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Billington, J orcid.org/0000-0003-0995-8875, Webster, RJ, Sherratt, TN et al. (2 more authors) (2020) The (under)use of eye-tracking in evolutionary ecology. Trends in Ecology and Evolution. TREE2645. ISSN 0169-5347

https://doi.org/10.1016/j.tree.2020.01.003

The (under)use of eye-tracking in evolutionary ecology

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Keywords: attention, vision, sensory ecology, eye-movement, visual search, gaze

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Highlights

- Sensory ecology has so far focused on the way organisms perceive their environments, but rarely drills down to consider the specific features of the environment that organisms attend to
- The speed and accuracy of decision making is central to the success of behavioural strategies in complex environments, so the choice and prioritization of information is paramount
- The unique spatio-temporal resolution of eye-tracking data offers great insight into attentional processing compared to other behavioural measures.
- Techniques and concepts from experimental psychology offer the potential for novel insights into animal behaviour through the incorporation of attentional sampling and filtering
- Eye-tracking approaches have given unique insights into how animals make the goal-directed decisions that represent the substrate of natural selection.

Abstract

To survive and pass on their genes, animals must perform many tasks that affect their fitness, such as mate-choice, foraging and predator avoidance. The ability to make rapid decisions is dependent on the information that needs to be sampled from the environment and how it is processed. We highlight the need to consider visual attention within sensory ecology and advocate the use of eye-tracking methods to better understand how animals prioritise the sampling of information from their environments prior to making a goal directed decision. We consider ways in which eye-tracking can be used to determine how animals work within attentional constraints and how environmental pressures may exploit these limitations.

Sensory ecology (see Glossary) studies the ways species sample information from their environment, and how they use this information to interact with the world around them. The ability of individuals to locate food, avoid predation (and other hazards), and acquire mate(s) is key to their reproductive success. Each of these activities involves making decisions based on the available sensory information, such as whether a habitat is safe or whether a potential mate is desirable. In the field of human psychology, eye-movements have a long history of being used as an objective physiological measure of the **cognitive** processing and information capture that occurs during everyday activities [1, 2]. Unlike other behavioural measures (e.g. reaction time or decision choice) tracking **eye-movements** affords a direct means of measuring the precise time and direction of visual **attention** during early scene sampling. We would argue that the spatio-temporal resolution offered by tracking eye-movements in non-humans provides a window into objectively measuring 1) how information is prioritised in order to make rapid, goal-directed decisions that represent a substrate of natural selection; and 2) how species evolve to exploit the limitations of information sampling in order to evade detection or capture.

The importance of (the limitations of) attention

Sensory ecologists explicitly acknowledge the substantial inter-specific variation in the way in which species acquire (sample) and process (filter and use) sensory information [3, 4] [see Box 1]. At a purely physiological level, this may include differences in the acuity of the various senses due to limitations within the sensory organs themselves. Much of this variation exists because a species will tend to evolve the ability to sample information relevant to their survival [5]. For example, many species possess a **foveated** visual system [6], resulting in heterogeneous spatial sampling of information across a viewed scene. In humans, acuity is highest at the point of **fixation** in the fovea (central 1 deg) and rapidly declines toward **peripheral** regions of the retina [7]. In order to offset this sampling limitation, eye-movement mechanisms enable active targeting of regions of the visual environment by directing light from prioritised regions onto the highest acuity part of the retina. Thus, in species with foveated vision, **overt** changes in gaze fixation indicate a shift in visual attention. These shifts can be stimulus-driven (‘bottom-up’) in that a particularly salient feature (e.g. movement and / or high contrast) draws attention involuntarily [8]. Alternatively, eye-movements can goal-driven (‘top-down’) with an emphasis on the perceiver possessing a prior search strategy [8, 9]. Any computational processor (such as the central nervous system) will have limited bandwidth and attentional resources that are finite. As a consequence, whilst animals are capable of dividing attention whilst engaging in tasks such as searching for multiple prey types, there is a cost to this division in terms of lower overall predation success rates [10] and increased chance of failing to detect a predator [11]. It is these fundamental limitations which drive the need for efficiency in scene processing and attentional allocation, thus allowing eye-tracking to be used to determine how information is prioritised prior to making a goal-directed decision.

Feasibility of using eye-tracking methodology in ecology

When using eye-tracking equipment, spatial accuracy (the calibration between the estimated and actual gaze direction) and precision (spread or dispersion) of the recorded raw gaze samples [12] are extremely important considerations, particularly when the visual task includes regions of interest that are separated by a small distance (<8º). Further, the temporal resolution of eye-tracking data can range from 60-1250Hz, with the choice of resolution being dictated by both the temporal properties of the visual task/ paradigm and data storage limitations.

More recent advances in technology are offer high specification devices which are more suitable for non-human studies. Remote (monitor mounted) camera eye-tracking devices intended for human use have already proved successful in ecological studies. Animals can be restrained in order to achieve this (much the same as a human participant with a chin rest or bite bar); however, it has also proven possible to train some animals to remain still in order to collect eye-tracking data. This has been successful in dogs, using an iView X_{TM} RED (SensoMotoric Instruments GmbH, Germany) with a reported accuracy of 1º [13], and in New World (*Callicebus cupreus*) and Old World (*Macaca mulatta*) monkeys using a Tobii Pro TX300 (Tobii Technology, Stockholm, Sweden) with minimal constraint in a baby seat [14] and modified transport box [15]. During free movement, traditional invasive devices, such as an implanted scleral search coil [16], can achieve very high levels of sensitivity (0.1º). Head plates surgically attached to parietal bones can allow binocular tracking [17] and provide a reasonable level of accuracy (<1º). Yorzinski and colleagues [18-20] have designed a device for tracking monocular eye-movements in the peafowl, which consists of a 25g wearable headpiece (eye-tracker and scene tracker) and a 345g backpack transmitter. Whilst these methods are still somewhat restricted to larger avian species, the device is reported to have 5º accuracy, allows for free movement in natural environments and is of no lasting detriment to the animal. In the longer term, studies need to define the mass of device that can be worn without impact on the behaviour of the animal, as has been done for GPS tracking devices in birds [21].

Software and analytical approaches are paramount to improving eye-tracking techniques; for example, an eye-tracking accuracy of <0.1º has been reported in archer fish using an innovative computational triangulation technique which can correct for the refractive properties of glass, water and air [22]. On land, head movement compensation algorithms have been found to improve the deviation in eye-tracking signals relative to targets during mobile eye-movements [23] and carefully synching of data is required in during binocular tracking in species with independent eye-movements such as chameleons and mantis shrimp [24, 25].

The present and future utility of eye-tracking in evolutionary ecology

Eye-tracking studies of non-primate animals have been scarce to date, but have already shown potential to provide greater insight into how animals manage to be successful at survival despite relatively limited attentional capabilities. The classic visual-search eye-tracking paradigms employed by experimental psychologists directly lend themselves to understanding how animals search the world during activities such as foraging or maintaining vigilance for predators. However, the uses are by no means restricted to this topic and there is potential for eye-tracking to improve our understanding of other crucial survival behaviours such as cooperation with conspecifics, sexual signalling, and controlling locomotion.

Fixation and **saccade** measures derived from **raw data** can be combined to create a more holistic temporal picture of scene processing via the creation of scan-path data [see Box 2], saliency-maps [26] and heat maps [see Figure 2]. Fixation and saccade patterns show some general rules that persist across taxa, allowing for inferences to be drawn regarding attentional processes across species. For example, as task difficulty increases, for a visual search task, the eye-movements switch from a systematic search strategy to an isotropic, more random search strategy [27]. Further, a stimulus that grabs attention in a bottom-up fashion induces a very rapid saccadic eye-movement response (<200ms in humans) [8], whilst top-down driven eye-movements can be slower (>200ms in humans) [8, 9]. The spatio-temporal resolution of eye-tracking allows the researcher to measure subtle changes in behaviour objectively, which may be missed with reaction time or decision choice data alone [see Box 2 for a detailed illustration]. This is particularly pertinent when decisions need to be made on-line on a moment to moment basis, such as during locomotion (see **Movement in a spatial world**).

Maximising fitness within attentional limitations

Animals are rarely afforded the luxury of hazard free foraging and it is necessary to divide attention between searching for a viable food source and the vigilance required to detect an approaching predators. Several avian eye-tracking studies to date have shown that animals are capable of rapidly modulating how they allocate attention in response to environmental changes in order to maximise fitness. For example, European starlings (*Sturnus vulgaris*) are more likely to fixate on the predator (versus non-threat) stimuli if they are present simultaneously [28, 29] and peafowl (*Pavo cristatus*) exhibit decreased fixation on conspecifics in the presence of a predator [20]. However, individual fixation durations on non-threat stimuli decrease, and there are more saccades per second when predator stimuli disappear, reflecting a shift toward 'scene searching' (i.e. more focussed foraging) in the absence of a visible threat [28]. Eye-movement monitoring has been singular in discovering peafowl sometimes mimic the defensive behaviours of conspecifics *before* fixating on the predator themselves. As peahens emit loud anti-predator calls [30], it is possible that group behaviour may reduce the demand on visual attention for the group as a whole, triggering heightened attention for predators in cases where threat is more likely and, therefore, reducing the energy invested in visual search for predators at other times [31].

Foraging for prey involves maximising the rate of energy gain and, even in the absence of threat, predators must become as proficient as possible in detecting (often cryptic) targets in order to maximise fitness within the limitations of available attentional resources. It has been proposed that animals adopt a 'search image' strategy; that is, a top-down driven search strategy that focusses on a single phenotype of cryptic prey to avoid the cognitive cost of having many different types of search target [10, 32-35]. In seeking to understand search image formation, many studies to date have relied on presenting a single target at any one time and, for example, modulating temporal abundance by controlling switch frequency between prey types across a number of trials [10, 34]. These approaches are undoubtedly rigorous and informative, but eye-tracking paradigms offer greater potential to understand the development of the search image under more naturalistic, free-viewing, conditions in which multiple targets are presented at any one time. Observing how foraging scan-paths are modulated under experimenter-manipulated changes in prey ratios, target spatio-temporal distributions and phenotype salience would allow researchers to directly measure if and how typical evolutionary pressures lead to increased top-down attentional sampling and/ or suppression of bottom-up driven involuntary eye-movements.

Exploiting the attentional limitations of the perceiver

Eye-tracking has provided a novel approach to clarify how animal colouration evolved to exploit the limits of both the visual sensory system and cognitive resources of the perceiver [33]. In particular, sensitive measures of overt attention such as final and total inspection time during visual search prior to capture [see Box 2] can be used in order to make comparisons across a broad range of concealment strategies. This offers a means of quantitatively validating computational approaches to quantifying camouflage [36], which in turn have wide-reaching implications for understanding the evolution of visual signalling. One particularly interesting defensive phenomenon is that some animals are thought to exhibit markings which are cryptic at a distance, yet aposematic at close range [37]. One can readily imagine a laboratory eye-tracking study in which target distance is experimentally manipulated whilst measuring predator saccadic eye-movements. A switch from top-down to bottom-up attentional reallocation (inferred from time to saccade initiation [8, 9]) could be then linked to tangible survival benefits (e.g. reaching plausible striking distance from prey).

The spatial acuity permissible with eye-tracking is unique in allowing for 'feature focussed' approaches when considering animal signalling in natural settings. Such approaches have proven successful in determining which elements of a peacock's plumage influence mate choice in different circumstances. Whilst the lower train of peacocks attracted the most attention overall, the upper train may be used as signal when the peahens were at a further distance [18] perhaps a consequence of its visibility in more cluttered environments [19]. These approaches may be useful when addressing topics such Batesian mimicry, where a harmless species (mimic) presents the phenotype of harmful species (model) in order to benefit from learned predator aversion [38]. Many mimics are ‘imperfect’ in that they do not fully match their model’s phenotype [39]. This may be driven by pressures such as a need to maintain camouflage [39] or thermoregulation [40]. However, the mimic phenotype is also driven by the sampling limitations of the predator [41, 42]. Thus, imperfect mimicry may still provide a survival benefit in that certain features may disproportionately influence predator choice, a hypothesis which would be testable by looking a fixation locations whilst assessing real-world or experimenter- manipulated models and mimics prior to capture.

Movement in a spatial world

The ability to navigate effectively through the environment underpins the success or failure of all the key survival behaviours, and fundamental eye mechanics, gaze behaviours and navigation strategies are inextricable linked to evolutionary demands [43]. During locomotion optic flow is an important visual signal for direction of movement in many species, including during flight in birds and moths [44, 45]. Given that decisions regarding trajectory and route path are made rapidly, we would argue that the temporal resolution provided by eye-tracking is essential in studying locomotion in visually guided animals. Data can be modelled in multiple ways in order to determine the timing, salience and utility of visual features during moment to moment motor planning [see Figure 2]. In humans, eye-movement patterns during locomotion comprise fixation and tracking of specific features in the scene (waypoints [46] or road-edges [47]). It has been shown that humans tend to steer towards where they are looking, and they look towards where they want to steer [48], as such, looking to a point 1-3s ahead seems to provide useful prospective information for guiding motor behaviours [47, 49] and constraining eye-movements proves to be detrimental to steering performance [50].

Eye-tracking studies have already provided us with some interesting insights into how animals interact with the spatial world, including tracking and scanning behaviours in species with eye architecture which is very different to the human [24, 25, 51, 52] [see Box 1]. However, the difficulty of using mobile eye-tracking in the field has meant that few eye-tracking studies have been done in non-humans during natural locomotion. However, the measurement of eye-movements in walking cats (*Felis catus*) found that as task demands increased there was heightened attention to path sections at a closer proximity to their body. The eye-movements of cats predominantly comprised of gaze shifts and fixations at points some 0.7-1.2 seconds ahead of them [16] indicating that visual attention was being directed to regions in order to sample information for use by the motor system in planning the next stride, a finding that parallels motor planning timings in humans remarkably well [47, 49] and bodes well for using human models as predictors of animal locomotion.

Concluding remarks

Visual attention has an important role to play in ecology and evolution research. It is hoped that adoption of eye-tracking will facilitate the measurement of visual attention to better explain how animals' make decisions to optimise fitness. Recent innovations in eye-tracking technology have afforded more opportunities for mobile eye-tracking and measurement of eye-movement in species with eye architecture very different to the human. It is timely that the field of ecology reconsiders the opportunities offered by eye-tracking, see Outstanding Questions.

Box 1: The diversity of animal eye-movements

Eye-movement behaviour is diverse across vertebrates, arthropods and crustaceans [53, 54] and is varied in terms of degree of acuity across retinal eccentricity, eye musculature, position, and amplitude of movements [43]. Species with either a rudimentary **area centralis** or highly developed foveal vision will benefit from shifting gaze, as this provides a powerful means to prioritise processing of their environment [55]. Those species that that lack eye musculature are restricted to repositioning gaze, and therefore attention, through head and body movements [53]. In such cases, techniques which track head/ body movements alone in order to determine gaze may be enough to make inferences regarding cognitive processes.

At first glance techniques borrowed from the field of psychology seem to lend themselves more easily to testing animals with a visual system more approximate to that of the human. However, eye-tracking studies may prove key in determining how non-mammalian vertebrate have evolved to vastly different architecture in order to tackle difficult tasks. For example, archer fish (*Toxotes jaculatrix)* lack the ability to make the **smooth pursuit** eye-movements humans use to track moving objects, yet have become skilled at tracking a moving prey for a short period in order to make a decision as to whether they can shoot a jet of water and achieve a hit. If they cannot, they make a predictive saccade to an anticipated location and direct a jet of water whilst the target remains in the high acuity area centralis [56]. Interestingly, these anticipatory saccade behaviours mimic those used by professional cricket batsmen to fixate on the bounce point of an approaching ball prior to it striking the ground [57].

Eye-tracking studies using species with independent eye-movements, such as the peacock mantis shrimp (*Odontodactylus scyllarus*) [24] and chameleons (*Chamaeleo* *chamaeleon*) [25] are consolidating the idea that the independence of eye-movements is task-dependant. For example, chameleons respond to threats at intermediate distances by repositioning on a perch at the opposite side to the threat and compressing their abdomens. Importantly, concurrent eye-tracking whilst measuring these responses to threat has found that the leading eye maintains fixation on the threat image, whilst the other (following) eye continues to scan the environment [25]. Such coordinated movements may act to update visual space and contribute to the precise repositioning seen in chameleons.

Box 2: Camouflage: exploiting the limits of perceiver visual attention

Eye-tracking has also provided a novel approach to clarify how animal colouration evolved to exploit the limits of both the visual sensory system and cognitive resources of the perceiver [33]. Background matching camouflage is a type of concealment whereby an animal resembles the visual features of its environment to evade visual detection. In contrast, disruptive colouration functions by the breaking up of salient features. Using humans as predators in a visual search task, Webster et al. [58] compared the influence of these two camouflage strategies on survival rates of target artificial moths. Time to identify prey was operationalised using both behavioural responses (*search time*: total time to detect target) and eye-movement measures (*inspection time*: total time fixation was within 1.5° of target, depicted by grey rectangle; and *fixation bouts*: number of times the gaze enters and leaves the 1.5° target zone prior to detection). As such, the eye-tracking data provides a much more detailed account of how long targets are the subject of overt attention before a capture decision is made.

Hypothetical searches with different search times, inspection times and fixation bouts are presented in (Figure iB) and (iC). In (B) search time is 3000ms and the scan-path shows that the target is detected the first time that the scan-path enters the target zone with a short inspection time. For comparison, the search depicted in (C) is also 3000ms in length but includes three fixation bouts within the target zone before detection occurs. Behavioural search time data alone would have led to the false conclusion that the two targets are equally difficult to detect, while eye-tracking data allowed a more complex picture regarding how the targets capture attention. By breaking down total time spent searching into different components, it becomes apparent that the target in (C) is more likely to evade detection under scrutiny of overt attention.

Webster et al. [58] used eye-tracking to provide a much more nuanced approach than simply estimating survivorship and/or capture time alone. Importantly, degree of disruptive colouration predicted inspection time, whilst background matching did not. Disruptive colouration also predicted fixation bouts over and above background matching metrics.

Glossary

Area centralis: A small region of the retina which is specialised for high acuity vision. Primates and other mammals have a sophisticated **foveated** visual system**,** comprising of the highest density of rods and cones in a higher acuity central region. In the human this high spatial resolution region makes up around 2 degrees of visual angle, with light from the point of fixation falling onto the foveal region.

Attention: a weakly defined phenomenon whereby limited **cognitive** resources are directed to a particular task (with a high load requiring resources to be withdrawn from other cognitive functions). **Overt attention** involves explicit, measurable, eye-movements to be directed to the attended point in space. **Covert attention** refers to attending to a point in space without an associated eye-movement.

Cognition (or cognitive processes): A process broadly defined as the act of processing sampled sensory signals for the purpose of providing information to produce effective goal directed decisions and behaviours. Whether or not these neural processes are carried out with any self- awareness by non-humans is beyond the scope of this opinion piece.

Fixation: When the eye remains directed toward the same location for a brief time-period to gather information around that point. For humans each fixation ensures that light from the point of fixation falls upon the highest spatial resolution **foveal region** of the eye.

Eye-movements: The use of an **eye-tracking** device for measuring eye-movements often comprising a camera system attached to the head or placed externally, near to the eye. Eye-movements comprise of movements of the musculature of the eye, head, and body in order to reposition gaze.

Peripheral vision: In humans, peripheral vision can be defined as the retinal regions outside of the high-resolution foveal region. Light falling on the periphery comes from parts of the scene not being looked at directly. The periphery has lower spatial resolution and also fewer colour sensitive receptors, but the periphery is particularly sensitive to certain classes of motion.

Raw data: Collected during a visual search task, comprising of Xeye Yeye gaze point coordinates which can be filtered and smoothed determine gaze sampling patterns relative to the properties of the visual stimulus.

Saccade: A short high-velocity eye-movement which acts to rotate the eye to ensure it is directed toward a different part of the visual scene. Saccades are usually followed by a period of **fixation** to allow the sampling of new visual information.

Sensory ecology: the study of how organisms acquire, process, and respond to information from their environment based on their ability to perceive it.

Smooth pursuit: Continuous eye-movements which track an object in the environment.

Figure text

Figure i. Eye-tracking during the detection of a camouflage target. Eye-tracking data superimposed on a tree bark background with an embedded moth target (A) along with two hypothetical searches (B) and (C). Red dots indicate regular samples of eye movement connected by yellow lines to approximate the scan-path (adapted from [58]).

Figure 1: Capturing human gaze behaviour during locomotion, demonstrating the versatility of eye-tracking data. Examples of gaze sampling during locomotion (driving in real environments) with gaze position measured as angular eye-position (degrees) relative to the centre of the vehicle. (A) Real time eye-tracking during driving; transparent circles represent fixation on four successive eye-tracker samples (frames), with reference to future path and road tangent point/ occlusion markings. (B) Heat maps indicate the proportion (percentage) of gaze fixations falling on the scene over the course of several driving trials (same as Key in 1(A)). (C) A birds-eye view of steering trajectories alongside fixation locations from three example participants steering a curve from an inside (red), middle (blue) and outside (green) starting position, demonstrating that participants steer towards where they look. Adapted from [48].

Acknowledgements: Jac Billington was funded by The Leverhulme Trust during the writing of this article.

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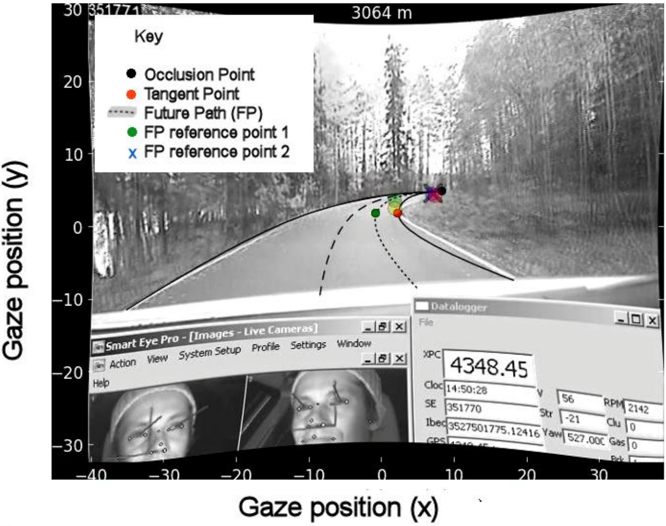
(A)



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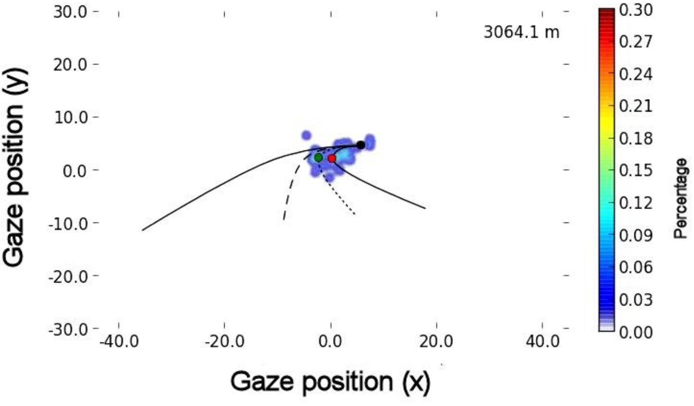

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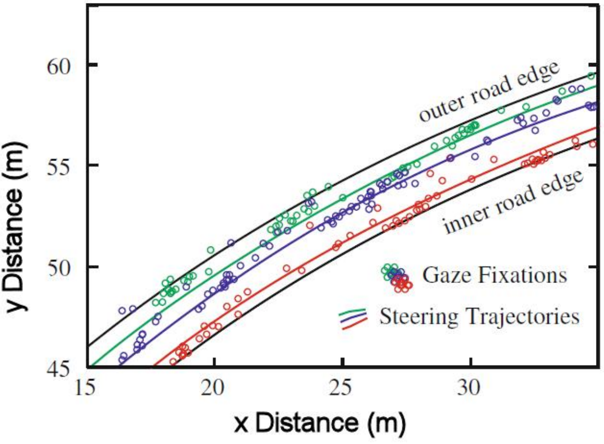

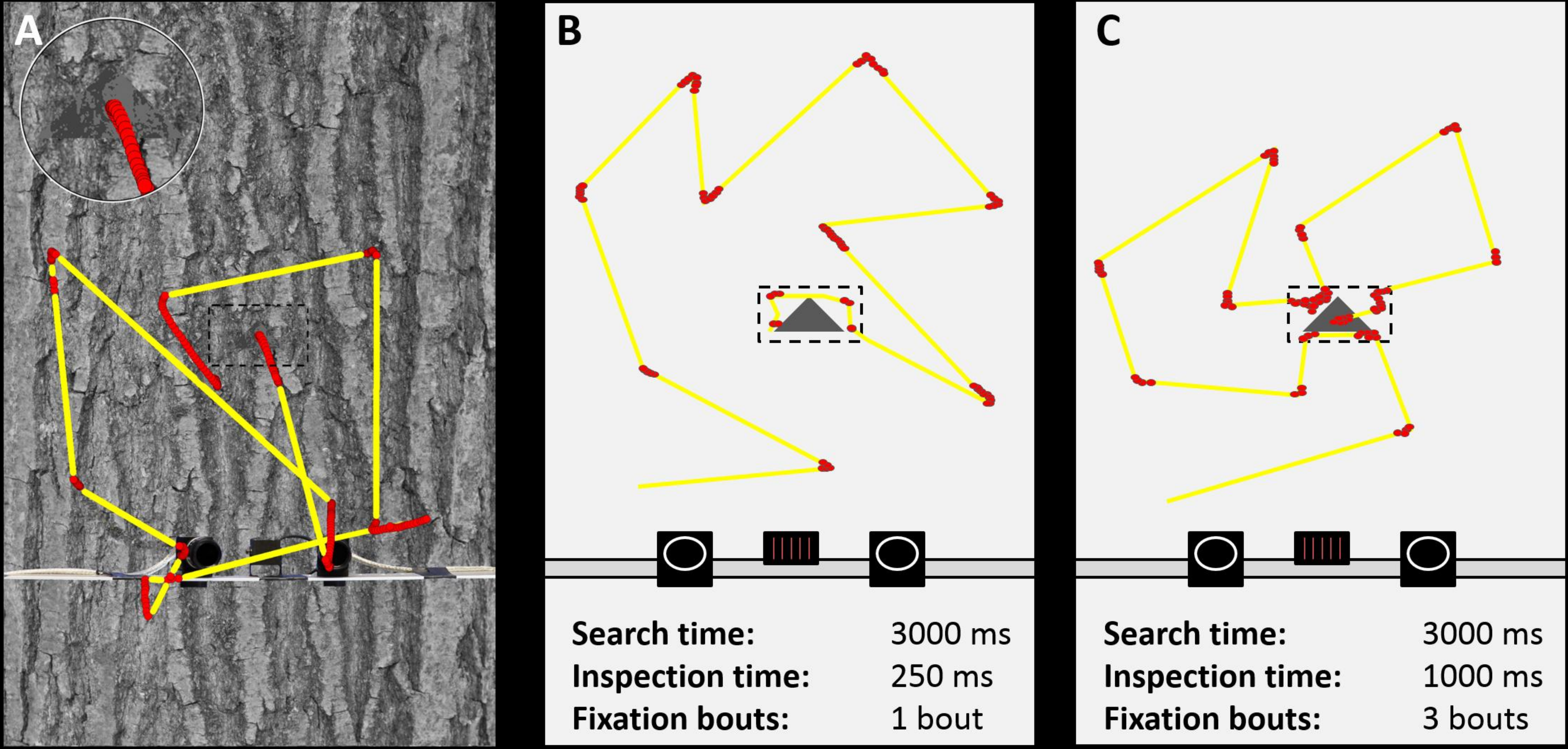
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The (under)use of eye-tracking in evolutionary ecology

Outstanding Questions

- How do animals prioritise information within complex sensory environments?
- (How) do animals learn to adopt different strategies when processing sensory information, and how flexible are those strategies under changing conditions?
- To what extent do the limits of attention and information processing on the part of the receiver determine the strength of selection on animal signalling?
- Can eye-tracking technology be used to validate computational approaches to quantifying conspicuousness of cryptic targets?
- Can eye-tracking technology improve our understanding of evolutionary phenomena such as the maintenance of imperfect mimicry and distance-dependent signalling?