Orienting to the sun improves camouflage for bilaterally symmetrical prey

VERONICA MAVROVOUNA[1], OLIVIER PENACCHIO[2] and WILLIAM L. ALLEN[1],*

[1]*Department of Biosciences, Swansea University, Singleton Campus, Swansea SA2 8PP, UK*
[2]*School of Psychology and Neuroscience, University of St Andrews, South Street, St Andrews, Fife KY16 9JP, UK*

Here, we investigate the camouflage consequences of animal orientation behaviour. Shadows can be a conspicuous cue to the presence of prey. For bilaterally symmetrical animals, light field modelling indicates that camouflage will be improved when an animal orients its longitudinal axis directly towards or away from the sun, because the appearance of shadows is minimized. We test this prediction with a field predation experiment, in which wild birds hunt for artificial camouflaged prey oriented with the longitudinal axis either parallel or perpendicular to the sun. We find that prey oriented parallel to the sun are 3.93 times more likely to survive than prey oriented perpendicular to the sun. This result demonstrates the strong orientation dependence of camouflage. Given the dramatic difference in survival of prey with different orientations, we suggest that camouflage should be investigated as an important determinant of the positional behaviour of animals.

ADDITIONAL KEYWORDS: antipredator – camouflage – countershading – orientation – predation – visual ecology.

INTRODUCTION

Orientation behaviour is a fundamental aspect of movement ecology for all motile organisms, with a major influence on sensory input, resource acquisition and other behavioural decisions (Jander, 1975). Orientation behaviour is known to be influenced by factors including thermoregulation (Waldschmidt, 1980), ultraviolet exposure (Braude *et al.*, 2001), sensation and communication (Weissburg, 2010), navigation (Guilford & Taylor, 2014), foraging (Červený *et al.*, 2011), mate attraction (White & Latty, 2020) and the cost of movement (Shepard *et al.*, 2013). Antipredator defences such as camouflage, however, are not frequently considered as a driver of animal orientation behaviour (Penacchio *et al.*, 2015a).

Previous work on camouflage and orientation behaviour has shown that some species of moth adopt body orientations that improve their camouflage while resting on backgrounds with anisotropic textures (Webster *et al.*, 2009; Kang *et al.*, 2012, 2015), and twig-mimic caterpillars have improved masquerade when

they adopt more twig-like body postures (Rowland *et al.*, 2020). However, these examples are restricted to highly cryptic animals that remain motionless for long periods of time. Here, we investigate whether the effect of body orientation on camouflage effectiveness might be much more general, owing to the relationship between orientation, shadows and visibility.

Shadows are an important cue to the presence and form of objects, including prey (Ramachandran, 1988). Countershading coloration, the tendency for animals to be lighter on surfaces that receive less illumination (Poulton, 1890; Thayer, 1896), can be an effective camouflage adaptation because it makes self-cast shadows on the undersides of animals less visible (Donohue *et al.*, 2020) and reduces recognizable cues to three-dimensional (3-D) form (Penacchio *et al.*, 2015b; Cuthill *et al.*, 2016; Ruxton *et al.*, 2019). However, the effectiveness of self-shadow concealment depends on the strength of shadows and where they fall. For example, countershading camouflage designed to hide self-cast shadows optimally in direct sunlight is less effective in cloudy conditions, because shadows are weaker and the countershading gradient remains visible (Penacchio *et al.*, 2015b; Cuthill *et al.*, 2016; Penacchio *et al.*, 2018).

*Corresponding author. E-mail: w.l.allen@swansea.ac.uk

The other important influence on where shadows fall is the orientation of the animal relative to the light source, typically the sun. The camouflage consequences of misalignment between camouflage phenotype and light direction were demonstrated by Rowland *et al.* (2008), who found that pastry caterpillars placed on the top surfaces of branches survived best when they were countershaded, and thus hid their self-cast shadows, whereas those placed on the underside of branches survived best when they were reverse countershaded. Most animals lack the ability to move 'upside-down', but all can rotate horizontally on the sagittal axis (yaw) with respect to the surface plane to change heading. Heading relative to the sun also influences where shadows fall and is therefore predicted to have wider camouflage consequences. The modelling work of Penacchio *et al.* (2015b) demonstrates that for bilaterally symmetrical animals with fixed coloration (i.e. most terrestrial animals), aligning the longitudinal axis parallel to the direction of the illumination is optimal, with deviation increasing internal and background contrast. In computer-based experiments featuring a simulated 3-D environment in which humans searched for targets, target deviations of $> 15°$ away from the orientation for which their camouflage was designed dramatically increased detection speed and search accuracy (Penacchio *et al.*, 2017).

Here, we aim to address the criticism of Stevens & Ruxton (2019) that most work on the role of orientation in camouflage has taken place in artificial scenarios by replicating human-predator laboratory-based study by Penacchio *et al.* (2017) in a natural environment with wild avian predators.

We predict that prey whose longitudinal axis is oriented parallel to the main direction of light will survive with higher probability than prey oriented perpendicular to the main direction of light. Support would indicate that camouflage might be an important influence on animal orientation behaviour, a hypothesis generally overlooked in the literature on animal orientation (Webster *et al.*, 2009; Kang *et al.*, 2012; Penacchio *et al.*, 2015a; Stevens & Ruxton, 2019).

MATERIAL AND METHODS

We undertook a field predation experiment, in which artificial 'caterpillars' (paper tubes baited with a mealworm) were placed on bramble leaves and left exposed to wild avian predators. In two treatments, prey were rotated on the sagittal axis manually at regular intervals to maintain a body orientation with the longitudinal axis either parallel or perpendicular to the sun. Time to predation was recorded as a measure of camouflage effectiveness.

TARGET DESIGN

Prey targets consisted of paper tubes 25 mm long and 7.86 mm in diameter, with optimal camouflage for the experimental light environment and background, designed and constructed following the methods of Cuthill *et al.* (2016), described in full in the Supporting Information (Appendix S1). An optimal countershading gradient was constructed for the experiment time and location (Clyne Valley Country Park, Swansea, UK: 51°36′23″N, 4°00′06″W) and printed on paper tubes in a colour that matched the average colour of the bramble *Rubus fruticosus* leaves used for presentation of stimuli.

PROCEDURE

The experiment ran over ten blocks on ten sunny days (16, 21–23 and 27–30 October and 3 and 4 November 2019). In each block, 30 targets (15 in each orientation treatment) were placed on bramble leaves ≤ 3 m either side of a 100-m-long transect. The transect was in an area of closed scrubland, selected because it had bramble plants on both sides of a path and had less than one person per hour foot traffic. The location has a relatively high density of insectivorous birds, providing the necessary levels of predation, with species such as the Eurasian wren (*Troglodytes troglodytes*), robin (*Erithacus rubecula*), blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*) seen foraging on or near the targets during the course of the experiment. The experimenter was vigilant to the possibility of being followed by individual predators to locate prey, but this was not noticed.

At the start of each block, the experimenter placed targets on bramble leaves by first identifying a suitable bramble leaf. The criteria were approximate horizontal orientation with respect to the ground, a minimum of 50 mm in width to ensure that the leaf remained the immediate background of prey as they were rotated, in a position that would not become shaded throughout the course of the experiment, and without any obvious damage or discoloration. A target was selected at random from a well-mixed box, with the target identity code printed inside the tube randomly assigning orientation treatment to the selected bramble leaf. A mealworm (*Tenebrio molitor*) larva, killed by freezing at –80 °C and then thawed, was positioned at one end of the paper cylinder, with ~2 mm protruding. This served as an edible reward for avian predators, with avian predation on the mealworm recorded as the measure of target visibility. The mealworm was attached to the inside of the tube by sliding a 25-mm-long stainless-steel dressmaking pin first through the thorax of the mealworm, then through the ventral inside surface of the target and then the bramble leaf, positioning the target in the approximate centre of the leaf. Targets

in the perpendicular treatment were oriented with the longitudinal axis of the tube 90° to the direction of the sun (Fig. 1). Targets in the parallel treatment were oriented with the mealworm end of the tube pointing towards the sun. This was done manually using the experimenter's estimate of the position of the sun. The location of each target was recorded on a hand-drawn map to aid target retrieval.

Targets were left exposed to predation for ~2 h either side of solar noon. During the experiment, solar noon varied minimally between 11.59 and 12.02 h (www.solar-noon.com); hence, in each block the experimenter began placing targets at 09.40 h, with it taking ~20 min to place all targets out. Mealworm predation was then checked every hour starting on the hour over a period of 4 h (checks beginning at 11.00, 12.00, 13.00 and 14.00 h). At each check, the target was scored as predated if the mealworm had been removed completely or partly. The experimenter assessed whether non-avian predation might have occurred by looking for slime trails left by gastropods or hollow exoskeletons left by arthropods. If the target was not at the expected location, possibly because of disturbance by wind, animals or the experimenter, or because of experimenter error in relocating the target, the experimenter searched thoroughly beneath the expected target location. If the target was found with the pin present but mealworm missing, it was recorded as predated. If the mealworm was still present, it was replaced on the bramble leaf and not recorded as predated. If the target could not be found or if the pin and mealworm were missing, it was censored from the analysis.

At each check, every target that had not been predated was rotated to maintain perpendicular or parallel alignment to the direction of the sun.

ANALYSIS

The observations of multiple species foraging on prey and that predators did not follow experimenters to locate prey, along with the timing of the experiment outside the breeding season when few individuals are territorial, give confidence that data do not exhibit a high degree of pseudoreplication (i.e. total predation owing to a very small number of individual predators).

Data were analysed using Cox proportional hazards regression (Cox, 1972) to test how prey orientation influenced target survival. Prey orientation was included as a categorical predictor (perpendicular vs. parallel) and block number as a continuous predictor. Analyses were conducted using the *survival* (Therneau & Lumley, 2020) and *rms* (Frank & Harrell, 2019) packages for R v.3.6.1 (R Core Team, 2018).

RESULTS

The weather remained sunny throughout the 4 h duration of all blocks, with only fleeting cumulus cloud presence. In total, 11 targets were lost (five parallel and six perpendicular; difference not significant). Eleven targets oriented parallel to the direction of the sun were predated by birds, whereas 38 targets with perpendicular orientation to the sun were predated (Fig. 2), a significant difference [Wald = 18.71, hazard ratio = 0.25 (95% confidence interval 0.13–0.50), $Z = 3.999$, $P = 0.00006$]. The proportional hazard assumption of Cox models was not violated ($P > 0.05$). There was a non-significant trend towards attack rates increasing in later blocks [hazard ratio = 1.09 (95% confidence interval 0.99–1.21), $Z = 1.780$, $P = 0.075$].
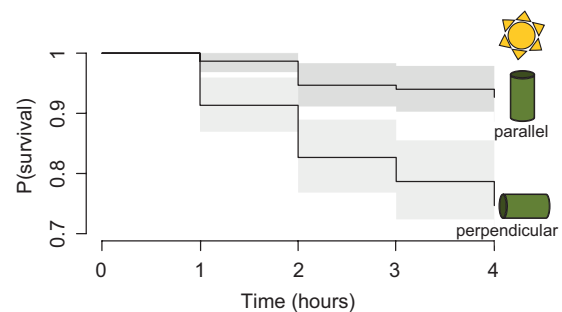

Figure 1. Examples of targets placed *in situ* in the two orientation conditions with respect to the direction of the sun: parallel or perpendicular. Suitable photographs of targets *in situ* were not taken during the experiment. These images were obtained at solar noon on 18 February 2021, when the sun is in the same position as on 25 October. Hence, we used the 25 October countershading pattern to make the targets shown in the figure. Given that the colour of bramble leaves differs in autumn and late winter, for illustrative purposes we recalculated the average bramble colour using the same methods and used this to print targets.

Figure 2. The survival probability of prey oriented parallel and perpendicular to the direction of the sun. Shaded areas denote 95% confidence intervals.

DISCUSSION

Our experiment addressed the importance of positional behaviour for camouflage (Stevens & Ruxton, 2019; Rowland *et al.*, 2020). We found that bilaterally symmetrical prey with bilaterally symmetrical background-matching countershading coloration were an estimated 3.93 times more likely to avoid avian predation when their longitudinal axis was oriented towards the sun compared with being oriented perpendicular to the sun. This confirms, in an ecologically relevant scenario using wild avian predators, the findings of computer based experiments with human predators (Penacchio *et al.*, 2017), light field modelling (Penacchio *et al.*, 2015a) and comparative analysis (Kamilar & Bradley, 2011).

The targets were designed to have optimal camouflage on bramble leaf backgrounds at solar noon at the location and light environment where the experiment took place when oriented with the longitudinal axis parallel to the direction of the sun. In this orientation, the similarity of the target colour to the background colour is maximized, the target's internal contrast when viewed by predators from all angles is minimized, and shadows falling on the left and right ventral surfaces will have been approximately symmetrical. Over the period when the experiment took place, the altitude of the sun at solar noon varied between 19 and 28°; hence, when viewed with the sun behind the predator, perpendicularly oriented targets had a large surface area almost fully illuminated, with no dorsal shadow cast (Fig. 1). Viewed from above, a shadow was visible on the side of the prey facing away from the sun. Thus, from these angles a predator would view a gradation in lightness over the body of the target created either by the countershading pattern or a shadow cast on an area not counteracted by countershading. This gradation would be expected to reduce the effectiveness of all the main mechanisms by which countershading might promote camouflage, including: (1) reduction of two-dimensional background matching viewed from above; (2) reduction of 3-D background matching viewed from the side; and (3) increased conspicuousness of 3-D cues to target shape and form (Kelley *et al.*, 2017; Ruxton *et al.*, 2019). With the sun in front of the predator, target radiance was much lower than the radiance of the sun, silhouetting the target and resulting in poor background matching. Additionally, perpendicular targets cast larger shadows on the leaf background, which might also have contributed to increased visibility. Most bilateral animals will cast larger shadows on substrates as they orient away from the sun, because transverse cross-sections generally have a smaller area than sagittal cross-sections. The effect on visibility of shadows cast by animals in

backgrounds has not been investigated extensively (Stevens & Ruxton, 2019). It is plausible that they are a useful cue in environments where shadows cast by animals are conspicuous or contain relevant shape information. All these effects on visibility are expected to occur to some degree for other simple and complex bilaterally symmetrical body shapes, although for some shapes, such as flat surfaces (e.g. lepidopteran wings), the body rotations that influence crypsis are expected to differ.

Comparative work shows that over evolutionary timescales, camouflage often adapts to the light environment experienced by animals in a way predicted by theory (Kamilar & Bradley, 2011; Santana *et al.*, 2011; Allen *et al.*, 2012; Ancillotto & Mori, 2017; Smithwick *et al.*, 2017). However, for most animals, camouflage coloration is fixed over short-term changes in the direction and intensity of light. Our result suggests that variable light environments mean that camouflage effectiveness is dependent on orientation behaviour (Kiltie, 1988; Rowland *et al.*, 2008). To gain the greatest camouflage benefit, bilateral animals must orient their longitudinal axis towards or away from the light source. Although the present experiment investigated only two orientations, the results of the study by Penacchio *et al.* (2017) suggest that visibility to human predators begins to increase rapidly for body azimuth, elevation or roll deviations > 15° from the reference orientation when the sun is at the zenith (elevation 90°), suggesting a tight range of body orientations where prey with optimal background matching and countershading coloration for one orientation retain effective camouflage.

The experiment was designed intentionally as an extreme scenario, testing the effect of orientation in direct light and at a time of year when the sun stays low in the sky. Nevertheless, the magnitude of the camouflage advantage for orienting parallel to the direction of light was unexpected. We would expect the orientation effect to be much reduced in overcast conditions or closed habitats where light is less directional and self-cast shadows are not so strong (Penacchio *et al.*, 2015a). We also expect the orientation effect to be smaller in latitudes and seasons when the sun tends to be closer to the zenith, because shadows will tend to be more symmetrical. However, it is worth noting that in these scenarios the sun is lower in the sky than in our experiment for a considerable portion of the day. For example, at the summer solstice, when the sun reaches its highest zenith, the sun is still below 28° for 38% of daylight hours and below 19° for 29% of daylight hours at the experimental location. There is no reason to suspect that there will be a qualitative shift in the relationship between orientation and camouflage for bilaterally symmetrical animals in environments where light is less directional. We do,

however, expect that countershading camouflage might evolve more readily and be more effective in environments where the direction, directionality and intensity of light are less variable.

Our result confirms the place of camouflage on the list of functions that could select for animal orientation behaviour and has interesting implications where these functions might work in unison or conflict. For instance, spiders (Suter, 1981), dragonflies (Tracy *et al.*, 1979), lizards (Bauwens *et al.*, 1996), tortoises (Coe, 2004) and ungulates (Hetem *et al.*, 2011) have been shown to orient to the sun to regulate the rate of solar heat gain. Basking with the long axis perpendicular to the direction of the sun maximizes the surface area exposed and, consequently, the rate of heat gain (Bulté & Blouin-Demers, 2010). Animals also adjust between perpendicular and parallel orientations to balance the rate of vitamin D_3 production vs. damaging ultraviolet absorption (Karsten *et al.*, 2009). The present result suggests that orienting perpendicular to the sun is likely to come at a cost to camouflage. Other potential drivers of orientation do not make conflicting demands. Foraging sparrows tend to orient towards the sun, possibly to facilitate detection of predators that hunt preferentially with the sun behind them to take advantage of solar glare for the prey (Carr & Lima, 2014). Organisms with simple positive or negative phototaxis, whatever its function, might also benefit from improved camouflage. The circumstances in which different functions dominate behaviour is a subject for further research.

The present experiment extends the importance of frontal plane orientation on camouflage effectiveness (Rowland *et al.*, 2008) to the sagittal plane. This is the more important plane for animals that have 'feet-down, head-up' body postures, using limbs to support the body on approximately horizontal surfaces, such as the majority of tetrapods. Some animals might be able to maintain the effectiveness of countershading camouflage while rotating away from the sun on the sagittal axis by rotating the longitudinal axis such that dark surfaces stay pointed towards the sun. It would be interesting to test this in animals that have considerable freedom of movement, but most body plans constrain longitudinal rotations to enable limbs to provide necessary support, balance and locomotion. Thus, our results predict that animals pursuing cryptic strategies should rotate on the sagittal axis to orient parallel to the sun, and those that do so will experience reduced predation. The artificial prey used in this study provide the necessary control over appearance to test the orientation effect stringently, but future work should aim to test whether real camouflaged prey with freedom of movement have reduced predation in body orientations predicted to minimize visibility.

DATA AVAILABILITY

The data from this study are available in Appendix S2.

REFERENCES

Allen WL, **Baddeley R**, **Cuthill IC**, **Scott-Samuel NE. 2012.** A quantitative test of the predicted relationship between countershading and lighting environment. *The American Naturalist* **180:** 762–776.

Ancillotto L, **Mori E. 2017.** Adaptive significance of coat colouration and patterns of Sciuromorpha (Rodentia). *Ethology Ecology & Evolution* **29:** 241–254.

Bauwens D, **Hertz PE**, **Castilla AM. 1996.** Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* **77:** 1818–1830.

Braude S, **Ciszek D**, **Berg NE**, **Shefferly N. 2001.** The ontogeny and distribution of countershading in colonies of the naked mole-rat (*Heterocephalus glaber*). *Journal of Zoology* **253:** 351–357.

Bulté G, **Blouin-Demers G. 2010.** Estimating the energetic significance of basking behaviour in a temperate-zone turtle. *Ecoscience* **17:** 387–393. doi: 10.2980/17-4-3377

Carr JM, **Lima SL. 2014.** Wintering birds avoid warm sunshine: predation and the costs of foraging in sunlight. *Oecologia* **174:** 713–721.

Červený J, **Begall S**, **Koubek P**, **Nováková P**, **Burda H. 2011.** Directional preference may enhance hunting accuracy in foraging foxes. *Biology Letters* **7:** 355–357.

Coe M. 2004. Orientation, movement and thermoregulation in the giant tortoises (*Testudo (Geochelone) gigantea*) of Aldabra Atoll, Seychelles. *Transactions of the Royal Society of South Africa* **59:** 73–77.

Cox DR. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)* **34:** 187–202. doi: 10.1111/j.2517-6161.1972.tb00899.x

Cuthill IC, **Sanghera NS**, **Penacchio O**, **Lovell PG**, **Ruxton GD**, **Harris JM. 2016.** Optimizing countershading camouflage. *Proceedings of the National Academy of Sciences of the United States of America* **113:** 13093–13097.

Donohue CG, **Hemmi JM**, **Kelley JL. 2020.** Countershading enhances camouflage by reducing prey contrast. *Proceedings of the Royal Society B: Biological Sciences* **287:** 20200477.

Frank E, **Harrell J. 2019.** *rms: regression modeling strategies*. R Package version 3.

Guilford T, **Taylor GK. 2014.** The sun compass revisited. *Animal Behaviour* **97:** 135–143.

Harrell FE. 2020. rms: Regression Modeling Strategies. R Package version 6.1-0. https://CRAN.R-project.org/package=rms

Hetem RS, **Strauss WM**, **Heusinkveld BG**, **De Bie S**, **Prins HHT**, **Van Wieren SE. 2011.** Energy advantages of orientation to solar radiation in three African ruminants. *Journal of Thermal Biology* **36:** 452–460.

Jander R. 1975. Ecological aspects of spatial orientation. *Annual Review of Ecology, Evolution, and Systematics* **6:** 171–188.

Kamilar JM, **Bradley BJ. 2011.** Countershading is related to positional behavior in primates. *Journal of Zoology* **283:** 227–233.

Kang C, **Stevens M**, **Moon J-y**, **Lee S-I**, **Jablonski PG. 2015.** Camouflage through behavior in moths: the role of background matching and disruptive coloration. *Behavioral Ecology* **26:** 45–54.

Kang C-K, **Moon J-Y**, **Lee S-I**, **Jablonski PG. 2012.** Camouflage through an active choice of a resting spot and body orientation in moths. *Journal of Evolutionary Biology* **25:** 1695–1702.

Karsten KB, **Ferguson GW**, **Chen TC**, **Holick MF. 2009.** Panther chameleons, *Furcifer pardalis*, behaviorally regulate optimal exposure to UV depending on dietary vitamin D$_3$ status. *Physiological and Biochemical Zoology: PBZ* **82:** 218–225.

Kelley JL, **Taylor I**, **Hart NS**, **Partridge JC. 2017.** Aquatic prey use countershading camouflage to match the visual background. *Behavioral Ecology* **28:** 1314–1322.

Kiltie RA. 1988. Countershading: universally deceptive or deceptively universal? *Trends in Ecology & Evolution* **3:** 21–23.

Penacchio O, **Cuthill IC**, **Lovell PG**, **Ruxton GD**, **Harris JM. 2015a.** Orientation to the sun by animals and its interaction with crypsis. *Functional Ecology* **29:** 1165–1177.

Penacchio O, **Harris JM**, **Lovell PG. 2017.** Establishing the behavioural limits for countershaded camouflage. *Scientific Reports* **7:** 13672.

Penacchio O, **Lovell PG**, **Cuthill IC**, **Ruxton GD**, **Harris JM. 2015b.** Three-dimensional camouflage: exploiting photons to conceal form. *The American Naturalist* **186:** 553–563.

Penacchio O, **Lovell PG**, **Harris JM. 2018.** Is countershading camouflage robust to lighting change due to weather? *Royal Society Open Science* **5:** 170801.

Poulton EB. 1890. *The colours of animals: their meaning and use, especially considered in the case of insects*. London: Kegan Paul, Trench Trübner, & Co.

Ramachandran VS. 1988. Perception of shape from shading. *Nature* **331:** 163–166.

R Core Team. **2018.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rowland HM, **Burriss RP**, **Skelhorn J. 2020.** The antipredator benefits of postural camouflage in peppered moth caterpillars. *Scientific Reports* **10:** 21654.

Rowland HM, **Cuthill IC**, **Harvey IF**, **Speed MP**, **Ruxton GD. 2008.** Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proceedings of the Royal Society B: Biological sciences* **275:** 2539–2545.

Ruxton GD, **Allen WL**, **Sherratt TN**, **Speed MP. 2019.** *Avoiding attack: the evolutionary ecology of crypsis, mimicry and warning signals*. Oxford: Oxford University Press.

Santana SE, **Dial TO**, **Eiting TP**, **Alfaro ME. 2011.** Roosting ecology and the evolution of pelage markings in bats. *PLoS One* **6:** e25845.

Shepard EL, **Wilson RP**, **Rees WG**, **Grundy E**, **Lambertucci SA**, **Vosper SB. 2013.** Energy landscapes shape animal movement ecology. *The American Naturalist* **182:** 298–312.

Smithwick FM, **Nicholls R**, **Cuthill IC**, **Vinther J. 2017.** Countershading and stripes in the theropod dinosaur *Sinosauropteryx* reveal heterogeneous habitats in the early Cretaceous Jehol biota. *Current Biology: CB* **27:** 3337–3343. e2.

Stevens M, **Ruxton GD. 2019.** The key role of behaviour in animal camouflage. *Biological Reviews of the Cambridge Philosophical Society* **94:** 116–134.

Suter RB. 1981. Behavioral thermoregulation: solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. *Behavioral Ecology and Sociobiology* **8:** 77–81.

Thayer AH. 1896. The law which underlies protective coloration. *The Auk* **13:** 124–129.

Therneau TM, **Lumley T. 2020.** Package 'survival'. *R Top Doc* **128:** 112.

Tracy CR, **Tracy BJ**, **Dobkin DS. 1979.** The role of posturing in behavioral thermoregulation by black dragons (*Hagenius brevistylus* Selys; Odonata). *Physiological Zoology* **52:** 565–571.

Waldschmidt S. 1980. Orientation to the sun by the iguanid lizards *Uta stansburiana* and *Sceloporus undulatus*: hourly and monthly variations. *Copeia* **1980:** 458–462.

Webster RJ, **Callahan A**, **Godin JG**, **Sherratt TN. 2009.** Behaviourally mediated crypsis in two nocturnal moths with contrasting appearance. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364:** 503–510.

Weissburg MJ. 2010. Waterborne chemical communication: Stimulus dispersal dynamics and orientation strategies in crustaceans. In: Breithaupt T. Thiel M. (eds) Chemical communication in crustaceans. New York, NY: Springer, Available at: https://doi.org/10.1007/978-0-387-77101-4_4.

White TE, **Latty T. 2020.** Flies improve the salience of iridescent sexual signals by orienting toward the sun. *Behavioral Ecology* **31:** 1401–1409.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Stimulus design.
Appendix S2. Experimental data.