



Evolution of visual system specialization in predatory arthropods[☆]

Paloma T Gonzalez-Bellido¹, Jennifer Talley² and
Elke K Buschbeck³

Under strong selective pressure for survival, image-forming vision set off an ongoing predatory arms race 500 million years ago. Since then, and particularly so in the arthropods, predatory behavior has driven a myriad of eye adaptations that increase visual performance. In this review, we provide examples of how different arthropod predators have achieved improvements in key visual features such as spatial and temporal resolution of their retina. We then describe morphological, neural and behavioral strategies used by animals in this group to gather crucial information about the prey, such as its distance, velocity and size. We also highlight the importance of head and body tracking movements to aid in categorizing the potential prey, and briefly mention the ongoing work on the sensorimotor transformations necessary for target interception.

Addresses

¹ Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA

² Air Force Research Laboratory, Munitions Directorate, Eglin AFB, FL 32542, USA

³ Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA

Corresponding author: Paloma T Gonzalez-Bellido (paloma@umn.edu)

Current Opinion in Insect Science 2022, 52:100914

This review comes from a themed issue on **Behavioural ecology**

Edited by **Joseph Parker**

Available online 26th March 2022

<https://doi.org/10.1016/j.cois.2022.100914>

2214-5745/© 2022 Elsevier Inc. All rights reserved.

Introduction

A successful visual predator relies on a sensor system that is extremely well adapted to its environment and ecological demands. For many predators, this includes the following attributes: the ability to see details in the visual environment, a visual system that is fast enough to track the movements of prey, the ability to correctly gauge the distance of the prey and the ability to plan

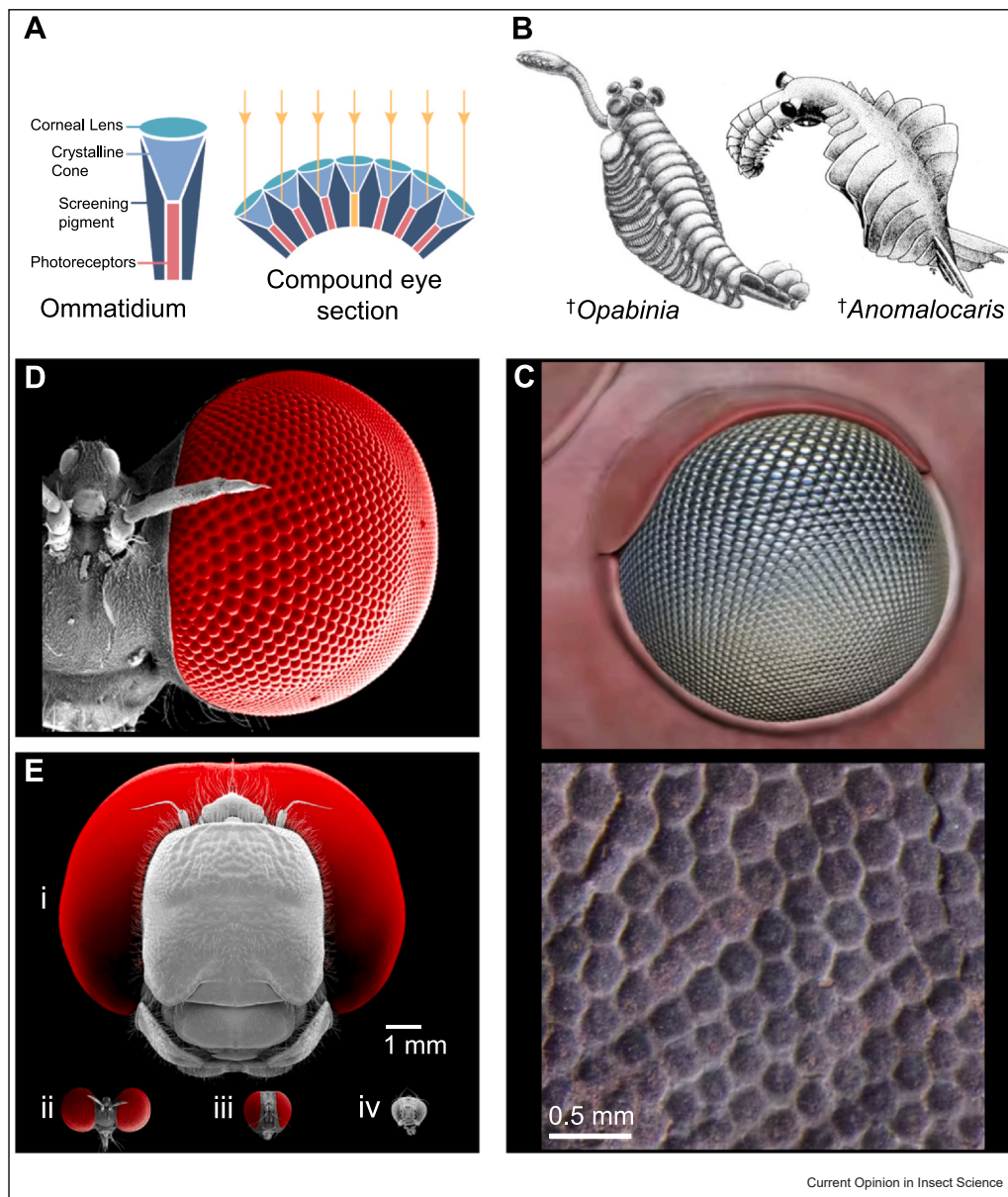
trajectories according to the prey's trajectory. Visual performance needs to be supported by adequate computational circuits. In the following sections, we summarize key eye features that improve visual performance and enable successful predation in the air, on land or in water.

Spatial resolution — “all the better to see you with” — the Wolf

The ability to perceive their environment as a high-resolution image gives an edge to most visually guided predators. Trilobites, some of the earliest-known arthropods that lived 530 mya, already had image-forming eyes of the compound type [1]. Compound eyes provide spatial resolution capabilities via the repetition of its sampling unit, called an ommatidium, each containing photoreceptor(s) and a lens, and pointing in a slightly different direction than its neighbors (Figure 1a). The emergence of predation during the early Cambrian (circa 541–520 mya), with parallel increases in digestive and visual abilities [2], likely drove the subsequent survival arm-races and diversity explosion [3]. Shortly after, *Opabinia regalis* (stim. 508 myo fossil), boasted a specialized proboscis for predation, and five compound eyes of different sizes [4] (Figure 1b), indicating that compound eyes within the same animal had already specialized for different roles. In addition, *Anomalocaris canadensis* (515 myo) boasted a 4 cm wide eye with > 30 000 lenses [5]. Investing in such a large number of ommatidia, while keeping each of them the same size, preserves sensitivity and results in higher spatial resolution. This performance increase allows the detection of potential prey from further away, and thus improves predation success. It also incurs a high energetic cost because the metabolic rate of photoreceptors is high and because the animal must carry the increased mass. For example, photoreceptors are responsible for 8% of a fly's metabolic resting rate [6]. The cost of information transfer tends to rise substantially with higher rates, with diminishing returns [7]. Indeed, compound eyes cannot attain the high resolution present in typical vertebrate camera-type eyes, without reaching outrageous proportions [8]. Hence, the widespread assumption that only arthropods with the largest bodies can bear eyes large enough to

[☆] Distribution statement A. Approved for public release: distribution unlimited PA # AFRL-2022-0268.

Figure 1



The compound eye is an ancient modular design. **(a)** The visual unit of the compound eye (ommatidium), is repeated to form a compound eye. The parameters of each ommatidium can be tuned to the needs of the wearer. **(b)** *Opabinia* and *Anomalocaris*, two visually guided Cambrian predators with well-developed compound eyes. **(c)** Artist's reconstruction of an *Anomalocaris Briggsi* eye (top), based on a fossil with larger lenses in the dorsal area (bottom). **(d)** The eye of the tiny robber fly *Holcocephala fusca* exhibits an extreme forward-facing fovea. **(e)** The heads of predatory species: (i) Dragonfly, (ii) Robber fly (iii) Killer fly, in comparison to that of a prey species (iv) the fruit fly. Image credits: Panels (a, d and e) by Sam Fabian. *Opabinia* drawing in panel (b) reproduced from [4] with CC BY 4.0 license; *Anomalocaris* drawing in (b) reproduced with permission from [71]. Images in (c) by Diego Garcia-Bellido and Katrina Kenny, reproduced with permission.

sustain a predatory lifestyle, as seen in dragonflies which can have 3000 ommatidia [9] and a visual acuity $\sim 0.3^\circ$ [10]. An intrinsic solution to this conundrum resides within the compound eye modular design. Localized changes to ommatidia parameters, which can occur within a few generations [11], can result in areas of increased resolution (termed acute zones or foveas) or

sensitivity (named bright zones). A dorsal specialization was already present in the *Anomalocaris Briggsi* eye (Figure 1c) [5], and is common in extant arthropods [12,13], but has been taken to extremes by the tiny Robber fly *Holcocephala fusca* (6 mm long body; Figure 1d). *Holcocephala* achieves visual (acceptance angle = 0.27°) and behavioral (object detection

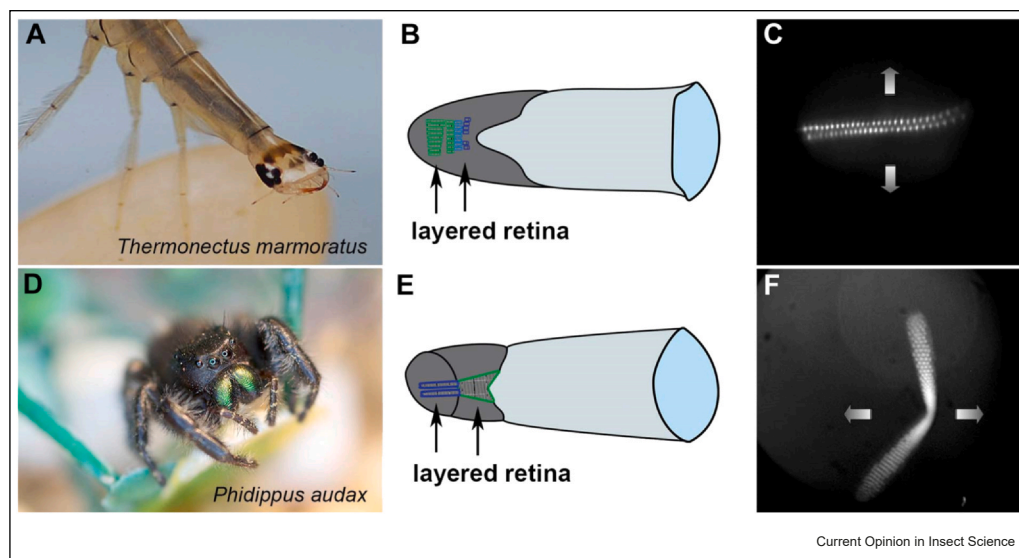
threshold = 0.13°) spatial resolution on par with the much larger dragonflies (Figure 1e). *Holcocephala* does so by dramatically flattening the cornea/retina, increasing the length of the pseudocone and reducing the width of the photoreceptor in the frontal area of its eye [14].

In contrast to the aquatic and aerial predators discussed above, tiger beetles are terrestrial arthropods. These medium-sized predators use their particularly well-developed compound eyes [15] to hunt a variety of other insects in relatively flat habitats. As their world is restricted to two dimensions, their compound eyes are adjusted accordingly; with a streak of high acuity matched to the horizon plane. This eye organization is particularly well suited for the flat environment and even allows them to use the elevation of their prey as a distance cue [16].

Widespread as compound eyes are in arthropod adults, the larvae of some predatory insects use another type of image-forming eye; ocellar-like simple eyes that are called stemmata. For example, each of the 12 stemmata (6 on each side of the head) of the tiger beetle larvae is capped by a large cuticular lens, which in the posterior eye serves ~5000 photoreceptors [17]. Tiger beetle larvae use their upwards facing stemmata to monitor the

environment for potential prey, such as small insects. Although all 12 stemmata work synergistically, the majority of the overlying space is sampled by two particularly large stemmata [18]. A somewhat similar organization is also found in the diving beetle larvae *Thermonectus marmoratus* [19,20] (Figure 2a). As the name ‘water tigers’ implies, these highly active larvae are voracious aquatic predators. The two principal eyes are large image-forming eyes that look directly forward and are important for visually guided prey capture [21]. The anatomies and functions of these tubular eyes (Figure 2b) are unusual in that they are divided into two relatively large and distinct retinas, namely, distal and proximal retinas. Both retinas expand horizontally, but are very narrow vertically (Figure 2c). These eyes are particularly interesting because they are characterized by unusual optics that involve bifocal lenses [22]. Of note is that the single-lens eyes are distributed to monitor different areas of space and have a layered retina, with a relatively small and unidirectional visual field. Both features are reminiscent of the eye organization in jumping spiders (Figure 2d) [13,23], which are well-known visual predators that can stalk their prey prior to pouncing on it [24]. Upon prey detection, a jumping spider will turn its body to bring the prey into view of their elaborate principal eyes [25] which have a

Figure 2



Similar simple eyes have evolved in predators of phylogenetically distant arthropod lineages. (a) Sunburst diving beetle larvae are sophisticated visual predators with 12 eyes, including four forward-facing principal eyes. They come into action when a prey is detected, and the larvae orients towards it. (b) The larvae's principal eyes are relatively long tubes with corneal lenses and a retina that has two layers that are sensitive to light of different colors. Drawing modified after [28,72]. (c) As illustrated by an ophthalmoscope image, the proximal retina of *T. marmoratus* presents as a horizontal stripe with two rows of photoreceptors. Although their eyes cannot move inside the head, the larvae perform scanning movements to expand their visual fields. (d) An eye organization that in many ways is similar exists in jumping spiders, which have 8 eyes, 2 of which (the anterior-medium eyes) are particularly large, serving as their principal eyes. (e) The spider's principal eyes share many characteristics with those of the diving beetle larvae, including their tubular shape, the presence of a corneal lens, and a retina with multiple layers that are sensitive to light of specific colors. (f) The jumping spider retina has the shape of a boomerang that can be moved right and left and even twist through movements of the eye tube. This allows the spider to expand its visual fields even though its body remains stationary.

boomerang-shaped retina with particularly high spatial acuity (Figure 2e), several layers and the ability to move to track prey internally without moving the body [26] (Figure 2f). Their tiered retinal layers placed at the focus distances of the different wavelengths compensate for chromatic aberration and are used in distance estimation [27,28].

Temporal resolution – “The velocity with which time flies is infinite” – Seneca

In addition to providing a high-resolution image of the stationary environment, the eyes of predators need to be fast to minimize motion blur. Motion blur is the ‘smear’ that degrades the image when the motion of the predator and/or the fleeing prey is faster than the photoreceptors’ temporal sampling rate. The compound eyes of arthropods excel at this task because they have rhabdomic photoreceptors, whose biochemical cascades allow for much faster kinematics than the ciliary counterparts [29]. Within Diptera (true flies), temporal dynamics are adapted to lifestyle: those of nocturnal animals (such as mosquitos), integrate light for the longest and thus are the slowest, whereas those of diurnal predators are the fastest [30]. While killer fly photoreceptors are the fastest recorded so far, they contain thrice the number of mitochondria profiles than those of fruit flies [31], highlighting the direct correlation between energetic cost and increased visual performance. Interestingly, although killer flies have decreased the diameter of their rhabdomeres to the apparent limit for transmitting light efficiently, their pseudocone is kept short and the cornea/retina is not flattened. Thus, their spatial resolution is still an order of magnitude worse than that of *Holcocephala* (see section above). As a result, killer flies can only hunt prey at short range [32]. Under such conditions, extreme investment into the best possible temporal resolution holds the key to survival as the physics of vision dictates stark trade-offs between spatial and temporal resolution (see [33] and spatial resolution below).

Resolution and sensitivity – “information is the resolution of uncertainty” Claude Shannon

Overall visual performance is always bound by the trade-off between sensitivity and resolution, both spatial and temporal. To increase spatial and temporal resolution, each photoreceptor must sample a smaller proportion of the environment and do so for a shorter period, respectively. Both result in fewer photons being collected by each detector, and thus negatively impact the signal-to-noise ratio of individual photoreceptors (see [34]). Spatial and temporal resolution challenges are exacerbated in compound eyes because each functional sampling unit requires its own lens, the size of which is limited by diffraction [35], but these are at least in part compensated for with the much higher temporal resolution

provided by rhabdomic photoreceptors [36]. Although life on the ground often has a slower pace, motion blur is also an issue for the fast-moving predators who run after their prey. For example, the eyes of tiger beetles are too slow to keep up with the rapid changes in their scenery while they chase after their prey. They effectively become blind in the middle of their pursuit and have to pause chasing to increase the visual information quality, before ultimately pouncing at their prey [15]. As a strategy to minimize the number of stops, tiger beetles use their rigidly held forward antennae as guides when they suffer from motion blur [37]. Self-induced motion blur is not a problem for their larvae because they are sit-and-wait predators that do not move until their prey is within jumping range [38]. Although aquatic diving beetle larvae do stalk their prey, their approach is relatively slow [21] when compared to that of aerial predators or tiger beetles, and the prey itself also moves relatively little preceding most attacks (EKB personal observation 2022). Hence, temporal resolution is less critical for them. Likewise, the hunting strategy of jumping spiders typically involves watching and stalking the prey [39] rather than rapid pursuit. Still, as exemplified by the reduced spatial resolution in the eyes of jumping spiders that hunt in dark environments [40], overall visual performance is always bound by the trade-off between spatial and temporal resolution. Once the limits of visual performance are reached, predators may recruit other senses to increase reliability. For example, although Ogre-faced spiders use the exceptional light sensitivity of their large principal eyes to cast their net and tangle their prey at night [41], they also recruit the auditory system to detect airborne prey [42].

Eye position and depth perception – “...nada hay verdad ni mentira, todo es según el color, del cristal con que se mira” – Campoamor

Post detection, the predator must decide if prey is suitable and can be caught. When making this decision, the predator benefits from gathering information like the velocity, size, type and distance to the object. A simple spatial rule of thumb would negate the need for distance information, as crabs do, by categorizing objects moving above the horizon as predators, and those below it as potential prey [43]. In addition, because many predatory arthropods have two eyes with overlapping fields of view, it gives them the potential for assessing distance through stereopsis; the ability to perceive the world in 3D by using the disparity in the images from both retinas. Although their small heads and relatively poor spatial resolution limit the distance at which this strategy is effective, stereovision has been proven in Mantids [44,45], and proposed to play a part in *Holcocephala* [14]. Stereopsis has evolved independently in arthropods, mollusks [46] and vertebrates, and consequently the neural basis of stereopsis in Mantids differs from that of

vertebrates [47]. In contrast, because killer flies attack insects outside of their potential stereopsis range, they rely on matched filters, or heuristics rules: if the perceived prey size and velocity match a preferred ratio, the attack is released [48]. Dragonflies with eyes fused on top of their head (holoptic eyes), also use heuristic rules to inform the attack [49]. This eye design is believed to have evolved in dragonflies that hunted in open fields, where close-range 3D perception is not paramount [50]. Damselflies, the dragonfly sister group with characteristically widely spaced eyes, integrate the binocular information from both eyes [51], but whether they exploit this ability for stereovision purposes remains to be shown. Visual information from multiple eyes may also play a role in prey capture by tiger beetle larvae, which have to correctly assess if the distance of a potential morsel is within their ~15 mm jumping range [52]. Based on an elegant study with occluded eyes and the addition of prisms, these larvae use both monocular and binocular clues [38]. The ability for some arthropods to correctly estimate distances monocularly also has been illustrated for aquatic diving beetle larvae [53] and behavioral experiments under different light conditions suggest that jumping spiders may use image-defocus cues to better assess the distance of potential prey [54].

**Gaze shifting for prey tracking and sampling
– “it is clear from our simulations that
batters, even professional batters, cannot
keep their eyes on the ball” – Professor A.
Terry Bahill**

Often the ability to see motion is an important ingredient for target detection [55]. After detection, many arthropods take the time to move their head and/or body, and actively visually track the potential prey before deciding whether to attack. Since their eyes are fixed to their heads, head tracking is the equivalent of eye tracking in vertebrates, but the actual tracking strategy is predator and purpose dependent. For example, because Libellulid dragonflies track potential prey with smooth head movements [49], this keeps the prey image on the fovea [56], and thus provides the highest possible image quality when categorizing prey and conditions, ahead of launching the attack. In contrast, the robber fly *Laphria saffrana* cues onto the wing beat frequency of the potential prey to categorize it, and does so through a ‘saccade and fixate’ strategy [57]. Similarly, the frequency of light flashes is exploited by predatory female fireflies to attract unsuspecting males of other species [58], and the ‘Saccade-and-fixate’ strategy is employed by many terrestrial species to stabilize their visual input via head and/or body movements [59]. For example, tiger beetles typically go through phases of evaluating the position of their prey, which is followed by an active pursuit informed by the position of the prey detected during the stop. While their typical

pursuit is open loop [15], closed-loop pursuit has been observed under laboratory conditions as well. Diving beetle larvae have a different approach. Sometimes they first detect a desired prey item from a distance, and orient towards it to bring it into the visual field of their principal eyes. Since the retina is extremely narrow vertically, they engage in vertical scanning movements during their approach to scout out the shape and position of their prospective victims [21]. Another predatory strategy is to remain stationary and allocate tracking to the eyes within an otherwise motionless body, as is the case in jumping spiders. Here too the boomerang-shaped retina needs to perform scanning movements in order to assess potential prey [26]. Recent work with a tracking device that allows following the gaze of the principal eyes during these scanning movements has revealed that they are directed by the spider’s lateral eyes [60], suggesting a sophisticated level of integration between the dispersed eye units.

**Approach strategy and neural underpinnings
“Still, intuitive assumptions about behavior is
only the starting point of systematic analysis,
for alone they do not yield many interesting
implications” – Gary Becker**

We have briefly reviewed the eye and visual tracking adaptations of predatory arthropods. Entire reviews could be dedicated to analysis of prey approach strategies and the neural processing that underpins them. Here, we will simply highlight that visual feedback [32,61] and internal models [62,63], appear to be used to different degrees by different species. In insects, visual information is routed from the optic lobes to the anterior tubercle of the brain [64] and onwards to integration centers, such as the central complex. From the lobula, visual information is also routed to the posterior ventral protocerebrum (PVL) and the lateral accessory lobe, brain areas that send projections to neck, legs and wings motor centers through the ventral nerve cord [65]. The fast PVL route is used by fruit flies to activate the escape response through a fast pathway that is mediated by their Giant Descending Neurons. Concurrently, the drive for catching a target is integrated with competing tasks, such as obstacle avoidance [66]. With a visual latency of circa 10 ms, we postulate that the Target Selective Descending Neurons (TSDNs) in killer flies [67] use a similar circuit that also bypasses central integration centers of the brain. TSDNs are cells that carry information about moving targets from the brain to the thoracic centers and were described first in dragonflies [68]. Recently, responses similar to those of dragonfly TSDNs have been reported in predatory and conspecifics targeting Diptera [69]. TSDNs form a tight bottleneck of information between the sensors and movement of the head and body. As such, we expect research about TSDN-like cells in a variety of predatory

arthropod groups to yield valuable information on multisensory integration and sensorimotor transformations. Of course, additional complexity needs to be considered, as internal states, for example, hunger is known to regulate predatory behavior [48,70].

Declaration of Competing Interest

Nothing declared.

Acknowledgements

This work was funded by the Air Force Office of Scientific Research (FA9550-18-1-0339 to PTGB) and by the National Science Foundation (IOS-1856241 to EKB).

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest.

1. Schoenemann B, Pärnaste H, Clarkson ENK: **Structure and function of a compound eye, more than half a billion years old.** *Proc Natl Acad Sci U S A* 2017, **114**:13489-13494.
2. Vannier J, Liu J, Lerosey-Aubril R, Vinther J, Daley AC: **Sophisticated digestive systems in early arthropods.** *Nat Commun* 2014, **5**:3641.
3. Fox D: **What sparked the Cambrian explosion?** *Nature* 2016, **530**:268-270.
4. Briggs DEG: **Extraordinary fossils reveal the nature of Cambrian life: a commentary on Whittington (1975) 'The enigmatic animal Opabinia regalis, Middle Cambrian, Burgess Shale, British Columbia'.** *Philos Trans R Soc Lond B Biol Sci* 2015, **370**:20140313.
5. Paterson JR, Edgecombe GD, García-Bellido DC: **Disparate compound eyes of Cambrian radiodonts reveal their developmental growth mode and diverse visual ecology.** *Sci Adv* 2020, **6**:eabc6721.
- Linking fossils with the visual abilities and ecological niches of the earliest arthropod predators known.
6. Laughlin SB, de Ruyter van Steveninck RR, Anderson JC: **The metabolic cost of neural information.** *Nat Neurosci* 1998, **1**:36-41.
7. Niven JE, Anderson JC, Laughlin SB: **Fly photoreceptors demonstrate energy-information trade-offs in neural coding.** *PLoS Biol* 2007, **5**:e116.
8. Kirschfeld K: **The resolution of lens and compound eyes.** *Proc Life Sci* 1976, **354**:370.
9. Sherk TE: **Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes.** *J Exp Zool* 1978, **203**:61-80.
10. Labhart T, Nilsson DE: **The dorsal eye of the dragonfly *Sympetrum*: specializations for prey detection against the blue sky.** *J Comp Physiol A* 1995, **176**:437-453.
11. Perl CD, Niven JE: **Differential scaling within an insect compound eye.** *Biol Lett* 2016, **12**:20160042.
12. In *Eyes to See: The Astonishing Variety of Vision in Nature*. Edited by Land MF. Oxford University Press; 2020.
13. Land MF, Nilsson D-E: *Animal Eyes*. OUP; 2012.
14. Wardill TJ, Fabian ST, Pettigrew AC, Stavenga DG, Nordström K, Gonzalez-Bellido PT: **A novel interception strategy in a miniature robber fly with extreme visual acuity.** *Curr Biol* 2017, **27**:854-859.
15. Gilbert C: **Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae).** *J Comp Physiol A Sens Neural Behav Physiol* 1997, **181**:217-230.
16. Layne JE, Chen PW, Gilbert C: **The role of target elevation in prey selection by tiger beetles (Carabidae: Cicindela spp.).** *J Exp Biol* 2006, **209**:4295-4303.
17. Toh Y, Okamura J-Y: **Morphological and optical properties of the corneal lens and retinal structure in the posterior large stemma of the tiger beetle larva.** *Vision Res* 2007, **47**:1756-1768.
18. Toh Y, Mizutani A: **Structure of the visual system of the larva of the tiger beetle (Cicindela chinensis).** *Cell Tissue Res* 1994, **278**:125-134.
19. Mandapaka K, Morgan RC, Buschbeck EK: **Twenty-eight retinas but only twelve eyes: an anatomical analysis of the larval visual system of the diving beetle *Thermonectus marmoratus* (Coleoptera: Dytiscidae).** *J Comp Neurol* 2006, **497**:166-181.
20. Stowasser A, Buschbeck EK: **How aquatic water-beetle larvae with small chambered eyes overcome challenges of hunting under water.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2014, **200**:911-922.
21. Buschbeck EK, Sbita SJ, Morgan RC: **Scanning behavior by larvae of the predacious diving beetle, *Thermonectus marmoratus* (Coleoptera: Dytiscidae) enlarges visual field prior to prey capture.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2007, **193**:973-982.
22. Stowasser A, Rapaport A, Layne JE, Morgan RC, Buschbeck EK: **Biological bifocal lenses with image separation.** *Curr Biol* 2010, **20**:1482-1486.
23. Blest AD, Price GD: **Retinal mosaics of the principal eyes of some jumping spiders (Salticidae: Araneae): adaptations for high visual acuity.** *Protoplasma* 1984, **120**:172-184.
24. Jackson RR, Pollard SD: **Predatory behavior of jumping spiders.** *Annu Rev Entomol* 1996, **41**:287-308.
25. Land MF: **Orientation by jumping spiders in the absence of visual feedback.** *J Exp Biol* 1971, **54**:119-139.
26. Land MF: **Movements of the retinæ of jumping spiders (Salticidae: dendryphantinae) in response to visual stimuli.** *J Exp Biol* 1969, **51**:471-493.
27. Blest AD, Hardie RC, McIntyre PD, Williams DS: **The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider.** *J Comp Physiol* 2004, **145**:227-239.
28. Land MF: **Structure of the retinæ of the principal eyes of jumping spiders (Salticidae: dendryphantinae) in relation to visual optics.** *J Exp Biol* 1969, **51**:443-470.
29. Morshedjian A, Fain GL: **The evolution of rod photoreceptors.** *Philos Trans R Soc Lond B Biol Sci* 2017, **372**.
30. Laughlin SB, Weckström M: **Fast and slow photoreceptors — a comparative study of the functional diversity of coding and conductances in the Diptera.** *J Comp Physiol A* 1993, **172**:593-609.
31. Gonzalez-Bellido PT, Wardill TJ, Juusola M: **Compound eyes and retinal information processing in miniature dipteran species match their specific ecological demands.** *Proc Natl Acad Sci U S A* 2011, **108**:4224-4229.
32. Fabian ST, Sumner ME, Wardill TJ, Rossoni S, Gonzalez-Bellido PT: **Interception by two predatory fly species is explained by a proportional navigation feedback controller.** *J R Soc Interface* 2018, **15**:20180466.
33. Meece M, Rathore S, Buschbeck EK: **Stark trade-offs and elegant solutions in arthropod visual systems.** *J Exp Biol* 2021, **224**:jeb215541.
34. Warrant EJ: **Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation.** *Vision Res* 1999, **39**:1611-1630.
35. Warrant EJ, McIntyre PD: **Arthropod eye design and the physical limits to spatial resolving power.** *Prog Neurobiol* 1993, **40**:413-461.
36. Fain GL, Hardie R, Laughlin SB: **Phototransduction and the evolution of photoreceptors.** *Curr Biol* 2010, **20**:R114-R124.

37. Zurek DB, Gilbert C: **Static antennae act as locomotory guides that compensate for visual motion blur in a diurnal, keen-eyed predator.** *Proc Biol Sci* 2014, **281**:20133072.
 38. Toh Y, Okamura JY: **Behavioural responses of the tiger beetle larva to moving objects: role of binocular and monocular vision.** *J Exp Biol* 2001, **204**:615-625.
 39. Forster L: **Vision and prey-catching strategies in jumping spiders.** *Am Sci* 1982, **70**:165-175.
 40. Cerveira AM, Nelson XJ, Jackson RR: **Spatial acuity-sensitivity trade-off in the principal eyes of a jumping spider: possible adaptations to a 'blended' lifestyle.** *J Comp Physiol A* 2021, **207**:437-448.
 41. Blest AD, Land MF: **The physiological optics of *Dinopis subrufus* L. Koch: a fish-lens in a spider.** *Proc R Soc Lond B Biol Sci* 1977, **196**:197-222.
 42. Stafstrom JA, Menda G, Nitzany EI, Hebets EA, Hoy RR: **Ogre-faced, net-casting spiders use auditory cues to detect airborne prey.** *Curr Biol* 2020, **30**:5033-5039 e5033.
- Evidence of multisensory integration for predation at the limits of visual detection.
43. Tomsic D, Sztarker J, Berón de Astrada M, Oliva D, Lanza E: **The predator and prey behaviors of crabs: from ecology to neural adaptations.** *J Exp Biol* 2017, **220**:2318-2327.
 44. Rossel S: **Binocular stereopsis in an insect.** *Nature* 1983, **302**:821-822.
 45. Nityananda V, Joubier C, Tan J, Tarawneh G, Read JCA: **Motion-in-depth perception and prey capture in the praying mantis *Sphodromantis lineola*.** *J Exp Biol* 2019, **222**:jeb198614.
 46. Feord RC, Sumner ME, Pusdekar S, Kalra L, Gonzalez-Bellido PT, Wardill TJ: **Cuttlefish use stereopsis to strike at prey.** *Sci Adv* 2020, **6**:eaay6036.
 47. Nityananda V, Tarawneh G, Henriksen S, Umeton D, Simmons A, Read JCA: **A novel form of stereo vision in the praying mantis.** *Curr Biol* 2018, **28**:588-593 e584.
 48. Wardill TJ, Knowles K, Barlow L, Tapia G, Nordström K, Olberg RM, Gonzalez-Bellido PT: **The killer fly hunger games: target size and speed predict decision to pursuit.** *Brain Behav Evol* 2015, **86**:28-37.
 49. Lin H-T, Leonardo A: **Heuristic rules underlying dragonfly prey selection and interception.** *Curr Biol* 2017, **27**:1124-1137.
 50. Nel A, Prokop J, Pecharová M, Engel MS, Garrouste R: **Palaeozoic giant dragonflies were hawkier predators.** *Sci Rep* 2018, **8**:12141.
 51. Supple JA, Pinto-Benito D, Khoo C, Wardill TJ, Fabian ST, Liu M, Pusdekar S, Galeano D, Pan J, Jiang S, et al.: **Binocular encoding in the damselfly pre-motor target tracking system.** *Curr Biol* 2020, **30**:645-656 e644.
- Eye location, distance and neural processing of prey information correlated with hunting strategies of two aerial predatory insect groups that diverged ~250 mya.
52. Mizutani A, Toh Y: **Behavioral analysis of two distinct visual responses in the larva of the tiger beetle (*Cicindela chinensis*).** *J Comp Physiol A* 1998, **182**:277-286.
 53. Bland K, Revetta NP, Stowasser A, Buschbeck EK: **Unilateral range finding in diving beetle larvae.** *J Exp Biol* 2014, **217**:327-330.
 54. Nagata T, Koyanagi M, Tsukamoto H, Saeki S, Isono K, Shichida Y, Tokunaga F, Kinoshita M, Arikawa K, Terakita A: **Depth perception from image defocus in a jumping spider.** *Science* 2012, **335**:469-471.
 55. Gonzalez-Bellido PT, Fabian ST, Nordström K: **Target detection in insects: optical, neural and behavioral optimizations.** *Curr Opin Neurobiol* 2016, **41**:122-128.
 56. Olberg RM, Seaman RC, Coats MI, Henry AF: **Eye movements and target fixation during dragonfly prey-interception flights.** *J Comp Physiol A* 2007, **193**:685-693.
 57. Talley J, Pusdekar S, Feltenberger A, Evers J., S. P., Wardill TJ, Gonzalez-Bellido PT: **Predictive saccades during prey categorization by the saffron robber fly (*Laphria saffrana*), a beetle predator.** In Preparation.
 58. Lloyd JE: **Aggressive mimicry in photuris fireflies: signal repertoires by femmes fatales.** *Science* 1975, **187**:452-453.
 59. Land MF: **The evolution of gaze shifting eye movements.** *Curr Opin Behav Neurosci* 2019, **41**:3-11.
- Excellent review on the importance and strategies for gaze control, which ultimately dictates what the animals sees.
60. Jakob EM, Long SM, Harland DP, Jackson RR, Carey A, Searles ME, Porter AH, Canavesi C, Rolland JP: **Lateral eyes direct principal eyes as jumping spiders track objects.** *Curr Biol* 2018, **28**:R1092-R1093.
- Division of labor and integration of signals between different eyes, for the purpose of predation.
61. Haselsteiner AF, Gilbert C, Jane Wang Z: **Tiger beetles pursue prey using a proportional control law with a delay of one half-stride.** *J R Soc Interface* 2014, **11**:20140216.
 62. Mischiati M, Lin H-T, Herold P, Imler E, Olberg R, Leonardo A: **Internal models direct dragonfly interception steering.** *Nature* 2015, **517**:333-338.
 63. Pusdekar S., Fabian ST, Talley J., Gonzalez-Bellido PT: **Interception strategy of the saffron Robber fly *Laphria saffrana*, a beetle predator.** In Prep.
 64. Wu M, Nern A, Williamson WR, Morimoto MM, Reiser MB, Card GM, Rubin GM: **Visual projection neurons in the *Drosophila* lobula link feature detection to distinct behavioral programs.** *Elife* 2016, **5**:e21022.
 65. Cheong HS, Siwanowicz I, Card GM: **Multi-regional circuits underlying visually guided decision-making in *Drosophila*.** *Curr Opin Neurobiol* 2020, **65**:77-87.
 66. Fabian ST, Sumner ME, Wardill TJ, Gonzalez-Bellido PT: **Avoiding obstacles while intercepting a moving target: a miniature fly's solution.** *J Exp Biol* 2022, **225**:jeb243568.
- Demonstration of a simple strategy integrating predatory drive with obstacle avoidance needs in a miniature robber fly.
67. Supple J: **Descending Premotor Target Tracking Systems in Flying Insects.** University of Cambridge; 2019 (vol Doctor of Philosophy (Ph.D.)).
 68. Olberg RM: **Identified target-selective visual interneurons descending from the dragonfly brain.** *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 1986, **159**:827-840.
 69. Nicholas S, Supple J, Leibbrandt R, Gonzalez-Bellido PT, Nordström K: **Integration of small- and wide-field visual features in target-selective descending neurons of both predatory and nonpredatory dipterans.** *J Neurosci* 2018, **38**:10725-10733.
 70. Bertsch DJ, Martin JP, Svenson GJ, Ritzmann RE: **Predatory behavior changes with satiety or increased insulin levels in the praying mantis (*Tenodera sinensis*).** *J Exp Biol* 2019, **222**:jeb197673.
 71. Collins D: **The "evolution" of *Anomalocaris* and its classification in the arthropod class *Dinocarida* (nov.) and order *Radiodonta* (nov.).** *J Paleontol* 1996, **70**:280-293.
 72. Harland DP, Jackson RR: **Eight-legged cats and how they see: a review of recent research on jumping spiders (Araneae: Salticidae).** *Cimbebasia* 2000, **16**:231-240.