Dappled light disrupts prey detection by masking movement

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Prey and ambush predators that rely on concealment face a major constraint: motion breaks their camouflage. However, dappled light is a common feature of sunny, vegetated habitats and can, when conditions are windy, become a source of dynamic visual noise. We tested the idea that this could mask movement, reducing the risk of detection. Newly hatched domestic fowl chicks, Gallus gallus domesticus, a proxy for wild forest-floor birds, were trained to peck moving, on-screen prey presented among two sources of dynamic dappled light: computer-simulated and that created with a mirror ball. Dynamic dapple, however produced, increased the chick's latency to both fixate and peck the prey. Furthermore, we show that dynamic visual noise masks motion in a way that static visual noise does not. This reduction in foraging efficiency should, we predict, have significant consequences for an organism's choice of habitat (as prey), foraging area (as predator) and its pattern of movement within a habitat.

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Think of the dappled lighting as leaves sway in the wind, or the complex reticulated patterns of light underwater (hereafter 'caustics') created by waves. Dynamic illumination is a common environmental phenomenon, both terrestrially and aquatically, yet investigations of how animals forage, and of visual search more generally, ignore this. Further, the direct influence of dynamic illumination upon behaviour in nonhumans is yet to be quantified.

This lack of research is somewhat surprising given that dynamic illumination increases visual complexity by introducing background motion noise. This is a known obstacle to signalling, particularly signals that are dynamic (Ord, Peters, Clucas, & Stamps, 2007; Peters, Hemmi, & Zeil, 2007, 2008). Indeed, the luminance profile of an environmental scene appears pertinent to the efficacy of motion-based signalling (Bian, Chandler, Pinilla, & Peters, 2019). In such cases, behaviour needs to be changed to maintain the signal-to-noise ratio (Merilaita, Scott-Samuel, & Cuthill, 2017) and increase the likelihood of that signal being received (Ord et al., 2007; Peters et al., 2007, 2008). Conversely, the opposite is true for camouflage: the prime objective here is to reduce the signal-to-noise ratio so that dynamic cues, such as organism movement, go undetected, falling within the distribution of this background motion noise (Fleishman, 1985, 1986). This is an important consideration as motion, in general, is said to 'break' camouflage (Cott, 1940; Cuthill, 2019; Hailman, 1977; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Rushton, Bradshaw, & Warren, 2007; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Stevens, Yule, & Ruxton, 2008; Zylinski, Osorio, & Shohet, 2009).

Data from visual search experiments on humans suggest how dynamic illumination may influence behaviour. Matchette, Cuthill, and Scott-Samuel (2018) investigated how prey detection was independently affected by the presence of dappled light and water caustics (both static and dynamic). When asked to capture moving prey items within computer-simulated scenes, human participants were significantly slower and more error-prone when viewing scenes with illumination that was dynamic as opposed to static. We therefore predict that such visual complexity will similarly mask prey movement for foraging animals. However, we cannot assume that other animals, even highly visual predators such as birds, respond to dynamic illumination in the same way as humans for two main reasons. First, the processing of luminance and colour information may differ. For example, birds have a different photoreceptor type, double cones, which seem to drive some or all of their luminance-based visual processing, while humans use pooled signals from medium- and long wave single cones (Osorio & Vorobyev, 2005). Second, there are differences in the neural structures controlling attentional mechanisms between mammals and other vertebrates (Sridharan, Schwarz, & Knudsen, 2014).
We adapted the paradigm of Matchette et al. (2018) for domestic fowl chicks, *Gallus gallus domesticus*, as a proxy for wild foraging birds. These birds are easily acquired and trained, and have become a common model system for general bird vision, cognition and behaviour (Lisney et al., 2011; Marino, 2017; Miller & Hollander, 2010; Skelhorn & Rowe, 2006; Skelhorn, Rowland, Speed, & Ruxton, 2010). The visual system of domestic fowl is also well characterized (Fantz, 1957; Ham & Osorio, 2007; Jarvis, Taylor, Prescott, Meeks, & Wathes, 2002; Lisney et al., 2011; Over & Moore, 1981) and they have an omnivorous diet that includes moving invertebrate prey (Marino, 2017). Soon after hatching, chicks will visually follow and peck appropriately at moving objects (Fantz, 1957; Over & Moore, 1981) meaning they are readily trained to a specific foraging task.

**METHODS**

**Set-Up: Housing Arena**

Forty newly hatched female domestic fowl chicks were obtained from Hy-Line International (www.hyline.com) and housed in the poultry facility of the University of Bristol Veterinary School for the duration of the experiment. As they were within 24 h of hatching, these chicks had no prior associations (either good or bad) with the type of lighting and screens used.

Upon arrival, each chick was given a unique combination of head, upper back and lower back markings using varying colours of nontoxic paint (Porcimark marking spray, Kruuse, www.kruuse.com) for identification and were housed in the same, 250x50 cm and 50 cm high, arena with wood chip as substrate. Any initial handling by experimenters was paired with a mealworm, *Tenebrio molitor*: this established a positive association with handling and familiarized chicks with the reward food item used in training and experimentation. The latter took place in a separate arena. Water and food were provided ad libitum, via water feeders and trays of chick starter crumb at substrate level (Farmgate, www.forfarmers.co.uk/poultry). The only exception to this was the removal of food trays for a short (30 min) pretrial food deprivation period to increase the chick’s motivation to forage in training and experimental trials.

The housing arena was subject to a light cycle that matched the ambient day-light cycle, achieved using ceiling daylight mimicking lamps (GEWISS, www.gewiss.com: twin 26 W LED) running in high-frequency (30 kHz+) ballasts, well above the ca. 60 Hz critical flicker fusion frequency of domestic fowl (e.g. Jarvis et al., 2002; Prescott, Wathes, & Jarvis, 2003). The ambient temperature was maintained at 25–28 °C using multiple 175 W infrared heat lamps (General Electric, www.gelighting.com) positioned on a light rail ca. 60 cm above the arena.

In addition to food and water, the housing arena also contained multiple objects that the chicks would encounter in the experimental arena, including a low perch, a hanging mirror ball (50 cm in diameter) and a computer monitor. This exposure minimized any neophobic responses to these items in the experimental arena. For example, the computer monitor was buried into the substrate such that chicks could walk over the screen in an identical manner to the experimental arena. Videos of training background scenes (see below) could then be presented on a continuous loop for the duration of the daylight hours.

**Set-Up: Experimental Arena**

The experimental arena, located across the room to the housing arena, was a cage measuring 250x50 cm and 50 cm high with wood chip substrate (Fig. 1a). At one end of this cage was a section (20x50 cm and 50 cm high) partitioned off using wire mesh. This created an independent ‘buddy area’: in all training and experimental trials, two chicks were placed in this space to reduce any potential distress for the experimental chicks due to social isolation. A quarter of the chicks (10) were immediately allocated a buddy chick role and played no part as experimental chicks. Throughout training and experimentation, buddy chicks were changed every 25 trials, or sooner if they themselves started to produce distress calls (<5% of trials). At the opposite end to the buddy arena was a horizontal wooden perch used to loosely segregate a ‘start pen’ from which chicks could begin each trial. To ensure an ambient temperature of 25–28 °C, as in the housing arena, a 175 W infrared heat lamp was also present.

The simulated scenes, stimuli and subsequent experimental task were created and executed in Unreal Engine 4 (Epic Games, www.unrealengine.com) and viewed at 0–20 cm from a gamma-corrected 20° Philips 200WS monitor (Philips, www.philips.co.uk), with a refresh rate of 75 Hz, an active LCD matrix and a resolution of 1680x1050 pixels. Because the flicker fusion frequency can sometimes exceed 75 Hz (Jarvis et al., 2002; Lisney et al., 2011), the use of a monitor with an active LCD matrix was desirable to ensure that any aversion to the screen (due to a refresh rate less than the flicker fusion frequency) was avoided (Oliveira et al., 2000). This monitor was positioned adjacent to the wire mesh and buried flush to the substrate.

Each simulated scene was monochromatic, covered a screen area of 1680x950 pixels with a mean luminance of 80 cd/m² and was viewed from a bird’s-eye perspective (Fig. 1b). The prey item was a (simulated) three-dimensional sphere with a matt surface and mean luminance equal to that of the background. When viewed from above, as in the experiment, the prey item was a circle of radius 18.7 pixels (Fig. 1c) with an apparent three-dimensional shape derived from the realistic projection of light to create shape-from-shading cues (Cook, Qadri, Kieres, & Commons-Miller, 2012). Prey items could appear at any random locus within one of two regions (210x650 pixels) of the scene and, once present, would follow a linear vector towards another random locus in the opposite region (Fig. 1b). Movement was fixed at a speed of 24 mm/s (6.9 degrees/s) and the prey item continued to move back and forth along this vector for the duration of the trial. This speed was chosen after pilot trials with a previous cohort of chicks, to ensure that moving prey items were detectable, but did not leave the screen too fast to be pecked. Time of appearance, location and subsequent movement vectors were random, picked from discrete uniform distributions using Unreal Engine’s random integer generator. Location regions were set such that prey items never left the viewed scene. An Akaso Brave 4 action camera (Akaso, www.akaso.org) was attached to the wire mesh above the monitor to record each trial from above. Recordings (4K resolution, 24 fps and 170° viewing angle) were then viewed post hoc to analyse the chicks’ behaviour and to measure their responses.

Two sources of dappled light were used, one created via a mirror ball and the other via computer simulations (henceforth ‘screen dapple’). For the former, a mirror ball (Showtec, www.showteco. uk; 500 mm diameter with 10x10 mm facets, suspended from a light rail) was used in conjunction with a spotlight (ArriLite 800, www.arrilite.com/lighting) to bathe the entire experimental arena in dappled light. The mirror ball could be left stationary or gently spun to create either static or dynamic dappled light (Fig. 1a). For the screen dapple treatments, Unreal Engine was used to create computer-simulated dappled forest light, identical to that used by Matchette et al. (2018; see Appendix). This dappled light could also be static or dynamic but was localized to the computer screen. There were therefore five treatments in total, in a 2x2+1 design: mirror ball static dapple, mirror ball dynamic dapple, screen static
dapple, screen dynamic dapple and no dapple illumination (henceforth termed ‘absent’).

Ethical note

All procedures were approved by the Animal Welfare and Ethical Review Body, University of Bristol (UIN/18/047). Several means were in place to minimize distress, including the use of a ‘buddy area’, appropriate ambient lighting and pre-exposure to all experimental apparatus. After the experiments, with veterinary approval, chicks were rehomed to local smallholders.

Protocol

Chicks were placed in the start pen and allowed to move towards the monitor to ‘forage’ for the prey item. If a chick correctly pecked the prey item, a food reward was immediately dropped next to the chick and the trial stopped. A time limit of 2 min was given per trial. This process was carried out five times sequentially for each chick for a given treatment.

Response measures were derived from video recordings. Once a chick had passed a threshold of 10 cm from the screen, at which point it was possible to detect the prey item, a timer was initiated which marked the start of the trial. The time of first fixation of the prey was recorded, as well as the time of the subsequent peck at the prey. ‘Fixation’ was superficially different to the cursory monocular scans that were common when a chick first entered the arena: the chick adjusts the orientation of its head in the direction of the prey item, allowing full binocular attention, at which point the neck extends and the chick begins to ‘stalk’ the prey item along its trajectory. Attack Latency (AL) was defined as the overall time from trial start to first correct peck. This comprised Fixation Latency (FL), the time from trial start to first fixation, and Peck Delay, the difference in time between the first fixation and the first correct peck. To check our response measures for experimenter bias, as well as their replicability, an independent referee recorded several response measures from a random sample of videos spanning all treatments which could be compared to the original experimenter recordings.

Training and Experimental Phases

Several training steps were necessary to introduce the task at hand, as well as each component of the experiment. Each step was conducted within the experimental arena where the stimuli were displayed on the monitor, with the screen set to white (Table A1). The first step introduced the computer-generated, spherical prey item. This step was critical to establish an association between the prey on the screen and reward. To achieve this, prey items remained stationary with a mealworm placed beside them (so as not to obscure the target). The second step introduced a moving prey item; a food reward was initially given once the chick had approached the prey item, which encouraged later pecking. The third and fourth steps then introduced a moving prey item in the presence of dappled light created via the mirror ball and computer simulations, respectively. Both forms of dappled light were initially introduced statically, then later dynamically. Each chick completed no more than three training blocks in a day, with at least a 1.5 h gap between each block. Owing to the narrow window for early chick learning, only chicks that attained 80% success rate (to peck the prey item and consume the reward) in a given training block would progress. Any chicks that failed to reach this criterion within the allocated blocks were converted to ‘buddy’ chicks. Of the remaining 30 chicks, 18 met the criterion and entered the experiment.

The experimental phase mimicked the format of the training phase, but with a more complex and context-relevant background. This comprised a single image of leaf litter, sourced from the software’s default asset package, which was tiled repeatedly to make-up a background scene (Fig. 1d). We used the selected background ‘out of the box’, with RGB range and mean values as supplied by Unreal Engine, as these were already judged to be realistic and, in any case, precise simulation of a real forest-floor background (which these chicks had never experienced) was unimportant for the experiment’s goals. The target luminance was then adjusted to match the mean background luminance. All treatments were run twice and in a randomized order, totalling 10 trials (2 x 5) per chick for each treatment. If a chick did not peck the target within 1 min, the trial ended and the chick was returned to the home arena.

Throughout the experimental phase, chicks pecked the target within 1 min in 82% of trials (mean Attack Latency 3.2 s, median 2.1 s, range 0.6–45.3 s) and all chicks did so in at least five of the 10 trials per treatment. Failures to peck were associated with individual chicks rather than particular treatments (only two chicks completed as few as five trials for a treatment and these two chicks completed < 10 trials for all and for four of the five, treatments, respectively).

Figure 1. (a) A photograph of the experimental arena in the presence of mirror ball dappled light. Chicks were lowered in at the start pen (denoted by the horizontal perch) and moved towards the stimuli monitor to forage. The buddy arena (beyond the monitor) was physically, but not visually, divided from the experimental arena with wire mesh. The recording device position can be seen on top of the wire mesh divider. (b) Screenshot of an experimental trial. The two regions denoted by the dashed yellow lines are the possible prey item appearance areas (no lines were present in the actual trials). The prey item (artifactly highlighted by a red circle) is midway through moving from one appearance area towards the other. (c) A close-up of the prey item outside the experimental context. (d) Screenshot of the tiled leaf litter image used as experimental backdrop. This image was converted to monochrome for the purpose of the experiment. (b–d) Reproduced with permission from Matchette et al. (2018).
Statistical Analyses

All statistical analyses were performed in R 3.3.2 (R Foundation for Statistical Computing, www.R-project.org) and utilized generalized linear mixed models (function glmer in the lme4 package; Bates et al., 2017). The response variables were Attack Latency, Fixation Latency and Peck Delay, all with gamma error and inverse link functions. The gamma link was used because of positive skew in the raw time data. The full model included the fixed effect treatment and the random effect of chick ID. The change in deviance between models with and without the predictors of interest was tested against a chi-square distribution with degrees of freedom equal to the difference in degrees of freedom between the models. Treatment effects were examined using a custom contrast matrix that represented the a priori comparisons of interest, that is, the main effects of Display (mirror ball versus screen dapple), Motion (static versus dynamic) and their interaction, plus a set of pairwise comparisons between each treatment and the dapple-absent control. This matrix has more contrasts than we have degrees of freedom, so we corrected for multiple testing using the Tukey procedure in multcomp (Hothorn, Bretz, & Westfall, 2008). The test statistic for these contrasts was the standardized normal deviate (z). For those interested in other comparisons, the full set of pairwise comparisons, using the Tukey procedure in multcomp, is also provided (Table 1).

To check our response measures for experimenter bias, as well as their replicability, nine, naïve, independent volunteers estimated both Fixation Latency and Peck Delay from 25 sample videos spanning all treatments. The 10 sets of timings for each of the response measures were then compared using the intraclass correlation coefficient (Shrout & Fleiss, 1979): function ICC from the R package psych (Revelle, 2017). Because bias is of interest as well as correlation, we also compared these nine volunteers’ data to those of the original experimenter using paired t tests (see Appendix).

RESULTS

When domestic fowl were presented with moving prey items, the Attack Latency was significantly longer when in the presence of dynamic computer-simulated dapple light than dynamic mirror ball dapple light, and both of these treatments had longer latencies than any other treatments (treatment $\chi^2_a = 269.87, P < 0.001$; Fig. 2, Table 1: Attack Latency). Breaking down this overall treatment effect, there was a significant interaction between Display and Motion ($z = 3.95, P < 0.001$) so, to establish why, mirror ball and screen dapple treatments were analysed separately. Dynamic dapple increased Attack Latency in both conditions, but more than twice as much with screen dapple (104% increase; $\chi^2_a = 178.77, P < 0.001$) than with mirror ball dapple (41% increase; $\chi^2_a = 56.07, P < 0.001$). Attack latency for both dynamic dapple treatments was significantly longer than in the dapple-absent control (mirror: $z = 5.31, P = 0.111$; screen: $z = 9.64, P = 0.111$). The Attack Latency under static mirror ball dapple did not differ from that in the absence of dappled light ($z = 2.30, P = 0.111$), but in the absence of dappled light it was longer than in the static screen dapple treatment ($z = 4.30, P < 0.001$).

These treatment differences were largely driven by Fixation Latency, with the pattern and significance of treatment differences matching those for Attack Latency (treatment $\chi^2_a = 601.87, P < 0.001$; Fig. 2, Table 1: Fixation Latency). There was a significant

Table 1

|          | A     | MS    | MD    | SS    | SD    |
|----------|-------|-------|-------|-------|-------|
| Attack   |       |       |       |       |       |
| Latency  | A     | 0.780 | <0.001| 0.136 | <0.001|
|          | MS    | 1.15  | <0.001| 0.779 | <0.001|
|          | MD    | -5.66 | -6.76 | -     | <0.001|
|          | SS    | 2.33  | 1.15  | 8.01  | <0.001|
|          | SD    | -10.30| -11.46| -4.71 | -12.77|
| Fixation | A     | -     | 0.712 | <0.001| 0.986 | <0.001|
| Latency  | MS    | 1.27  | -     | <0.001| 0.380 | <0.001|
|          | MD    | -4.23 | -5.46 | -     | 0.002 | <0.001|
|          | SS    | -0.52 | -1.79 | 3.75  | -     | <0.001|
|          | SD    | -17.61| -18.74| -13.29| -17.23|
| Peck     | Abs   | -     | 0.562 | <0.001| 0.001 | 0.684 |
| Delay    | MS    | -1.50 | -     | <0.001| 0.158 | 1     |
|          | MD    | 4.19  | 5.65  | -     | <0.001| <0.001|
|          | SS    | -3.80 | -2.26 | -7.99 | -     | 0.103 |
|          | SD    | -1.31 | 0.19  | -5.46 | 2.45  |

Lower-left-hand triangle of each matrix are Tukey-type t tests; upper-right-hand triangles are corresponding P values. Dapple treatments were: A: dapple absent; MS: mirror ball static; MD: mirror ball dynamic; SS: screen static; SD: screen dynamic.
interaction between Display and Motion ($z = 7.09, P < 0.001$). Analysing mirror ball and screen dapple treatments separately, dynamic dapple increased Fixation Latency in both conditions, but far more with screen dapple (164% increase; $\chi^2 = 247.70, P < 0.001$) than with mirror ball dapple (19% increase; $\chi^2 = 15.35, P < 0.001$). Attack Latency for both dynamic dapple treatments was significantly longer than in the dapple-absent control (mirror: $z = 3.06, P = 0.013$; screen: $z = 16.43, P < 0.001$). The Attack Latencies under static mirror ball dapple and screen dapple did not differ from that in the absence of dappled light ($z = 0.48, P = 0.984, z = -0.55, P = 0.975$, respectively).

The treatment differences in the delay from fixation to pecking were significant but smaller ($\chi^2 = 108.58, P < 0.001$; Fig. 2, Table 1: Peck Delay). There was no significant interaction between Display and Motion ($z = 0.184, P = 1.000$) but significant main effects of Screen and Motion. Dynamic dapple increased Peck Delay by 53% compared to static ($z = -7.47, P < 0.001$) and mirror dapple increased it by 86% compared to screen-based dapple ($z = -5.26, P < 0.001$). Compared to the dapple-absent control, dynamic mirror dapple increased Peck Delay ($z = -4.45, P < 0.001$), static screen dapple reduced it ($z = 5.50, P < 0.001$), and both static mirror ($z = 2.39, P = 0.093$) and dynamic screen dapple ($z = 0.78, P = 0.916$) showed no significant difference.

**DISCUSSION**

The ability of domestic fowl to forage for on-screen prey is influenced by the presence of dynamic dappled light in the same manner as in humans (Matchette et al., 2018). Moreover, this effect is consistent irrespective of the method used to create the dynamic dappled light: both screen dapple and mirror ball dapple increased the latency to fixate and to attack relative to their static counterparts.

These data could be explained in several ways. They could be a consequence of (1) a neophobic response to the dynamic dappled light. Neophobia is a common response of domestic fowl and, therefore, we tried to ensure this was minimized: chicks were familiarized with each independent experimental feature during the task at hand induced by the dappled light. This seems surprising because a scene with dappled light has a higher contrast range than one without and therefore would appear more visually complex (Dimitrova & Merilaia, 2010; Dimitrova, Stobbe, Schaefer, & Merilaia, 2009; Xiao & Cuthill, 2016). Further, these multiple high-contrast light points, particularly for static mirror ball dapple, might act as distractors (Dimitrova et al., 2009). Nevertheless, the chicks did not appear to be affected: indeed, Peck Delay was slightly but significantly longer for scenes with an absence of dappled light than static screen dappled light. A key take-home message is therefore that static noise does not mask dynamic signals (the moving target), but dynamic noise does.

An important methodological note is that, although the two sources of dappled light differed in their ‘scope of influence’ (global or limited to screen), they also differed in terms of spatial structure and the dynamic of dappling. Of the two, screen dapple was a more realistic recreation as it was modelled to match the spatiotemporal properties of real forest dapple flicker. In contrast, mirror ball dapple represented a more predictable light flicker, a product of the uniform mirror ball facets: light spots that move along a parallel trajectory at roughly a constant speed and spacing. In addition, owing to its top-down projection, mirror ball dapple could be momentarily occluded by the chick itself and may not consistently project upon an area that the chick is investigating, possibly resulting in a blurring effect. Indeed, this may be the reason for the differences in Fixation Latency between the two dynamic treatments and why there was minimal effect of static mirror ball dapple versus the absent control. Nevertheless, mirror ball dapple provided an alternative form of dapple that, when dynamic, still influenced the ability of chicks to forage successfully.

The presence of dynamic illumination within a habitat has been closely associated with aspects of concealment, coloration and perception. For example, the vertical barring and vermiculation of fish patterns have been linked to the influence of water caustics (McFarland & Loew, 1983), while some felid coats may be similarly influenced by the presence of dappled light within a habitat (Allen, Baddeley, Cuthill, & Scott-Samuel, 2012). The intensity of water caustic flicker could also have played a significant role in the initial evolution of colour vision (Maximov, 2000). Moreover, the inconsistencies of signal (e.g. in time, space, angle of view and perceived hue), caused by moving through inconsistent illumination, is likely to disrupt the ability to bind the features of an individual into a single percept (Espinosa & Cuthill, 2014; Murali, 2018), as well as influence the perception of group movement (Murali, Kumari, & Kodandaramaiah, 2019).

Thus, one may expect dynamic illumination, such as dappled light, to have a wider remit of influence, extending to visually mediated behaviours: where organisms choose to live (as prey), forage (as predators) and display (sexual signals), as well as the pattern of movement used by an organism within a habitat. For example, for mobile prey during periods of dynamic dappled light, when the relative safety of movement outweighs that when dappled light is static, one may expect an increase in foraging and commutes between shelters, in conjunction with a lesser need for group or protean movement. A shift towards nonforaging behaviours or foraging techniques associated with nonvisual senses may also be expected in predators under the same conditions. Moreover, the distracting effect of dappled light is likely to be highly variable, mirroring the variability of governing forces across microhabitats (Peters, Hemmi, & Zell, 2008): namely light intensity and plant motion (which itself is a function of wind speed, plant structure and topography; Bian et al., 2019).

**Author Contributions**

All authors contributed to the conception and design of the study, as well as drafting the manuscript; S.M. programmed the
Appendix

Screen dapple generation

Part of this section (in quotes) is reproduced with permission from Matchette et al. (2018).

The simulated scene was created and executed in Unreal Engine 4 (Epic Games, www.unrealengine.com). Each experimental zone comprised (from bottom up) the floor, spawn areas, prey item, camera item, tree static mesh collection and lighting systems. Each component had its own settings and ‘blueprints’ that could be coded to alter performance and behaviour. We used multiple experimental zones.

‘The floor component was a standard plane static mesh, coated in a default material acquired from the free demonstration asset package, ‘Kite Demo’. The material attached to the floor component’ (‘forest_path_001A’) ‘was a tiled, high-quality image of leaf litter (Fig. 1). This formed the backdrop to all dappled light trials in this experiment. Set just upon this were two transparent box meshes that would act as ‘spawn’ (appearance) areas. For any given trial, a prey item would appear at a random location within one appearance area (the ‘origin’ point); while another random location would be selected from the opposite appearance area (the ‘destination’ point) to create a random movement vector for the prey item. The prey item was then set to move (at any desired speed) along the random vector. Upon arrival, the prey item would reverse the movement (at the same speed) back towards the origin point. Once here, the process would repeat until the end of the trial.

‘Above this ground activity, a camera item was positioned, which would provide the player view for each trial. The camera item was rotated 90 degrees to the floor component and had equalized RGB values, creating a monochrome bird’s-eye view of the leaf litter backdrop. Between this component and the lighting systems were a collection of randomly positioned, pre-made model tree static meshes, also of the ‘Kite Demo’ assets package. When paired with the lighting systems above, these cast the characteristic dappled light shadows across the floor component. Each experimental zone had a unique arrangement of trees and therefore a unique arrangement of shadows. Crucially, a highly editable noise component could be added to create a range of dappled light flickers and dynamic shadows, to mimic the changing strength of wind. High above each zone was a directional light source and a skylight. Each had an intensity scale which would alter both the light intensity (brightness) and the shadow intensity (darkness).’

Repeatability and bias

For Fixation Latency, the intraclass correlation coefficient was 0.82 (95% confidence interval 0.73–0.90; $F_{24,216} = 47.0, P < 0.001$). In pairwise tests, there was no difference between the original experimenter’s data and those of the nine naïve volunteers (range of mean differences -0.05 to 0.04 s, five means being negative and four positive; 0.12 < $t_{24} < 0.99, 0.334 < P < 0.907$). For Peck Delay, the intraclass correlation coefficient was 0.98 (95% confidence interval 0.96–0.99; $F_{24,216} = 462.0, P < 0.001$). In pairwise tests, there was no difference between the original experimenter’s data and those of eight of the nine naïve volunteers (range of mean differences -0.04 to 0.05 s, five means being negative and four positive; 0.05 < $t_{24} < 1.84, 0.079 < P < 0.962$). One person’s Peck Delay times were significantly longer than the original experimenter’s (mean difference: 0.25 s; $t_{24} = 4.19, P < 0.001$), but also significantly longer than those of the other eight naïve volunteers (range of mean differences 3.13–3.90 s; 3.13 < $t_{24} < 4.79, all P < 0.001$). Therefore, this volunteer was the outlier and the original experimenter’s data were unbiased compared to those of the others. The original experimenter’s data were therefore considered suitable estimates for further analysis.

Table A1

| Treatment | Screen | Prey item | Dappled light | No. of trials per chick |
|-----------|--------|-----------|---------------|------------------------|
| Treatment 1 | Leaf litter | Moving | Absent | 10 |
| Treatment 2 | Leaf litter | Moving | Mirror ball static | 10 |
| Treatment 3 | Leaf litter | Moving | Mirror ball dynamic | 10 |
| Treatment 4 | Leaf litter | Moving | Screen static | 10 |
| Treatment 5 | Leaf litter | Moving | Screen dynamic | 10 |