

BINOCULAR VISION IN THEROPOD DINOSAURS

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ABSTRACT—The binocular fields of view of seven theropod dinosaurs are mapped using sculpted life reconstructions of their heads and techniques adopted from ophthalmic field perimetry. The tall, narrow snout and laterally facing eyes of the allosauroids *Allosaurus* and *Carcharodontosaurus* restricted binocular vision to a region only approximately 20° wide, comparable to that of modern crocodiles. In contrast, the coelurosaurs *Daspletosaurus*, *Tyrannosaurus*, *Nanotyrannus*, *Velociraptor*, and *Troodon* had cranial designs that afforded binocular fields between 45–60° in width, similar to those of modern raptorial birds. Binocular field width and predatory style (ambush versus pursuit) is examined for extant taxa, along with a discussion of cranial adaptations that enhance binocular vision. The progressive increase in frontal vision in the tyrannosaurids culminates in broader binocular overlap than that of a modern hawk. The visual acuity and the limiting far point for stereopsis is estimated for *Tyrannosaurus* based on reptilian and avian models.

INTRODUCTION

In most vertebrates, the optical design of the eye results in a retinal image or monocular field of view (MFoV) between 160 and 170° in diameter (Walls, 1942). The orbits are oriented anterolaterally such that in virtually all species the optic axes are directed at least slightly anteriorly, i.e., optic axis divergence (AD) is less than 180°. Consequently, the fields of view covered by the left and right eyes overlap partially, providing a region of space directly ahead of the animal visible to both eyes simultaneously, i.e. binocularly.

The region of overlap, the binocular field of view (BFoV), affords the animal several visual advantages. Binocularly-driven neurons, cells in the central nervous system that receive input from two neural pathways, can use ‘probability summation’ of the two statistically independent signals to suppress uncorrelated neural noise and thereby gain a slight enhancement in the detection of low contrast luminance features—an advantage for nocturnal vision (Thorn and Boynton, 1974). A wide anterior field of binocular vision can also assist in the perception of the direction of travel during locomotion (Jones and Lee, 1981), and binocularly driven neurons sensitive to the direction of motion can discriminate objects moving in depth towards the observer (Regan et al., 1979), also useful in locomotion. The most dramatic advantage of binocular vision, however, is the perception of depth and the range of objects seen within the BFoV: nearer objects appear sharply delineated in depth against the surrounding background, subtle variations in curvature across the surface are revealed, and the distance to target points can be judged—all without requiring the observer to reveal itself by moving its head.

Lateral separation between the two eyes results in a pair of images from slightly different perspectives: consequently, a nearby target point seen binocularly will project to a slightly different relative location on the left and right retinæ. This ‘binocular parallax,’ analogous to the motion parallax induced by head movement and the parallax used by surveyors in triangulation, can support the perception of the range or absolute distance of a given target, such as the determination of whether prey is within striking range. The more sophisticated perceptual process of ‘stereopsis’ (= ‘seeing solid’) derives from detecting differences in binocular parallax, known as binocular disparities (Mayhew and Longuet-Higgins, 1982). Stereopsis permits the perception of surface curvature and relief across regions where binocular disparity varies continuously and the detection of surface boundaries where disparity varies discontinuously. Objects

appear sharply demarcated in depth against their background, thus ‘breaking’ camouflage. While the spatial information provided by binocular depth perception is similar to that induced by shifting the head laterally or bobbing vertically, stereopsis has the advantage for predation of not revealing the presence of the predator by self-movement.

Binocular depth perception is not exclusively associated with predators, nor is binocular depth perception all-or-none, as it is often oversimplified. It is also frequently thought that a wide BFoV is associated exclusively with predators. A rabbit (141° AD, 27–32° BFoV), for instance, has a wider binocular field than a crocodilian (144° AD, 24–26° BFoV); a cow (114° AD, 52° BFoV) has more than a tawny owl (55° AD, 48° BFoV) (Walls, 1942; Martin, 1993).

The neural processes of stereopsis require the detection of binocular disparities of only minutes or seconds of arc. Resolving finer visual detail permits detection of finer binocular disparities, which translates to distinguishing smaller differences in distances (or, informally, to ‘see in depth’ out to greater distances). Spatial acuity can be enhanced by increasing the retinal image scale (either optically or by increasing eye diameter), or by increasing retina receptor density (usually within a fovea or ‘area centralis’). For a given visual acuity, increasing the interpupillary separation increases the disparity proportionally; i.e., other factors being equal, doubling the separation between eyes doubles binocular depth acuity, a capability discussed later for *Tyrannosaurus*.

Binocular Vision and Functional Stereopsis

In human vision, for which binocular depth perception is best understood, stereopsis was first shown to be achievable purely on the basis of binocular disparities using random dot stereograms that appear featureless monocularly but reveal depth when fused (Julesz, 1971). Binocular stereopsis provides a functionally independent means of detecting the presence and layout of objects in visual space in the absence of any other visual cues. While surface curvature in depth and object boundaries where depth is discontinuous can be achieved by stereopsis alone, binocular depth perception is most accurate when the visual system integrates disparity information with other depth cues that co-occur in natural scenes (e.g., accommodation, vergence, retinal motion induced by head movements, and monocular three-dimensional cues such as shading and texture gradients; Foley, 1978, 1980; Stevens, 1996).

Binocular stereopsis has been incontrovertibly demonstrated for only a few non-mammalian species. While neurophysiological studies on a variety of mammalian and avian species have demonstrated the existence of neurons that are driven binocularly, the most convincing demonstration of stereopsis is behavioral, e.g., using stereo goggles and a behavioral task requiring the detection of depth in random dot stereograms in the falcon (Fox et al., 1977), the pigeon (McFadden and Wild, 1986), and the barn owl (van der Willigen et al., 1998). Vertebrates with binocular fields wider than roughly 20° almost invariably derive some form of distance perception (at least the perception of range if not full stereopsis) from binocular disparity information (Pettigrew, 1991). The pigeon achieves stereopsis with only 22° overlap (Martin, 1993). While some concern has been expressed that binocular overlap does not necessarily imply stereopsis (e.g., Molnar, 1991), the few known exceptions are highly specialized avians that might be regarded as 'secondarily stereo-blind,' such as the nocturnal oilbird, which lives in totally dark caves, and the swift (Pettigrew, 1986).

In many birds, coordinated motor behavior involving eye convergence, accommodative changes with fixation changes, and head movements suggest that stereopsis integrates with other perceptual processes, in activities such as pecking in pigeons (McFadden, 1990, 1994) and prying in starlings (Martin, 1986). Compared to mammalian stereopsis, however, avian stereopsis is more restricted in the range over which it is effective, and within that range, depth perception is relatively coarser than the mammalian counterpart. This suggests that neural processing occurs at a greater expense of disparity resolution than in mammals (McFadden, 1993). The spatial directions of greatest binocular sensitivity and monocular spatial acuity are often distinct in birds. Falconiforms, for example, have highly divergent eyes and are bifoveate, with a central fovea aligned with the optic axis that supports the finest spatial acuity and a second more temporally located fovea specialized for binocular vision (Frost et al., 1990). Bifoveate birds alternate between aligning their head with the direction of a target in order to fixate it binocularly, and rotating their head by AD/2 (e.g., by ~45° for the falcon) to permit scrutiny of spatial details (Tucker, 2000). In contrast, mammals, with their single fovea but fine control of convergent eye movements, simultaneously achieve their finest detail vision and stereo acuity along a single, dynamically shifting direction of gaze.

This study concerns theropod dinosaurs, so the relationship between BFoV width and predatory style will be examined for reptilian and avian predators. The degree of binocular overlap is substantially greater in those reptiles that use binocular vision in predation than in those that merely detect prey on the basis of their motion. While most diurnal snakes require their prey to move to be detected, those with cranial and visual specializations for binocular vision have nearly 20° greater BFoV than those snakes not specialized binocularly (e.g., the tree snake *Dryophis prasinus* has BFoV width of 46° compared to 20–24° in *Coluber* and *Tarbophis*; Walls, 1942). A similar increment is found in the BFoV of snapping versus herbivorous turtles (38° versus 18°), and raptorial birds have at least 20° greater overlap than granivorous birds (Walls, 1942). While a narrow field would be sufficient for judging the range of a fixated point, a broader field would further allow perception of the three-dimensional layout ahead of the animal as it pursues prey or appraises its situation.

Tradeoff Between Binocular and Monocular Panoramic Vision

The more anteriorly directed the eyes, the greater the width of the BFoV—an increase achieved generally at the expense of the total field of view (TFoV), the panorama visible without head or eye movements. The tradeoff between TFoV and binocular overlap is often regarded as a feature that can be used to distin-

guish the vision of prey versus predator. While the frontal eyes of foxes and the lateral eyes of hares come to mind, this familiar truism neglects the importance of vigilance for predators as well as prey animals, particularly when some predators are in fact themselves prey, as with small snakes and lizards. Most lizards have very laterally placed eyes, with 146–172° AD, 144–160° MFoV, and only 10–20° BFoV. The varanid *V. griseus* has the least divergence, 146°, and the greatest binocular overlap, 32° (Walls, 1942).

The optic axes of the eyes of crocodylians diverge by ~144°, and each eye takes in a MFoV of 152–160°, providing a broad TFoV but only ~25° BFoV (Walls, 1942). The cranial modifications that give crocodylians pronounced periscopy (for nearly submerged stealth) place the orbits substantially above the nasal and frontal bones of the snout. With little further remodeling, crocodylians could seemingly have evolved orbits that faced directly forward, with parallel optic axes. The fact that crocodylian eyes have remained strongly divergent may indicate a balance struck between the needs for panoramic versus frontal vision. A BFoV of ~25° is apparently sufficient for this form of ambush predation, allowing surveillance of the surroundings.

In comparison to reptilian vision, avian and mammalian vision acquired more sophisticated solutions to the tradeoff of binocular versus total field of view. Rather than create a broad panorama using widely divergent eyes, as in the crocodile, felids achieve nearly the same total panorama yet simultaneously exhibit the widest BFoV among vertebrates (200° MFoV, 130° BFoV, and 270° TFoV) through the extraordinary curvature of the cornea.

Some mammals, such as rabbits and horses, and some birds, such as sparrows, chickens, pigeons, and starlings, can vary AD, allowing the animal to shift between optimizing for binocular overlap and optimizing for panoramic vision. A starling, for example, can shift between 43° binocular overlap to viewing nearly the entire hemisphere with the eyes everted (Martin, 1986). A rabbit has ~32° BFoV while peacefully occupied; then, if alarmed, it can shift to a wide panorama in which its two monocular fields actually overlap posteriorly (Walls, 1942; Zuidam and Collewijn, 1979). Such flexibility is not found in reptilian vision.

Binocular Overlap for Ambush Versus Pursuit Predation

A slab-sided or oreinorostral (Busbey, 1995) cranial design, with anterolaterally facing eyes, is characteristic of vertebrates that are not specialized for binocular vision yet nonetheless achieve some BFoV. The width w_B of the unspecialized BFoV is approximated by the expression $w_B \approx 2(w_N - AD/2)$, where w_N is the angular width of the retinal image measured from the optic axis nasally ($w_N = MFoV/2$ for a symmetrical eye). The reptilian MFoV $\approx 160^\circ$, hence $w_N \approx 80^\circ$. Given a moderately narrow snout, AD $\approx 140^\circ$, hence the default BFoV width is ~20° for a reptile that has no specialization for binocular vision. While such a narrow BFoV projects temporally in each retina, these regions can nonetheless provide the optical and neurophysiological basis for depth perception in some species (McFadden and Wild, 1986; Pettigrew, 1986).

While it is noted that the crocodylian BFoV of ~25° might represent a compromise between binocular depth perception and panoramic surveillance, other reptilian ambush predators that engage in precisely timed strikes may have an additional 10–20° BFoV width. While BFoV width does not exceed 45° in modern reptiles, greater widths are characteristic of many avians including modern raptors and some cursorial, secondarily flightless ratites. By analogy, a theropod dinosaur with BFoV wider than that of extant reptilian ambush predators had the potential of achieving more sophisticated stereopsis, spatial judgments of depth, and the layout of three-dimensional space, and may have engaged in more active pursuit predation.

MAPPING THE BFoV OF REPRESENTATIVE THEROPOD DINOSAURS

How did the BFoV of theropods compare to that of extant reptiles and birds? Towards answering this, life reconstructions of the heads of seven theropods were sculpted for this study. A new perimetry procedure was developed and applied to the reconstructions.

Method

Mapping the BFoV by Perimetry—In ophthalmology, the spatial extent of an individual's visual fields can be mapped spatially by a method called visual field perimetry (Lloyd, 1936). With the patient's head immobilized and gaze fixed directly forward, a visual stimulus such as a point of light is then presented at different visual directions and the subject reports whether the stimulus is seen. In a common application of perimetry the functional field of vision of each eye is mapped, which in a normally sighted individual is delimited by the nose and forehead surrounding the eye. The map is usually plotted in polar coordinates with the origin corresponding to a line of sight directly ahead of the observer. Superimposing the plots for the two eyes reveals the region of overlap, i.e., the BFoV.

The BFoV of the author was self-mapped for this study. Using a chin rest, and with one eye open at a time, marks were inscribed on a vertical glass plate indicating the maximum contralateral field visible by that eye. The plot was then transferred from glass to paper, then digitized, converted by a computer algorithm from linear to angular deflections, and plotted (the human BFoV will be used as a comparison reference for the theropod counterparts). The human BFoV is widest along the horizontal meridian, approximately 110° in this case. As in other BFoV plots, the left and right margins correspond to the contour of the nose as seen by the right and left eyes, respectively.

Mapping the BFoV of a Reconstruction by Inverse Perimetry—Conventional perimetry can be reversed in direction to map the field 'from the outside in' as constrained by the shape of the head, the placement of the orbits and the surrounding soft tissue. The principle underlying 'inverse perimetry' is that a line of sight just visible (e.g., that just grazes the snout) from the point of view of the subject will be likewise for the external observer. In this study, a life model of a theropod was placed in a fixture, with the long axis of the head horizontal and perpendicular to a

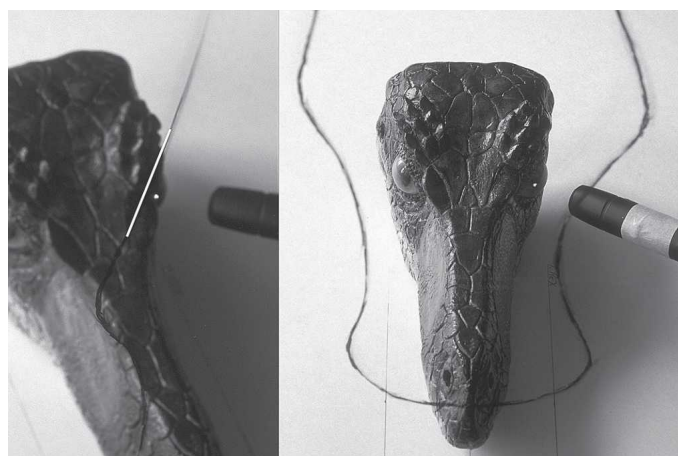


FIGURE 1. Inverse perimetry performed on *Velociraptor mongoliensis*. A glass plate placed between model and observer is used to trace the locus where the glint of the laser reflecting off the eye is just obscured by the snout (segment highlighted in A). Completed tracing is shown from an anterior view in B. This (Condon Museum F38609) and other reconstructions by Garfield Minott.

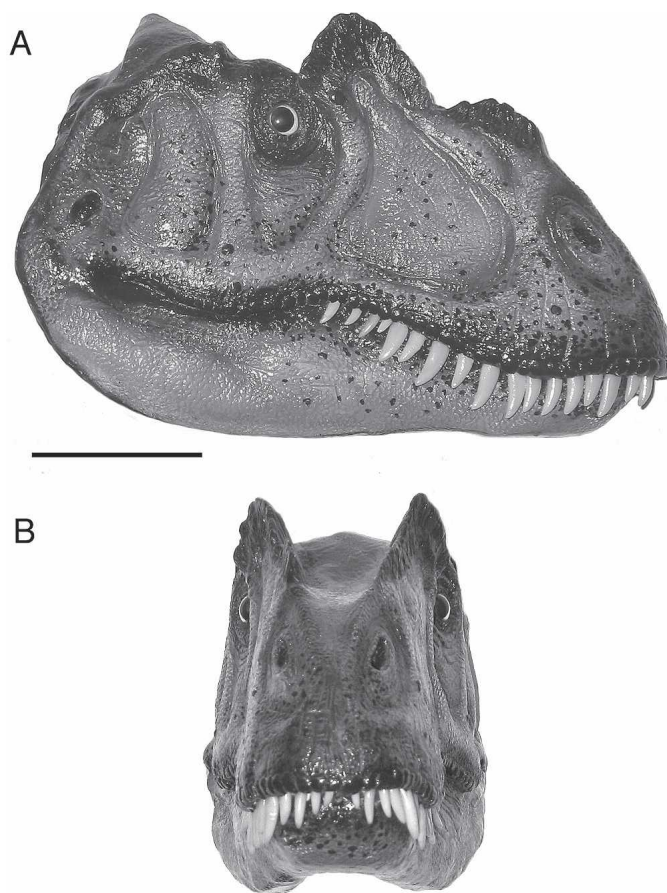


FIGURE 2. The narrow-set eyes, tall rostrum, and prominent lacrimals greatly limit the width of the region of binocular vision for *Allosaurus fragilis*. Reconstruction (Condon Museum F38604) in (A) lateral view, (B) anterior view, based on (Madsen, 1976). Scale bar equals 5 cm.

vertical glass plate placed before the snout. A mark was placed on the glass to indicate the intersection of the long axis of the head with the plane of the glass; the interpupillary distance and distance from pupil to glass were recorded for the subsequent computations.

A continuous locus was then plotted directly on the glass marking how far contralaterally the pupil can be seen before obstruction. To map the right contour of the BFoV, for instance, the model's left eye was illuminated and the author tracked how far to his left the illuminated spot could be seen before being obscured by the reconstruction's snout (Fig. 1). By marking this line of sight on the glass as elevation was varied, a continuous curve was traced. After completing the traces for both eyes, the contours on the glass were transferred to paper, digitized, and mathematically converted to polar coordinates using the same algorithm as created the human BFoV plot. The trigonometry performed by the software was verified for selected points at known distances from the origin, and the maximum BFoV width for each model was confirmed by physical measurements taken several meters from the model.

Life reconstructions were created of the allosauroids *Allosaurus* and *Carcharodontosaurus* and of five coelurosaurs: *Velociraptor*, *Tyrannosaurus*, *Troödon*, *Daspletosaurus*, and *Nanotyrannus* (Figs. 1–7). All models were provided with taxidermic eyes so that the corneal region, illuminated by a laser, would be visible when viewed through the glass plate at some distance from the model. The models (F38604–38609) are deposited in

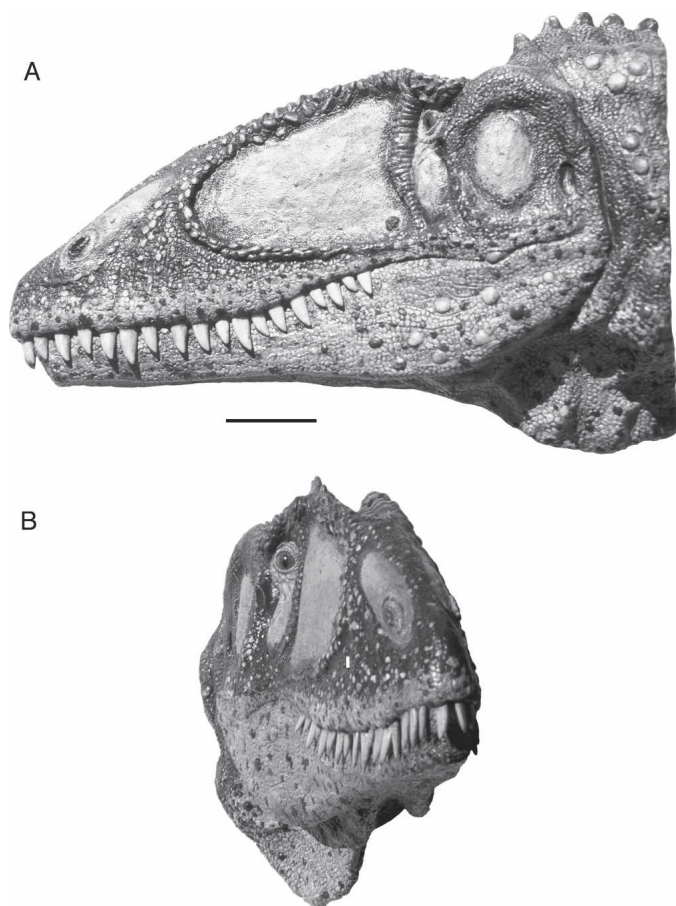


FIGURE 3. **A**, Reconstruction (Condon Museum F38605) of *Carcharodontosaurus saharicus* based on an earlier reconstruction sculpted for Paul Sereno and the National Geographic Society. **B**, the tall, elongate rostrum severely limits binocular vision at low elevations. Scale bar equals 5 cm.

the Condon Museum, Department of Geological Sciences, University of Oregon.

RESULTS AND DISCUSSION

The BFoV for *Allosaurus* is approximately 20° in width and rather uniform over elevation (Fig. 8), while that of *Carcharodontosaurus* broadens for very high elevations of the line of sight, where contralateral vision is less obstructed by the snout. Might that region been of functional significance visually? In general, it would be advantageous to direct the region of greatest binocular overlap ahead of the animal, by tilting the head accordingly. For example, in the pterosaur *Anhanguera suntanae*, a steeply downturned head posture would have aligned the region of maximal binocular vision with the horizon ahead of the animal (Witmer et al., 2003). For *Carcharodontosaurus*, a downward head tilt of approximately 40° (and eyes rotated upward to compensate) would have been required to bring that region to the horizontal. To also permit detail vision along the long axis of the rostrum would then have required either bifoveate retinæ or large-amplitude eye rotations. It is therefore questionable that the BFoV in *Carcharodontosaurus* at high elevations of the line of sight contributed distance perception for predation. The elevation of maximum BFoV width is more plausibly an indicator of habitual head posture in some of the coelurosaurs in this study, where the great-

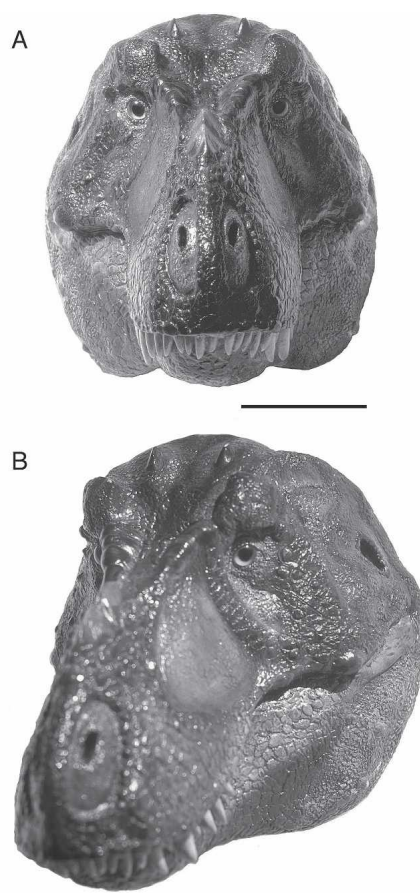


FIGURE 4. **A**, anterior view of *Tyrannosaurus rex* showing excellent anterior vision above and aside the snout. Scale bar equals 5 cm. **B**, the right eye is just visible from this lateral view, which represents the left extreme of the BFoV for this eye elevation. Reconstruction (Condon Museum 38608) derived from a cast of American Museum of Natural History specimen 5027.

est BFoV width occurs at more moderate elevations (see below).

The BFoVs of the tyrannosaurids (Fig. 9) are significantly broader than those of the allosauroids. The BFoV reaches 40° at about 12° elevation. The pronounced hour-glass shape for *Daspletosaurus* is attributable to the relatively narrow inter-pupillary separation and the protrusion of the lacrimals and frontals into the field of view, producing the greatest reduction in field width at approximately 25° elevation. As discussed for *Carcharodontosaurus*, the broader BFoV near 50° elevation was unlikely to contribute to binocular depth perception. The BFoV for *Tyrannosaurus* is more uniformly broad and reaches a maximum of ~55° width at an elevation around 10°. *Tyrannosaurus* had wider binocular vision than modern hawks, and the maximum width would have been directed across a horizontal swath of its surrounds by orienting the snout about 10° below the horizon. The absence of dorsal rugosity and lacrimal horns in *Nanotyrannus* resulted in a still wider BFoV. Note that the substantial left-right asymmetry (Fig. 9) is due to subtly different positions of the taxidermic eyes in the left and right orbits.

Figure 10 shows the BFoV plots for *Velociraptor* and *Troodon*. Maximum BFoV width for *Velociraptor* is ~55° at 10° elevation. The BFoV narrows, creating an hour-glass shape similar to, but slightly broader than, that of *Daspletosaurus*. While the

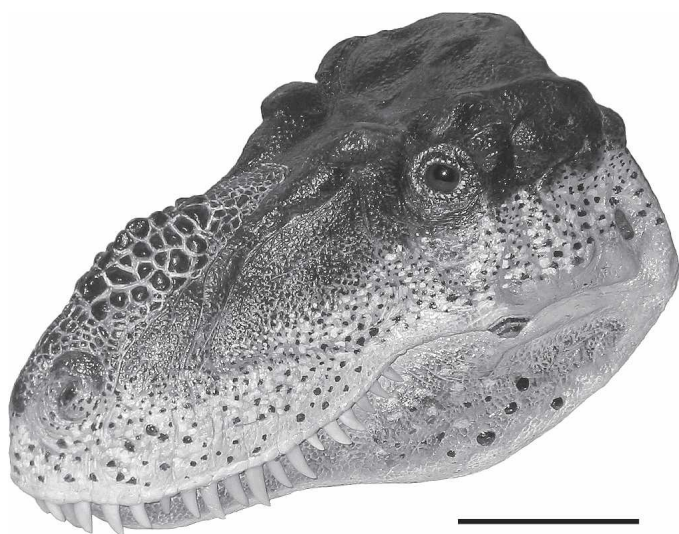


FIGURE 5. A model (Condon Museum F38606) of *Daspletosaurus torosus* based on the holotype (Canadian Museum of Nature, Aylmer, Quebec, specimen 8506: Russell, 1970). Scale bar equals 5 cm.



FIGURE 7. *Troodon formosus* reconstruction (Condon Museum F38610 based on “*Stenonychosaurus inequalis*” (Russell and Séguin, 1982). Scale bar equals 5 cm.

snout of the reconstruction of *Velociraptor* used in this study is very narrow (Fig. 1), the maxillae were in fact slightly narrower and more nearly vertical (Norell and Makovicky, 1998) than in the reconstruction. The mapped BFoV is, therefore, a conservative estimate of the binocular vision achieved by *Velociraptor*.

Troodon has a remarkable 60° BFoV, and a head tilt of approximately 20° would align the region of maximum overlap with the horizon. The wide spacing of the eyes within the cranium allows *Troodon* considerable binocular vision for lines of sight below the axis of the head, as also observed in many modern birds and in *Tyrannosaurus* (Fig. 9).

VISUAL IMPLICATIONS

The maximum binocular overlap for the allosauroid design was slightly less than that of extant crocodilians and close to that predicted for the basal oreinirostral cranial design. The descend-

ing ramus of the lacrimals acted as medially placed blinders in restricting contralateral vision, while dorsally, binocular vision was further limited by lacrimal horns and other rugose features along the snout. These allosauroids, by analogy to modern ambush predators, would have detected prey on the basis of motion parallax between prey and background (induced by either the prey’s motion or the predator’s self motion). As in crocodilians, the narrow BFoV might have provided allosauroids sufficient binocular depth perception for judging prey distances and timing attacks.

Far more binocular overlap was found in the coelurosaurs. The BFoV of tyrannosaurids (35–55°) was comparable to that of



FIGURE 6. *Nanotyrannus lancensis* model (Condon Museum F38607) on Cleveland Museum of Natural History specimen 754: Bakker et al., 1988). Scale bar equals 5 cm.

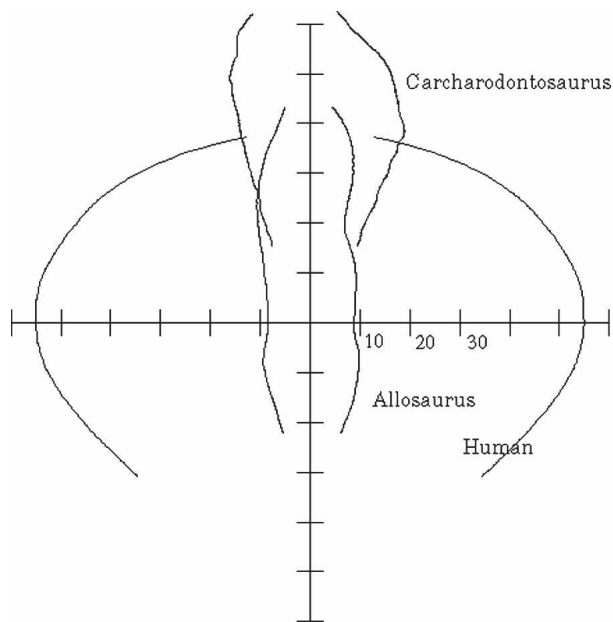


FIGURE 8. The BFoVs of *Allosaurus* and *Carcharodontosaurus* are superimposed on the Human BFoV. *Allosaurus* has slightly less binocular overlap than do modern crocodilians. The region of moderate BFoV for *Carcharodontosaurus* is of unlikely utility due to its elevation (see text).

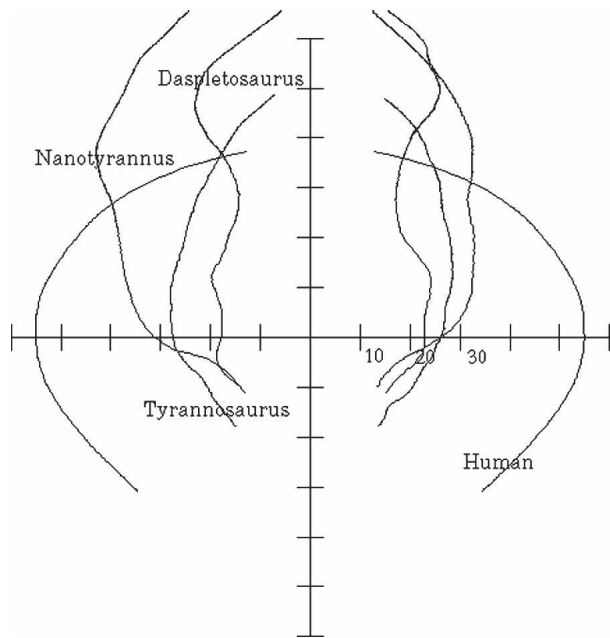


FIGURE 9. *Daspletosaurus*, *Nanotyrannus*, and *Tyrannosaurus* all have broad BFoV at low, hence usable, eye elevations. The hourglass-shaped BFoV for *Daspletosaurus* derives from restrictions to forward vision caused by the lacrimals and nasal rugosity. In *Tyrannosaurus* the maximum overlap occurs for $\sim 10^\circ$ of elevation, consistent with a slight downward slope to the head for a maximum binocular view of the horizontal plane.

modern hawks and that of *Velociraptor* and *Troodon* ($55\text{--}60^\circ$) was comparable to that of owls and substantially greater than that achieved by any extant reptiles. This degree of binocular vision requires extensive cranial modifications, including: depressing the frontals and nasals relative to the orbits, assuming a downward tilt of the cranium, widening inter-orbital separation, mediolaterally narrowing and curving the descending ramus of the lacrimals and maxillae (in the extreme producing “cheek grooves,” for example in *Dryophis* and similar tree snakes), and lateral expansion of the postorbital cranium to permit more anteriorly oriented orbits. Optical specializations such as rostral asymmetry of the optic axis and horizontally elongate pupils further increase BFoV width, but are not likely to be preserved in the fossil record.

Remodeling of the cranium can more than double the width of binocular overlap, permitting the highly specialized panoramic binocular vision associated with stereopsis and the accurate perception of three-dimensional space exhibited by both cursorial prey and active pursuit predators. While small birdlike theropods such as *Velociraptor* and *Troodon* exhibit the above suite of binocular specializations, these modifications also became increasingly pronounced in tyrannosaurids.

The Progression of Binocular Vision in Tyrannosaurids

Binocular field width is enhanced by narrowing and lowering the rostrum, and, by broadening the postorbital cranium, increasing the inter-orbital separation and decreasing optic axis divergence. In part, these specializations have been noted to be more characteristic of phylogenetically derived versus primitive tyrannosaurids: “The narrow snout and broad temporal region is characteristic of *Nanotyrannus* and *Tyrannosaurus*, although *Tarbosaurus* and to a lesser extent *Daspletosaurus* are intermediate between these taxa and albertosaurines” (Currie, 2003). The lowering of the rostrum relative to the orbits and postorbital

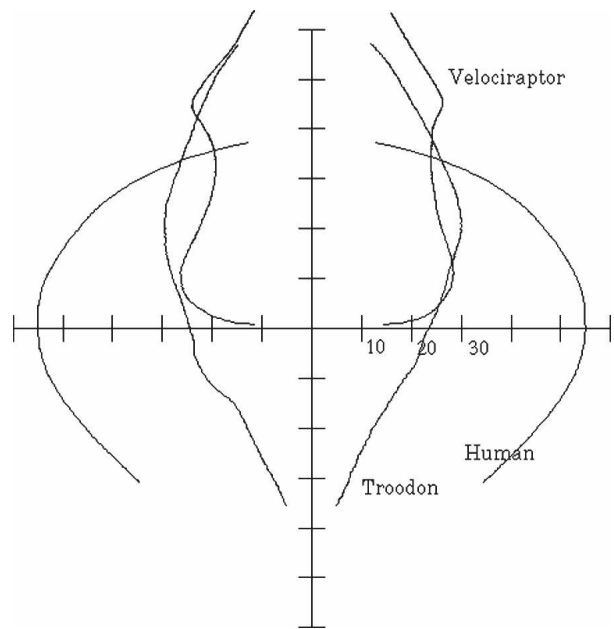


FIGURE 10. *Velociraptor* and *Troodon* have binocular fields matching or exceeding those of extant raptorial birds. Note that while the BFoV of *Troodon* reaches a maximum at $\sim 20^\circ$ elevation, it also has a significant ventral extension, in common with some modern birds.

cranium is also progressively characteristic of phylogenetically derived tyrannosaurids (Fig. 11). These osteological modifications, along with a progressive increase in orbit diameter (see below), and the appearance of cheek grooves (Fig. 12A), suggest that stereopsis played an increasing role in the lives of the tyrannosaurids, a trend inconsistent with the suggestion that the lineage terminated in an obligatory scavenger, as will be discussed below.

Estimating the Spatial Acuity of *Tyrannosaurus*—Doubt has been cast on the predatory capability of *Tyrannosaurus rex* (Horner, 1994; Horner and Lessem, 1993; Horner and Dobb, 1997), wherein the eyes were characterized as “beady” and thereby inappropriate for detecting distant prey. While orbit size is indeed negatively allometric with skull length, theropod orbits nonetheless increase in absolute size with increasing skull length (Chure, 2000; Farlow and Holtz, 2002; Holtz, 2003). For example, compare the equally long (11.5 m) theropods, *Tyrannosaurus rex* (Black Hills Institute of Geological Research specimen ‘Stan,’ BHI-3033) and the allosauroid *Acrocanthosaurus atokensis* (Currie and Carpenter, 2000). The skull of the *Tyrannosaurus* specimen (139.5 cm length from premaxillae to quadrate) was 13% longer than *Acrocanthosaurus* (123 cm), but the orbital opening (120 mm vs. 115 mm from lacrimal to postorbital) was only 4% larger. Nonetheless, the orbit for this *Tyrannosaurus rex* specimen was approximately 140 mm in diameter, as defined by a best fit to the spherical suborbital regions of the lacrimal and postorbitals (Neal Larson, pers. comm., February, 2004; see Fig. 12B). An eye fitting such an orbit was probably close to the structural limit for terrestrial vertebrates (Lawrence and Fowler, 2002).

As eye size increases, other optical parameters remaining constant, retinal image scale increases proportionately. Hence, for a given density of retinal receptors, visual acuity increases linearly with focal length (Barlow, 1986; Martin, 1993). A larger eye does not result in a brighter retinal image; brightness is governed by focal ratio, not focal length. Light sensitivity can be increased by pooling the responses of retinal receptors (Snyder et al., 1977), but at the expense of visual acuity. Crepuscular animals compro-

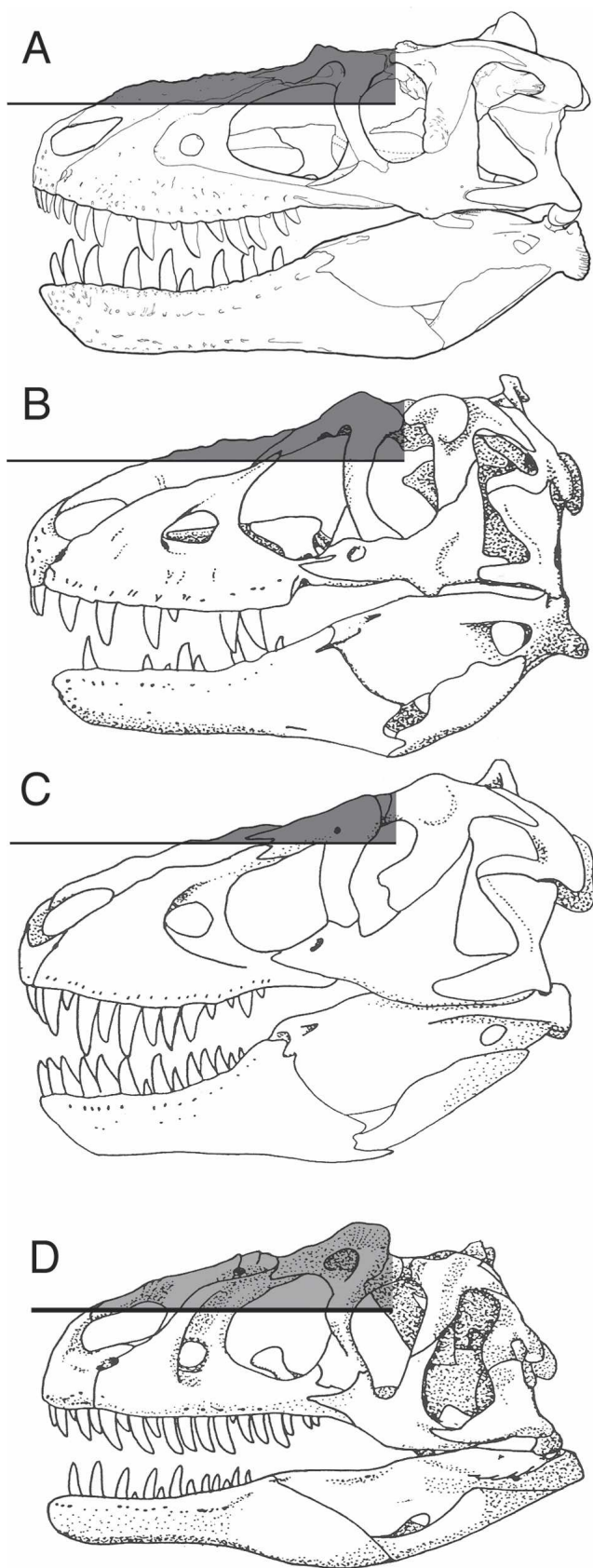


FIGURE 11. Left (top to bottom): shading indicates progressive reduction in interference by the rostrum on binocular vision in (A) *Gorgosaurus libratus*, (B) *Daspletosaurus torosus*, and (C) *Tyrannosaurus rex*. D, *Allosaurus fragilis* for comparison. *Gorgosaurus* based on Carr (1999); others adapted from Molnar et al. (1990).

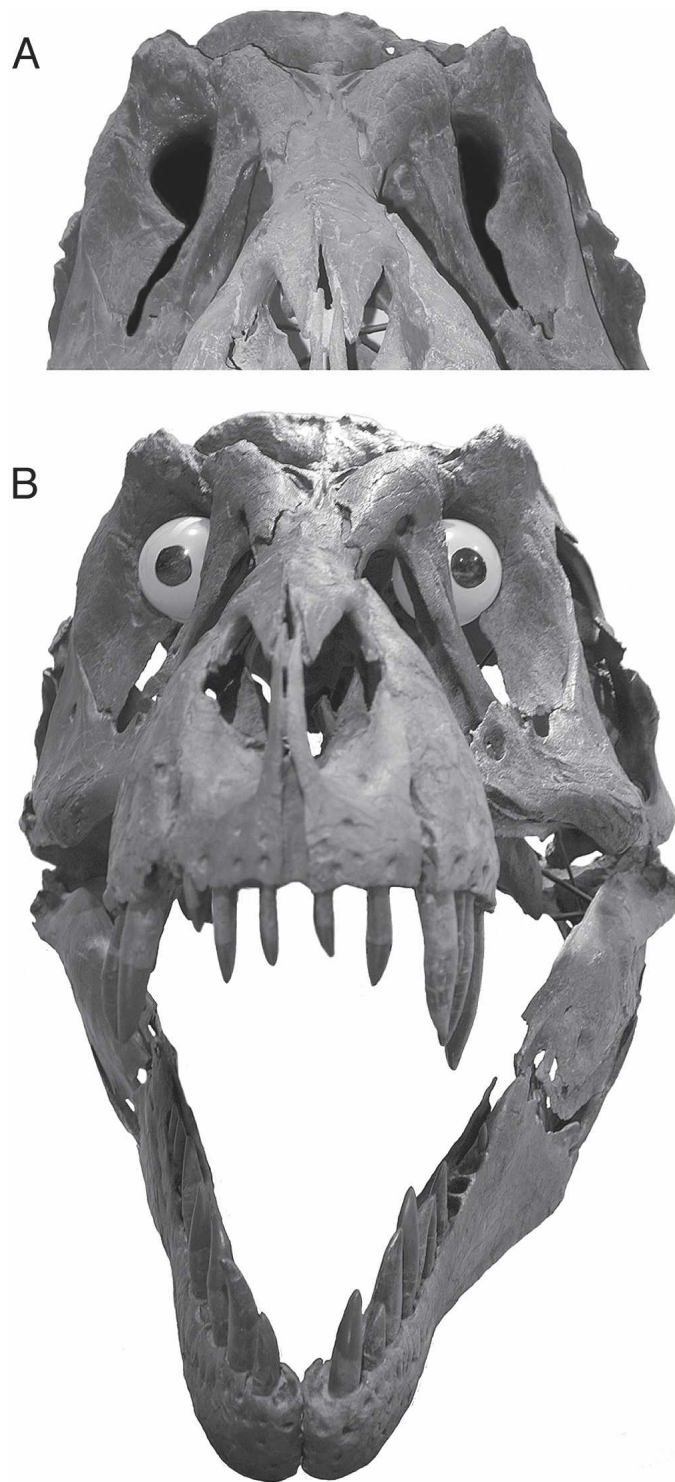


FIGURE 12. A, anterior view of *Tyrannosaurus rex* specimen 'Stan' (Black Hills Institute of Geologic Research specimen BHI-3033; a cast of this specimen is Royal Tyrrell Museum of Palaeontology TMP-1998.86.01). Narrowed frontals and medially curved lacrimals and maxillae formed 'cheek grooves' (see text) that assisted in broadening frontal vision. B, orbits filled with inflated elastic spherical membranes to determine orbit diameter (photograph courtesy Neal Larson, Black Hills Institute of Geologic Research).

mise resolution and detection of visual details in the first place: eye size is proportional to the product of acuity and the square root of sensitivity (Land, 1981). A larger eye, therefore, permits achievement of a given spatial resolution at lower light levels (Motani et al., 1999; Humphries and Ruxton, 2002). A diurnal animal, however, has no need for receptor pooling; hence, all of the increase in eye size can be invested entirely in proportionately greater visual acuity.

For reference in the acuity discussion that follows, the human eye (24.5 mm axial length) at best can resolve a 'minimum angle of resolution' (MAR) of 0.5', i.e., distinguish from uniform grey a sinusoidal grating of spatial frequency 60 cycles/degree (Campbell and Green, 1965). The MAR of 0.5' corresponds to a Snellen fraction of 20/10, while the familiar 20/20 corresponds to a MAR of 1.0'.

To estimate the visual acuity of *Tyrannosaurus*, with an orbit approximately 140 mm in diameter, it is first necessary to hypothesize the retinal image scale achieved by the eye that fitted such an orbit. Retinal image scale, and hence spatial acuity, is governed in part by the posterior nodal distance (PND), which in turn depends on eye shape. In avians, such as most passerines, and in reptiles, such as lizards and crocodylians, the axial length of the eye is less than the diameter measured transverse to the optic axis. Orbit diameter would thus considerably overestimate the PND in 'flat' eyes. In diurnal raptorial birds the eyes are 'globose,' more nearly spherical, providing a larger PND for a given orbit diameter. There is no clear osteological indication, unfortunately, as to whether the eyes of *Tyrannosaurus* were flat or globose. A bracketing approach will therefore be taken, based on a reptilian and two avian extant models, all possessing very large eyes for which optic capabilities are known. The alligator (20 mm axial length), represents a nocturnal or crepuscular model, that while sensitive, can resolve only 11' (Walls, 1942). The two large-eyed avian models, the ostrich (axial length 50 mm, i.e., twice that of the human eye, MAR = 3' or about 20/60) represents a compromise between acuity for cursorial behavior and sensitivity for nocturnal vision, while the diurnal eagle eye (35 mm axial length) represents an extreme specialization for visual acuity.

To apply an extant model to *Tyrannosaurus*, it is necessary to scale the eye relative to the orbit. The alligator eye measures 22 mm mediolaterally, filling only about 0.65 of the 34 mm orbital opening (Ray Wilhite, pers. comm., March, 2004). However, since the orbit of the alligator accommodates soft tissues for specialization not expected for *Tyrannosaurus*, such as the ability to withdraw the eye into the skull using retractor bulbi muscles, and the Harderian glands associated with aquatic habits (Schwab and Brooks, 2002), the eye of *Tyrannosaurus* probably occupied more than 0.65 the diameter of the orbital opening. The large (approximately 50 mm diameter) equine eye, for example, is similarly entirely enclosed by a bony orbit, and fills 0.75 of the height and 0.85 of the width of the orbit (Barnett et al., 2004). Thus, using the range 0.65–0.85, the corresponding eye diameter for *Tyrannosaurus* would have been 91–119 mm. Based on the crocodylian visual acuity model, the theropod would then have proportionally resolved roughly 2.0–2.7', i.e., 20/40 to 20/50 vision, but with the nocturnal light sensitivity of the alligator.

With image brightness similar to that of the great horned owl (Boire et al., 2001), the ostrich achieves better acuity than the 5.5' resolved by the domestic cat (Walls, 1942). Scaled proportionally to fit the orbit of *Tyrannosaurus*, the eye would resolve 1.4–1.7' (about 20/30). By this model, *Tyrannosaurus* would have had close to human acuity, yet owl-like nocturnal light sensitivity.

Alternatively, a diurnal *Tyrannosaurus*, with eyes like those of extant raptorial birds, scaled accordingly, could have theoretically achieved extraordinary visual acuity due to its great scale. Visual acuity is fundamentally limited by foveal receptor spacing

(of nearly 2 μm in hawks) and posterior nodal distance (which proportionately determines image scale), not chromatic aberration (Barlow, 1986). The falcon can resolve a grating of 160 cycles/degree (Fox et al., 1976) or about 2.6 times human acuity, and the larger eye of the eagle achieves as much as 3.6 times human acuity (Shlaer, 1972). Such capabilities, scaled proportionally on the basis of orbit diameters while matching the eagle's receptor spacing and optics, would have provided *Tyrannosaurus* with over 13 times human acuity.

While *Tyrannosaurus* is unlikely to have had acuity as fine as predicted by the most optimistic diurnal avian model, nor as coarse as that predicted by a nocturnal reptile, there is much latitude between these brackets for *Tyrannosaurus* to have greatly surpassed human vision in both acuity and sensitivity.

Estimating the Stereo Acuity of *Tyrannosaurus*—In addition to their great size, the eyes of *Tyrannosaurus* were broadly separated within the cranium. The pupils are assumed to have been approximately in the plane of the skull, with OA = 90° or less, and capable of clear vision past the lacrimals, resulting in an interpupillary separation of about 400 mm, compared to about 65 mm for a human. What binocular capabilities might have been achieved by a visual system of this scale?

A measure of binocular acuity is the 'limiting far point' (Ogle, 1962), the greatest distance at which an object can be viewed as distinguished from infinity. The limiting distance D can be expressed in terms of the interpupillary separation I and the threshold binocular disparity δ_t , according to the following expression, which has been applied to avian stereopsis (McFadden, 1993):

$$D = I/2 / \tan(\delta_t/2)$$

For human vision this equation predicts D = 1.3 km for an estimate of $\delta_t = 10'$ (Reading, 1983). Objects closer than this limiting far point will appear to stand out in depth relative to, say, the horizon. To readily break camouflage, objects must be substantially closer than this distance.

To estimate the limiting far point for *Tyrannosaurus*, an avian form of stereopsis will be assumed, whereupon the disparity threshold of δ_t for *Tyrannosaurus* would have been substantially coarser than its visual acuity. In the pigeon δ_t is ~9.5' (McFadden, 1993), about 6 times coarser than its visual acuity (Hodos et al., 1976). In the falcon, while δ_t has not been measured, stereopsis is most sensitive for disparities between 8–12' (Fox et al., 1976), which is 60 times coarser than its visual acuity.

The disparity threshold δ_t for *Tyrannosaurus* can be estimated as the product of the estimated visual acuity MAR and the assumed δ_t /MAR ratio. Using the ostrich model for acuity (MAR = 1.6') and the pigeon model for the δ_t /MAR ratio, *Tyrannosaurus* would have had a disparity threshold $\delta_t = 9.6'$, similar to that of the pigeon. The computed limiting far point D is ~140 m, a distance of some utility for predation and locomotion.

Using the eagle model for visual acuity (MAR = 0.039') and the falcon for δ_t /MAR results in $\delta_t = 2.3'$ and D is ~0.6 km. This is a direct scaling of the optics and the stereopsis processing of a modern raptor to the eye size and interpupillary separation of *Tyrannosaurus*. Finally, it is not unreasonable to substitute the finer δ_t /MAR ratio of the pigeon for that of the falcon, which yields $\delta_t = 0.23'$ and a remarkable limiting far point of about 6 km, substantially better than human ability.

The potential visual superiority of *Tyrannosaurus* probably extended beyond spatial acuities. Rowe (2000) concluded, on the basis of the Extant Phylogenetic Bracket method (Witmer, 1995), that dinosaurs may have had color vision based on four cone types, and color contrast enhancements provided by pigmented oil droplets—features that permit better color perception than that achieved by mammals. One might therefore envision an alert, hungry *Tyrannosaurus rex*, raising its head to maximum height, its keen olfactory sensitivity catching the scent of

living prey and not just carrion (Farlow, 1994; Brochu, 2000; Farlow and Holtz, 2002), then using its vision to segregate the prey from the background vegetation on the basis of stereopsis, detected prey movements, and subtle color contrasts.

The binocular capabilities provided by a BFoV 55° wide and broadly separated, large eyes (with acuities perhaps better than human) would allow not only observation of distant prey, but also accurate perception of the three-dimensional arrangement of potential obstacles to avoid during pursuit predation (Farlow et al., 1995). For ambush predation, these binocular and spatial acuities would have been more than adequate for judging the timing and direction of a terminal lunge. For obligate scavenging, these visual acuities would have been superfluous.

In summary, given (1) the strong correlation between (at least limited) binocular depth perception in those extant vertebrates possessing more than roughly 20° overlap (and full stereopsis in those vertebrates with about twice that amount), (2) the correlation between BFoV width and spatial ability (e.g., cursoriality), and (3) the extent of the remodeling of the cranium required to achieve a BFoV of 55° or greater, it would seem most parsimonious to conclude that the coelurosaurs included in this study all achieved functional stereopsis and all used that capability for spatially demanding tasks. In particular, due to its great scale and broad frontal vision, *Tyrannosaurus rex*, of all sighted observers to have ever lived, might have experienced the most spectacular view of the three-dimensional world.

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