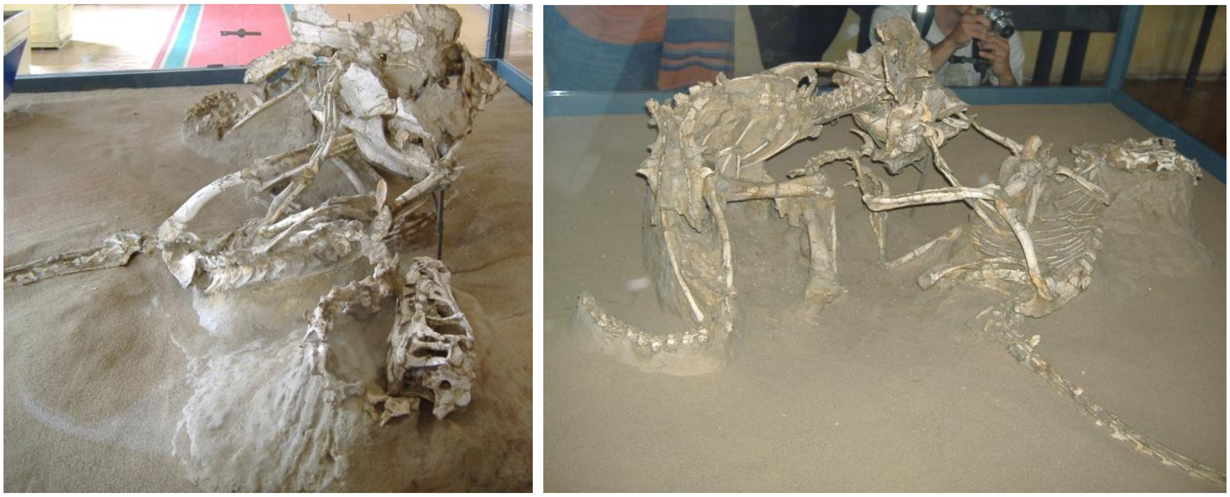
Learning objective 6.2: Suggest predatory behaviours and styles in carnivorous dinosaurs.

Not all carnivores are alike, and there are many different hunting styles among extant predators. Some hunters are ambush predators, which lie in wait until prey comes within striking distance – a good example of this kind of hunting strategy is a crocodile, waiting for prey to enter the water, then lunging. Other hunters stalk and pursue prey, and may rely on stealth to approach quietly and then strike. Still others, like wolves, may pursue prey over long distances, using their endurance to tire out and eventually overtake their prey.

Predatory animals can hunt alone or in groups. Some hunters work cooperatively in order to acquire prey that would be too difficult to kill on their own, and we call these social predators. Hunting behaviours can be diverse even among closely related animals. For example, tigers are solitary hunters, lions hunt cooperatively, and cheetahs sometimes hunt alone and sometimes hunt in pairs or small groups.

Were any predatory dinosaurs capable of social hunting? In Dry Island Buffalo Jump Provincial Park in Alberta, a bonebed of the tyrannosaurid theropod *Albertosaurus* preserves the remains of more than 20 individuals. This seems to suggest that *Albertosaurus* may have lived in groups rather than as solitary individuals. But if you remember our lesson on taphonomy, there are other reasons why many individual dinosaurs may have collected in one spot. However, the geological and taphonomic evidence at Dry Island suggests that these *Albertosaurus* represented a single pack that met some catastrophic end. It appears that at least some theropod dinosaurs formed groups, and therefore may have been social hunters.

An incredible fossil, called the "Fighting Dinosaurs", from Mongolia preserves a *Velociraptor* (a dromaeosaurid theropod) and a *Protoceratops* (a ceratopsian) seemingly interacting with each other. One hand of the *Velociraptor* is in the mouth of the *Protoceratops*, and the other is holding on to the frill of the *Protoceratops*. The *Velociraptor's* sickle-shaped claw is positioned in the throat of the *Protoceratops*. This amazing fossil pair seems to be a snapshot of a *Velociraptor* in the midst of killing a *Protoceratops*, and provides support for the use of the sickle-shaped toe claw as a predatory adaptation. This is one of the best examples of an interaction between two dinosaurs that we know of. Based on this



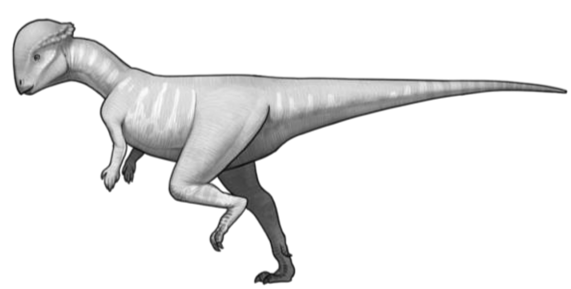
The Fighting Dinosaurs at the Mongolian Natural History Museum. Photos by V. Arbour.

fossil, we might guess that *Velociraptor* was a solitary hunter. However, maybe other *Velociraptor* were present, but were able to escape whatever killed the Fighting Dinosaurs.

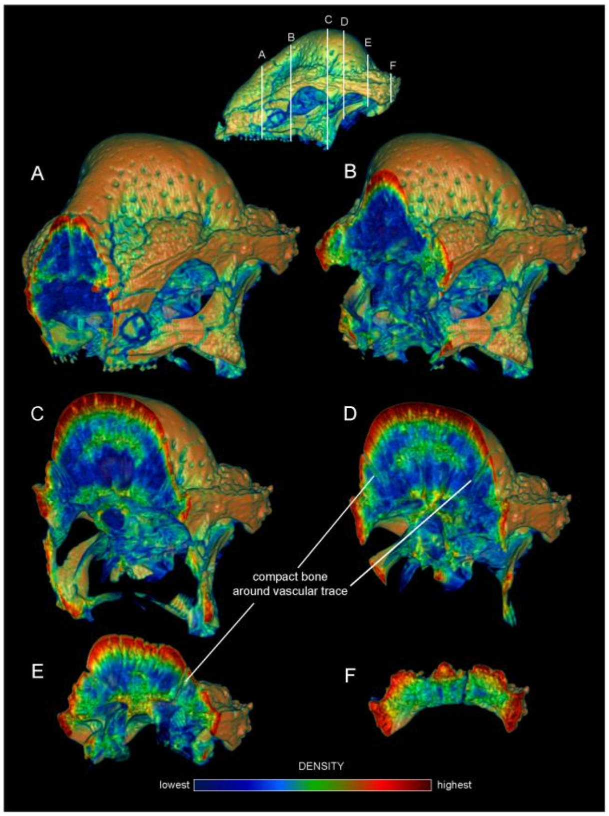
6.3 Suggest potential intraspecific behaviours in dinosaurs

Violence is not always limited to interactions between predators and prey or even between members of two different competing species. It is common for members of the same species to fight over territory, mates, food resources, and for social rank within a group. Fighting and aggressive displays between members of the same species are called agonistic behaviors. Because agonistic behaviors are common, so are adaptations that facilitate them. The antlers of an elk are one example. Male elk use their antlers in head-to-head shoving competitions. This kind of competition that determines which of two individuals is the strongest without either combatant risking serious injury is a special kind of agonistic behavior called **ritualized agonistic combat**.

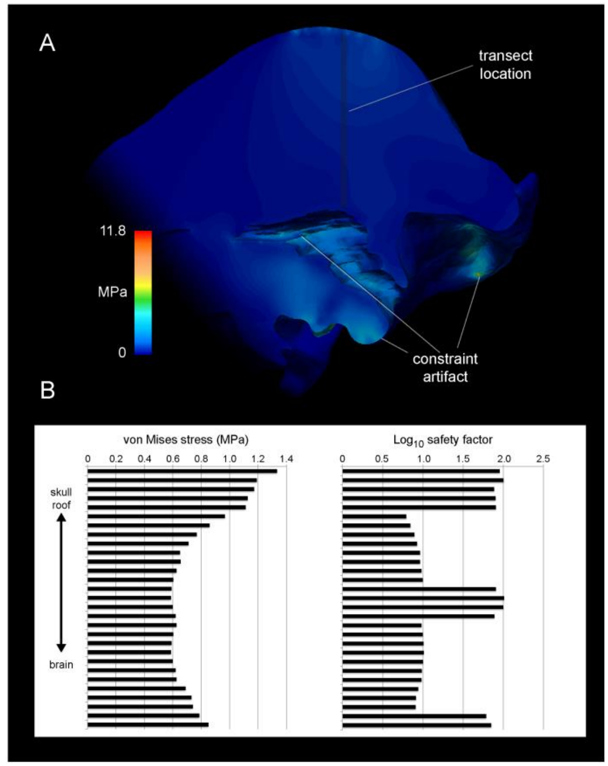
It has long been suspected that the thick domed skulls of many pachycephalosaurs were adaptations for agonistic head butting competitions. Finite element analyses of pachycephalosaur skulls have supported this hypothesis. Like modern animals that engage in ritualized agonistic head butting, such as musk oxen and big horn sheep, pachycephalosaur skulls were strong enough to withstand severe impact forces and had special mechanical stress reducing adaptations.



***Stegoceras* by Joy Ang.**



CT scans of the *Stegoceras* skull UALVP 2 were converted into 3D models. From these, the relative bone density can be shown as different colours, with red representing high density bone and blue representing low density bone. The bone in the dome also has a strut-like appearance, which is similar to the structure in modern head-butting animals. Bottom image from: Snively E, Theodor JM. 2011. Common functional correlates of head-strike behavior in the pachycephalosaur *Stegoceras validum* (Ornithischia, Dinosauria) and combative artiodactyls. PLOS ONE 6:e21422.



The results of a finite element analysis on the dome of UALVP 2 – in the top image, we are looking at a sagittal (lengthwise) cross-section through the dome, and the cavity towards the bottom of the skull is where the brain was housed. The graph below shows how much stress (pressure) there was from the top of the dome to the brain, and the absolute stress values were all low enough that *Stegoceras* would not have given itself brain damage from head-butting. Image from: Snively E, Theodor JM. 2011. Common functional correlates of head-strike behavior in the pachycephalosaur *Stegoceras validum* (Ornithischia, Dinosauria) and combative artiodactyls. PLOS ONE 6:e21422.

6.4 Identify other fossil evidence for defensive, predatory, or other intraspecific behaviours in dinosaurs

There can be strength in numbers, and both predators and prey may benefit from forming groups. Predators that form packs may be able to cooperatively bring down prey that is too dangerous or difficult to be attacked by an individual. It is usually more difficult to sneak up on an alert group than on a single alert individual. Prey that band together in a herd benefit from the additional sets of watchful eyes (and alert ears and noses). Some prey herds may also mount collective offenses against predators that would be too dangerous to challenge alone.

Evidence of dinosaurs forming groups comes from a variety of social display adaptations and adaptations relating to agonistic behaviors and from trackways and monospecific bonebeds. Some sauropod and ornithopod trackways show many sets of footprints, all from the same species of dinosaur and all heading in the same direction. These trackways suggest that the dinosaurs that made them were traveling together as a group. **Monospecific bonebeds** are large accumulations of fossil bones that are all from multiple individuals of the same species. Monospecific bonebeds are known for many kinds of dinosaurs, including ceratopsians, hadrosaurs, and tyrannosaurs (like the *Albertosaurus* at Dry Island).

A healthy dinosaur ecosystem was filled with many different kinds of dinosaur species, and it is improbable that a large random fossil-sample of any such ecosystem would yield multiple bones from only a single species. Monospecific bonebeds, therefore, are often interpreted as nonrandom samples, and an explanation is needed for why only one species is included. One obvious explanation for this nonrandom sample is that the particular species was traveling in a group and that the group collectively met the fate that ultimately resulted in their fossilization (such as dying in a flash flood, a mud or rock slide, or a massive volcanic ash fall).

A *Centrosaurus* herd panics in a flood. Large numbers of *Centrosaurus* bones from many individuals have been found in localized areas in Dinosaur Provincial Park, which suggests that these animals may have travelled in groups. (Jan Sovak)

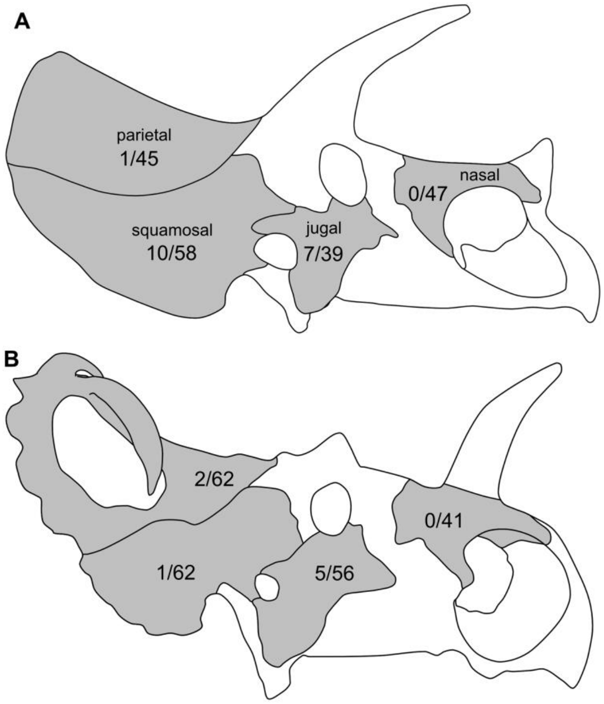
Many monospecific bonebeds are formed from the disarticulated skeletons of many individuals, like the *Edmontosaurus* bonebed we studied in lesson 2. However, sometimes we find articulated skeletons in close association with one another, and this is very strong support for social behaviour. A locality called Bayan Mandahu in China preserved the articulated skeletons of juvenile ankylosaurs called *Pinacosaurus*, lined up next to each other like they had laid down to sleep. This is very good evidence that juvenile *Pinacosaurus* traveled in groups.

***Pinacosaurus* skeletons at Bayan Mandahu. Photo by P. Currie.**

Adult *Pinacosaurus* have never been found in groups or bonebeds, which suggests that, while juvenile *Pinacosaurus* were social dinosaurs, adult *Pinacosaurus* lived solitary lives. Behaviours may change ontogenetically, and so can skeletal adaptations for attack and defense. Juvenile *Pinacosaurus* lacked the heavy armour of adult ankylosaurs, which may be why they lived in groups as juveniles. On the other side of the dinosaur family tree, juvenile tyrannosaurs may have employed different hunting strategies compared to adults. Juvenile tyrannosaurs had proportionately longer legs, which would have made them more fleet-footed than the stockier, more heavily-built adults. Perhaps young tyrannosaurs hunted smaller and faster prey, while adults were better able to attack larger and slower prey. Alternatively, the more cursorial limbs of young tyrannosaurs may have been a defensive strategy that helped the youngsters to avoid themselves becoming prey for adults.

Another source of potential information about dinosaur inter- or intraspecific interactions is the presence of pathologies. Palaeopathologies can include healed injuries or other evidence of diseases, such as infections, cancer, or arthritis. The cause of many pathologies can have multiple interpretations, so it is important to be cautious when extrapolating from evidence of pathologies. Nevertheless, they can provide some interesting clues about dinosaur behaviour. For example, several tyrannosaur skulls show signs of healed bite marks that can only have been made by other tyrannosaurs. Because the injuries had time to heal, these bite marks cannot have been formed by a tyrannosaur killing and feeding on the carcass of another. **Nonlethal face biting** is a common agonistic behavior among modern carnivores, such as crocodiles, and so tyrannosaurs may have engaged in a similar behaviour.

Adaptations that serve in predator defense may also be used in agonistic behaviors. A study examining healed injuries on skulls of two different species of ceratopsians found that injuries on the squamosal bone were more common in *Triceratops* than in *Centrosaurus*. This provides some evidence that *Triceratops* may have locked horns during intraspecific competitions similar to those of modern deer, cattle, and rhinos. The large orbital horns in *Triceratops* would touch the squamosal of an



Frequency of healed injuries on the skull bones of *Triceratops* (top) and *Centrosaurus* (bottom). From: Farke AA, Wolfe EDS, Tanke DH. 2009. Evidence of combat in *Triceratops*. PLOS ONE 4:e4252.

opponent, causing injuries. *Centrosaurus* has smaller orbital horns, and there weren't as many healed injuries on the squamosal, which might mean that the orbital horns were too small to cause injuries in that area, or that *Centrosaurus* did not use its cranial ornamentation for fighting.

Understanding dinosaur behaviours is one of the most interesting parts of palaeontology, but it is important to understand the limits of the evidence we have available. While we can find evidence in support of many behaviours, we cannot 'prove' that a dinosaur definitely did or did not do certain behaviours. For example, the anatomy of ankylosaur tails suggests they were adapted for tail-clubbing, and the results of finite element analyses show that they could use their tails for clubbing, but we can't say that ankylosaurids definitely used their tails for tail clubbing. If they did use their tails for clubbing, we also can't say right now whether they used them mainly as defensive weapons against predators, or whether they used them in intraspecific combat. Generally speaking, the more lines of evidence you can find to support a given hypothesis about dinosaur behaviour, the more confident we can be in our conclusions about that behaviour. Studying the behaviours and adaptations of modern animals, doing biomechanicals tests, collecting evidence from bonebeds and trackways, and looking for pathologies in skeletons are all excellent ways to investigate the behaviour of dinosaurs and other extinct organisms.

Supplementary Materials.

Tetrapod Zoology: Heinrich's digitial *Kentrosaurus*. [Blog post]

The Open Source Paleontologist: *Triceratops* Combat? [Blog post]

Laelaps: Gnarly fossil tells of a torn dinosaur tail. [Blog post]

Laelaps: Tracks hint at the social life of tyrant dinosaurs. [Blog post]

Laelaps: Social sauropods. [Blog post]

Videos of extant animal behaviours from ARKive:

Pack-hunting in African wild dogs - these are highly social mammals that bring down prey as a team and share the food among themselves.
Ambush predation in Nile crocodiles - at the other extreme, crocodiles tend to sit-and-wait for prey to approach, then lunge. Although many crocodiles are

hunting in this small area, they are not generally working cooperatively, and so this is not considered 'pack hunting'.

Muskox head-butting – a possible analogue for pachycephalosaurs.

Bighorn sheep head-butting - a possible analogue for pachycephalosaurs.

Oryx sparring – note the injuries inflicted by the horns!

Giraffe necking – perhaps not unlike ankylosaur tail clubbing, except using heads and necks instead of tails.

Reindeer herding – just one example of many extant animals that form large herds for protection against predators.