

## Research



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# Evolutionary history limits species' ability to match colour sensitivity to available habitat light

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The spectrum of light that an animal sees—from ultraviolet to far red light—is governed by the number and wavelength sensitivity of a family of retinal proteins called opsins. It has been hypothesized that the spectrum of light available in an environment influences the range of colours that a species has evolved to see. However, invertebrates and vertebrates use phylogenetically distinct opsins in their retinas, and it remains unclear whether these distinct opsins influence what animals see, or how they adapt to their light environments. Systematically using published visual sensitivity data from across animal phyla, we found that terrestrial animals are more sensitive to shorter and longer wavelengths of light than aquatic animals and that invertebrates are more sensitive to shorter wavelengths of light than vertebrates. Using phylogenetically controlled analyses, we found that closed and open canopy habitat species have different spectral sensitivities when comparing across the Metazoa and excluding habitat generalists, while deepwater animals are no more sensitive to shorter wavelengths of light than shallow-water animals. Our results suggest that animals do adapt to their light environment; however, the invertebrate–vertebrate evolutionary divergence may limit the degree to which animals can perform visual tuning.

## 1. Introduction

Animals use vision for many tasks, including finding prey, avoiding toxic animals and plants, identifying predators, assessing mate quality and navigating their environment [1–5]. In many cases, the objects of interest to the animal need to be distinguished from the background [6,7]. For example, foragers more easily detect food that contrasts with the background than food that does not [8–12]. Signals that contrast with background colours and patterns are also used for mating displays [13–18]. Furthermore, many species' body colour patterns have evolved to be simultaneously cryptic to predators but conspicuous to conspecifics [19–21]. Finally, contrasting colours can improve animals' ability to learn the meaning of signals, as when chicks learn to avoid bitter, aposematically coloured food [2,3,22].

An animal's ability to detect visual information depends upon the wavelengths and intensity of light in its habitat (the 'light environment') [6,23,24]. This varies by habitat: forests and estuarine environments possess a yellow-green cast [24–26]. Likewise, blue light dominates the water column at depth [23,24]. Animals' signalling behaviours, choice of microhabitat and visual physiology are thus expected to co-evolve to suit their light environment [6].

Sighted species' photoreceptors (the light-absorbing neurons which enable vision) are theorized to have undergone adaptation to best absorb the light in their environments [23]. This process, called visual tuning, is made possible by both filtering pigments [27–35] and differences in the amino acid sequences of photosensitive proteins called opsins [23]. Visual tuning shifts wavelengths of maximum sensitivity in species as diverse as birds, fish and mammals [23,36–46]. Although visual tuning has been extensively studied in fish [47,48], a systematic study of visual tuning in terrestrial animals has not yet

occurred; neither have terrestrial animals been systematically compared to aquatic species. Aquatic and terrestrial animals are found in a variety of light environments, and multiple phyla have transitioned from water to terrestrial habitats. Additionally, studies of animals that transition from aquatic larvae to terrestrial adults have found that these species change their visual pigment expression patterns to match their changing light environment [49–53]. Understanding whether phylogeny constrains the extent of visual tuning, particularly during these water-to-land transitions, is critical for understanding the evolutionary ecology of animal vision.

If opsin tuning faces phylogenetic constraints, the evolutionary history of vision may have shaped the degree to which phyla have adapted to their light environments. The types of opsins differ between chordates and other phyla [54]. Chordates use c-opsins in cilia-bearing photoreceptors to transduce photons into vision, while non-chordate animals use r-opsins in rhabdomere-bearing photoreceptors [55]. C- and r-opsins diverged before 400 Ma, were probably both present in the urbilaterian [55], and may have induced different degrees of visual tuning between chordates and non-chordates.

The diverse habitats in which animals live, combined with the long evolutionary history of visual pigments, lead to several questions. First, have transitions from aquatic to terrestrial habitats influenced species' visual sensitivities? And, are differences in animals' visual sensitivities associated with the c-opsin/r-opsin divergence? Second, do animals that live in visual environments that filter short and long wavelengths of light, such as closed-canopy forests and estuarine habitats, see wavelengths more similarly to each other than to open terrestrial or open-water aquatic environments, in which short and long wavelengths are less (if at all) strongly filtered? And, if there is an effect of habitat greenness, is this effect outweighed by phylogeny?

To answer these questions, we performed a phylogenetically weighted systematic analysis of the maximum and minimum wavelength of visual sensitivity, as well as the range of visual sensitivity, across animals.

## 2. Material and methods

### (a) Paper selection

We conducted Google Scholar searches in October 2017 and January 2018. Our first search used the search pattern 'visual pigment' OR opsin OR 'absorbance spectrum' ' $\lambda$  max' -human -man -men -woman -women -'Homo sapiens' -disease -regeneration. Our second search used the pattern visual pigment, opsin sensitivity, absorbance spectrum. For both searches, we excluded citations and patents.

We reviewed candidate articles using a three-step process. First, we identified research articles and review papers that examined visual physiology. We screened these articles to determine that they used microspectrophotometry, electrophysiology, pigment extraction, or *in vitro* mRNA expression followed by spectrophotometry to measure visual sensitivity or visual pigment absorption from at least two animals. Finally, we only considered studies using wild caught or full-spectrum reared animals, as artificial lighting can affect visual sensitivity [56,57].

For review articles, we determined whether the authors had included measurements of the mean wavelength of peak sensitivity ( $\lambda_{\text{max}}$ ) of some population in the article's figures or tables. We downloaded the corresponding primary sources and filtered them using the process described above.

### (b) Visual pigment sensitivity data

We recorded the (1) mean wavelength of peak sensitivity ( $\lambda_{\text{max}}$ ) for each visual pigment measured; (2) number of animals measured ( $n$ ); (3) standard deviation of the mean  $\lambda_{\text{max}}$  (s.d.) (when available) and (4) where animals were caught (when available). We calculated sampling error for  $\lambda_{\text{max}}$  when possible.

### (c) Habitat data

We classified each species using the following standardized data sources: field guides [58–60], public databases (BugGuide, bugguide.net, Butterflies and Moths of North America, butterfliesandmoths.org, FishBase fishbase.org, SealifeBase sealifebase.org, IUCN Redlist iucnredlist.org) and online encyclopaedias including Animal Diversity Web (animaldiversity.org) and Encyclopedia of Life (eol.org). We classified species as terrestrial or aquatic and then defined terrestrial sub-habitats based on canopy density. Rainforest and temperate forest were designated as 'closed' habitats; woodland as 'intermediate' canopy density; and shrubland, grassland and desert as 'open' habitats [25].

Aquatic habitats included river, stream, pond, lake, coastal, estuarine, open-water marine, bottom-dwelling marine, abyssopelagic, abyssodemersal, bathypelagic and bathydemersal habitats. We recategorized these habitats into three habitat types based on salinity. River, stream, pond and lake habitats were considered 'freshwater' habitats; coastal, near shore and estuarine animals were considered 'coastal', and other open-water and bottom-living, non-coastal marine animals were considered 'other marine'. We also recategorized these habitats into two habitat types based on whether light was abundant or not. Deep-water, abyssopelagic, abyssodemersal, bathypelagic and bathydemersal habitats receive little or no sunlight due to their depth in the water column and were considered 'lightless' habitats. All other habitats were considered 'lit' habitats.

Finally, we used FishBase, SealifeBase or field guides to identify the minimum and maximum depths for each species. We then used these data to calculate average depth per species ( $D_{\text{average}} = (D_{\text{max}} + D_{\text{min}}) \times 2^{-1}$ ).

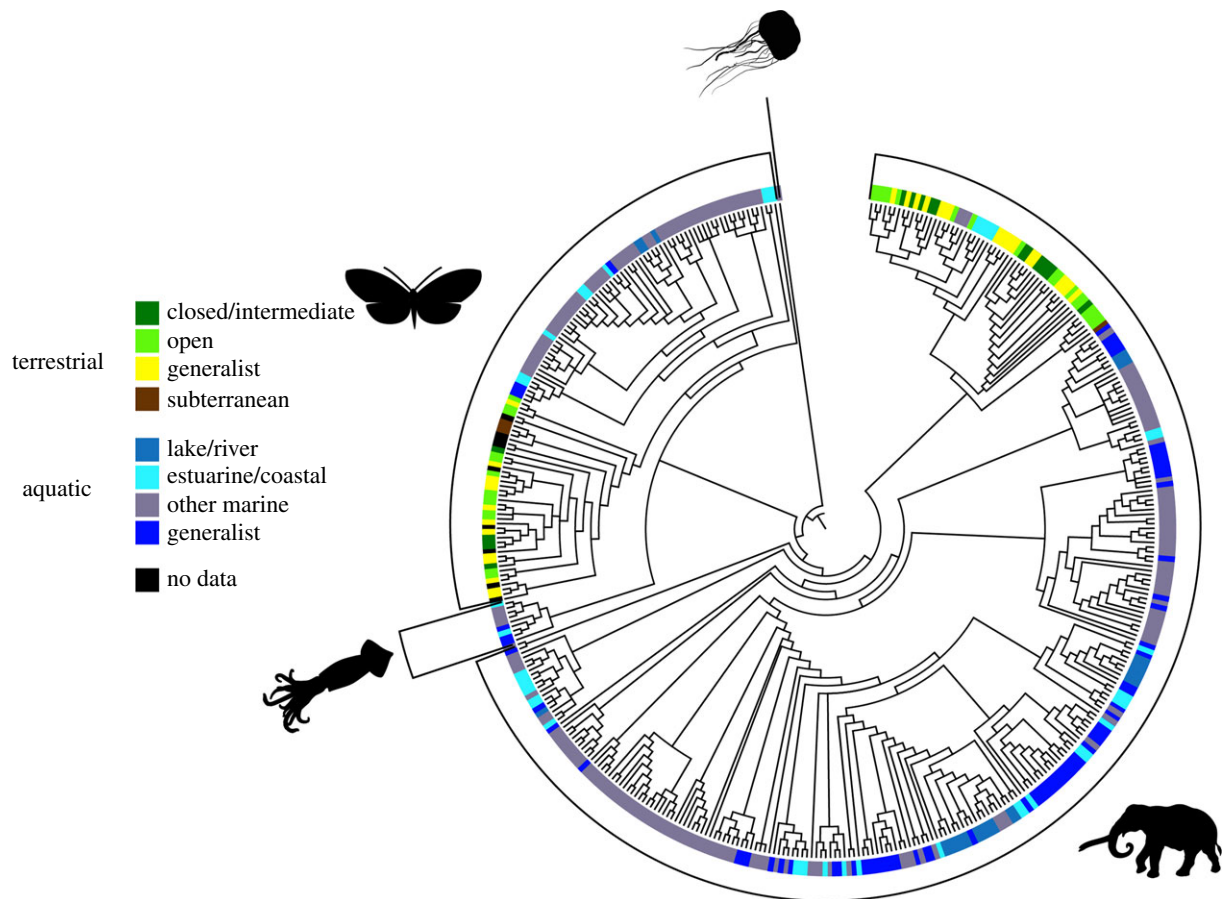
### (d) Phylogenetic control

To control for the effect of phylogeny on visual sensitivity we built a phylogenetic tree of all animals in our analysis (figure 1). We acquired data from the Open Tree of Life (tree.opentreeoflife.org) database using the function `tnrs_match_names` in the R package `rotl` [61]. We generated a phylogenetic tree using default arguments (`context_name = 'All life'`, `do_approximate_matching = TRUE`, `ids = NULL`, `include_suppressed = FALSE`), and excluded species flagged as *incertae sedis* (25 species) and species which had no sequencing data in the Open Tree of Life database (six species). We created an induced subtree with the resulting data using the function `tol_induced_subtree` in the package `rotl`.

We used the root function in *ape* [62] to root the tree using *S. cerevisiae* (ottid: 5262624) from tree.opentreeoflife.org) as the outgroup. We computed branch lengths using the `compute.brln` function in *ape* using default parameters (`method = 'Grafen'`, `power = 1`). Finally, we randomly resolved polytomies using the `multi2di` function in *ape* with default parameters (`random = TRUE`, `equiprob = TRUE`). Subtrees of the primary tree were constructed as needed using the `drop.tips` function in *ape*.

### (e) Statistical analyses

We first determined whether broad habitat or lineage influences the longest  $\lambda_{\text{max}}$ , shortest  $\lambda_{\text{max}}$ , and range of  $\lambda_{\text{max}}$ . As there was only one transition between invertebrates and vertebrates, and only a few (three) transitions between aquatic and terrestrial habitat, phylogenetic controls would have been underpowered,



**Figure 1.** Our phylogeny of species used in the meta-regressions. Both chordates and non-chordates experienced transitions from aquatic to terrestrial environments, and terrestrial chordates experienced a return to aquatic environments from terrestrial environments. Silhouettes representing sampled Metazoan phyla, clockwise from top: jellyfish: cnidarians; elephant: chordates; squid: mollusks; butterfly: arthropods. (Online version in colour.)

so we used the non-phylogenetically controlled glm function in R to construct generalized linear models with the formula  $\lambda_{\max} \sim \text{broad habitat} \times \text{lineage}$ .

We then subset our overall dataset for terrestrial animals and conducted a set of statistical analyses specific to terrestrial animals. To determine whether phylogeny influenced the effect of terrestrial habitat canopy type (closed; intermediate, open; or generalists, i.e. animals living in both closed or intermediate and open canopy habitats) on longest  $\lambda_{\max}$ , shortest  $\lambda_{\max}$ , and range of  $\lambda_{\max}$ , we used the *phylolm* function in the *phylolm* [63] package for R with the formulae  $\lambda_{\max} \sim \text{closed terrestrial} + \text{open terrestrial}$  and  $\lambda_{\max} \sim \text{intermediate terrestrial} + \text{open terrestrial}$  fitted using the lambda model and with a bootstrap of 100. However, since there were only two species that were intermediate habitat specialists, and they had similar visual spectra to those in closed canopies, we combined closed and intermediate habitat treatments into a single treatment and re-ran the *phylolm* using the new treatment levels (closed\_intermediate versus open generalist).

We then subset our overall dataset for aquatic animals and conducted a set of statistical analyses specific to aquatic animals. We examined the effects of depth on visual sensitivities of aquatic animals. To determine whether phylogeny could explain extant differences in minimum, maximum, or average depth of habitat among longest  $\lambda_{\max}$ , shortest  $\lambda_{\max}$ , and range of  $\lambda_{\max}$  among aquatic species, we used the *phylolm* function in the *phylolm* package for R with the formula  $\lambda_{\max} \sim \text{depth}$  fitted using the lambda model and with a bootstrap of 100. For these models, we used a subtree of our overall phylogenetic tree (see above), which omitted all terrestrial species.

Finally, we subset our overall dataset for open terrestrial, closed terrestrial animals and lit habitat aquatic (both freshwater and coastal) animals and conducted the following analyses. To

determine whether phylogeny could explain extant differences in longest  $\lambda_{\max}$ , shortest  $\lambda_{\max}$ , and range of  $\lambda_{\max}$  between animals living in these four habitat types we used the *phylolm* function in the *phylolm* package for R using the formulae  $\lambda_{\max} \sim \text{coastal-aquatic} + \text{freshwater-aquatic} + \text{terrestrial-closed}$  and  $\lambda_{\max} \sim \text{coastal-aquatic} + \text{freshwater-aquatic} + \text{terrestrial-open}$ , fitted using the lambda model and with a bootstrap of 100.

### 3. Results

Our dataset included 1114 opsins from 446 species, from a total of 156 articles (See the electronic supplementary material: electronic supplementary material, table S1). Of these, 868 opsins were recorded from 355 aquatic species, and 246 opsins were recorded from 91 terrestrial species.

There are few (three) transitions from either aquatic to terrestrial species or from terrestrial to aquatic species, with two of these transitions in the vertebrate dataset and one in the invertebrate dataset (figure 1) and one transition from invertebrate species to vertebrate species. Controlling phylogeny in these cases would result in an unacceptably small sample size, so we used the glm function in R to construct generalized linear models with the formula  $\lambda_{\max} \sim \text{broad habitat} \times \text{lineage}$ .

#### (a) Terrestrial species were maximally sensitive to longer wavelengths of light than aquatic species

Terrestrial species were maximally sensitive to longer wavelengths of light than aquatic species, independent of lineage



(invertebrate or vertebrate) (GLM,  $n = 433$ : habitat  $p = 3.83 \times 10^{-8}$ ,  $t = 5.600$ , lineage  $p = 0.309$ ,  $t = -1.019$ ; interaction:  $p = 0.595$ ,  $t = -0.532$ ;  $\lambda_{\max}$  longest long-wavelength terrestrial species:  $535 \pm 41.6$  nm, aquatic species:  $506 \pm 30.6$  nm, invertebrates:  $513 \pm 38.9$  nm, vertebrates:  $512 \pm 33.0$  nm) (figure 2a; electronic supplementary material, table S2).

### (b) Terrestrial species saw shorter wavelengths of light than aquatic species

Terrestrial species were maximally sensitive to shorter wavelengths of light than aquatic species; however, there was a significant interaction between habitat and lineage: aquatic vertebrates were more sensitive to short wavelengths than aquatic invertebrates and terrestrial invertebrates were more sensitive to short wavelengths than terrestrial vertebrates (GLM,  $n = 433$ : habitat  $p = 0.045$ ,  $t = -2.012$ , lineage  $p = 0.051$ ,  $t = 1.960$ , interaction:  $p = 2.34 \times 10^{-3}$ ;  $t = -3.061$ ;  $\lambda_{\max}$  shortest short-wavelength terrestrial species:  $442 \pm 79.2$  nm, aquatic species:  $476 \pm 39.3$  nm; invertebrates:  $466 \pm 70.2$  nm, vertebrates:  $471 \pm 41.3$  nm; figure 2b; electronic supplementary material, table S2).

### (c) Terrestrial species and invertebrates saw a larger range of wavelengths of light than aquatic species and vertebrates

Terrestrial species saw a larger range of wavelengths of light than aquatic species. In addition, there was a significant interaction between habitat and lineage: aquatic invertebrates saw a narrower range of wavelengths of light than aquatic vertebrates, but terrestrial invertebrates saw a broader range of wavelengths of light than terrestrial vertebrates. (GLM,  $n = 443$ : habitat  $p = 2.51 \times 10^{-6}$ ,  $t = 4.772$ , lineage  $p = 0.03$ ,  $t = -2.184$ , interaction:  $p = 0.00261$ ;  $t = 2.232$ ;  $\lambda_{\max}$  range terrestrial species:  $92 \pm 85.6$  nm, aquatic species:  $30.9 \pm 51.6$  nm; invertebrates:  $47.2 \pm 80.4$  nm, vertebrates:  $40.7 \pm 56.7$  nm; figure 2c; electronic supplementary material, tables S3 and S4).

### (d) Forest-woodland and open habitat species have similar spectral sensitivities

When considering all terrestrial species, including generalists, when examining the effect of more fine-grained habitat on visual sensitivity, we found that there was an influence of phylogenetic structure on the longest wavelengths of light ( $\lambda_{\text{Pagel}} = 0.878$ ) and on the range in wavelengths of light ( $\lambda_{\text{Pagel}} = 0.823$ ) that animals can best see. However, we found that there was no effect of phylogenetic structure on the shortest wavelengths of light ( $\lambda_{\text{Pagel}} \ll 0.01$ ) that animals can best see. We found that there was no effect of tree canopy openness on longest  $\lambda_{\max}$ , shortest  $\lambda_{\max}$ , and range of  $\lambda_{\max}$  (electronic supplementary material, table S3).

### (e) Habitat depth did not influence sensitivity to long, short or range of wavelengths of light

When examining the effect of minimum depth on visual sensitivity, we found that there was no influence of phylogenetic structure on the effect of minimum depth had on the longest wavelengths of light aquatic animals could see ( $\lambda_{\text{Pagel}} \ll 0.01$ ). There was an influence of phylogenetic structure on the effect

that maximum and average depth had on the longest wavelengths of light aquatic animals could see (electronic supplementary material, table S5). Likewise, there was an influence of phylogenetic structure on the effect of minimum, maximum and average depth had upon the shortest wavelengths and range of wavelengths of light that aquatic animals could see (electronic supplementary material, table S5). We found that neither minimum, maximum, nor average depth influenced the longest, shortest or range in  $\lambda_{\max}$  that a species could see (see the electronic supplementary material, figures S2–S4, electronic supplementary material, table S5).

### (f) Animals in coastal and freshwater habitats saw shorter wavelengths of light while animals in forest + intermediate or open-canopy habitats saw longer wavelengths of light

When examining the effect of fine-grained habitat on visual sensitivity, we found that there was no influence of phylogenetic structure on the longest or shortest wavelengths of light animals could see ( $\lambda_{\text{Pagel}} \ll 0.01$ ). We found that coastal and freshwater animals had similar longest  $\lambda_{\max}$  and shortest  $\lambda_{\max}$ . The longest and shortest  $\lambda_{\max}$  of animals living in coastal and freshwater habitats were shorter than that of animals living in closed or open terrestrial habitats. We found that, when we excluded habitat generalists from our analysis (relative to our analysis of all terrestrial animals, above), the longest and shortest  $\lambda_{\max}$  of animals living in open terrestrial habitats were shorter than that of animals living in closed habitats (figure 3 and table 1).

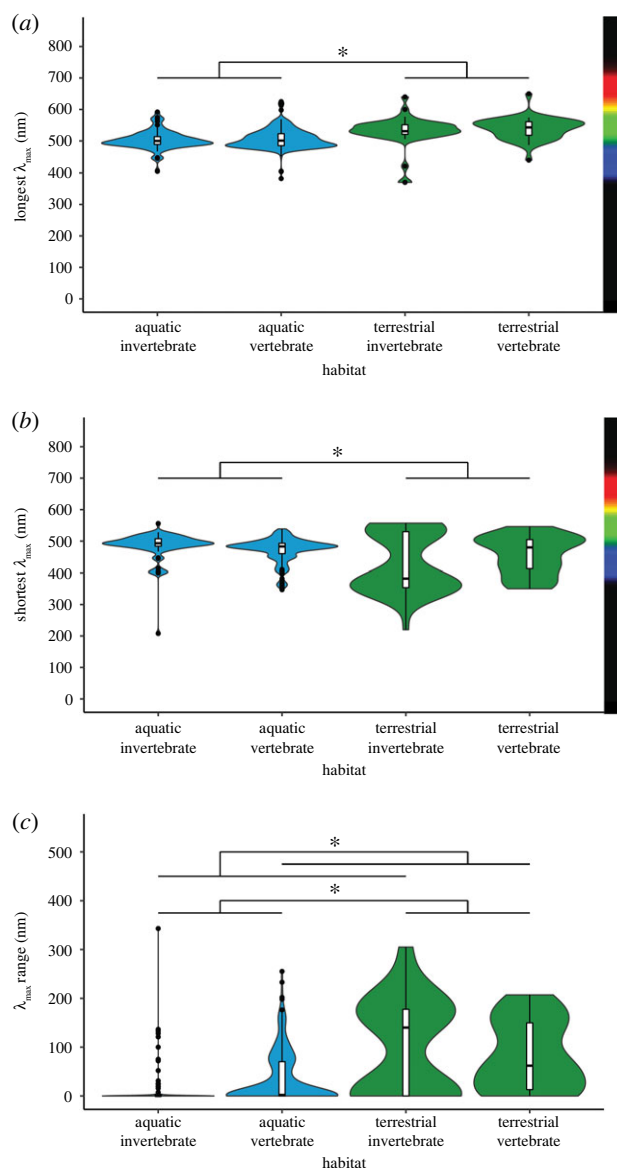
### (g) Open terrestrial animals had a broader visual range than coastal or freshwater animals

When examining the effect of fine-grained habitat on visual sensitivity, we found that there was an influence of phylogenetic structure on the range of wavelengths of light animals could see ( $\lambda_{\text{Pagel}} = 0.226$ ). We found that open terrestrial animals had a wider visual range than aquatic freshwater or coastal animals, while there was no significant effect between any other pairs of habitats on visual range (figure 3 and table 1).

## 4. Discussion

### (a) The transition from aquatic to terrestrial habitats has influenced animal vision

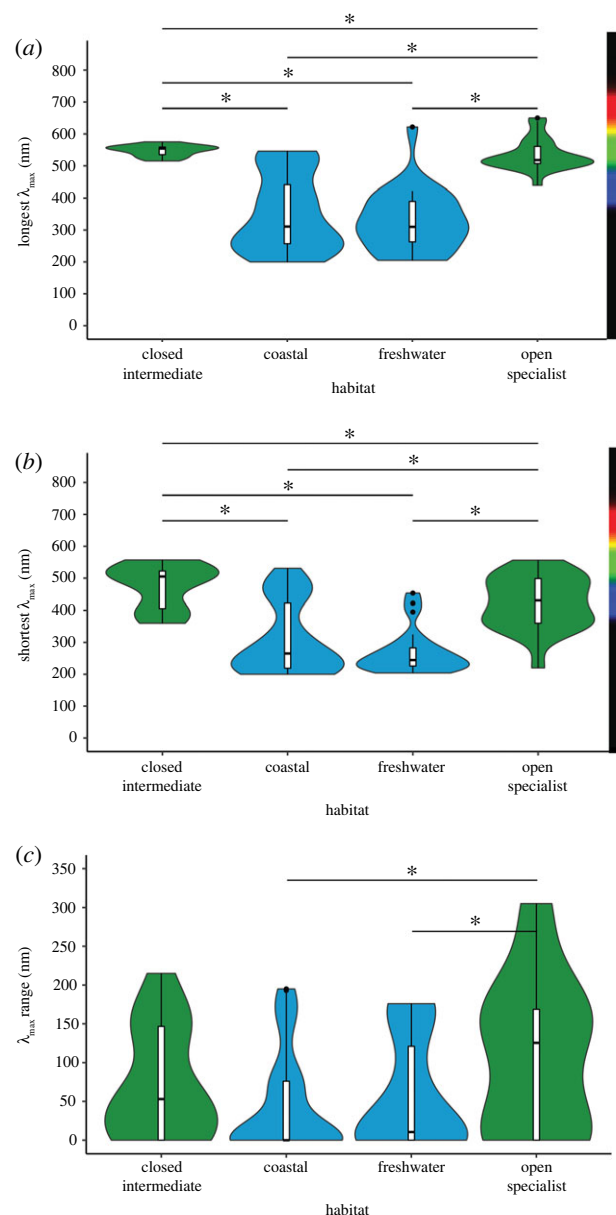
We found that terrestrial species see longer long-wavelength light and a larger range of wavelengths of light overall compared to aquatic species. Few other studies have broadly investigated the effect of the evolutionary transition between aquatic and terrestrial habitats on colour vision. However, transitions from aquatic to terrestrial life stages that lead to the development of different visual abilities can indicate the necessity of different strategies for perceiving the world [49]. Such studies have been conducted within single species: for example, in several species of dragonfly adults have short wavelength-shifted vision, among other differences [49,50], and similar transitions have been observed in southern leopard frogs [64]. Just as animal development favours the expression of environmentally matched opsins over an intra-generational time scale, our results suggest that



**Figure 2.** Effect of coarse habitat and lineage on mean visual pigment sensitivity. (a) Longest opsin: aquatic invertebrates:  $n = 78$ ,  $\mu = 503.3$  nm; aquatic vertebrates:  $n = 273$ ,  $\mu = 507.6$  nm; terrestrial invertebrates:  $n = 43$ ,  $\mu = 530.3$  nm; terrestrial vertebrates:  $n = 39$ ,  $\mu = 539.1$  nm. (b) Shortest opsin: aquatic invertebrates:  $n = 78$ ,  $\mu = 485.3$  nm; aquatic vertebrates:  $n = 273$ ,  $\mu = 473.0$  nm; terrestrial invertebrates:  $n = 43$ ,  $\mu = 430.1$  nm; terrestrial vertebrates:  $n = 39$ ,  $\mu = 456.1$  nm. (c) Opsin range: aquatic invertebrates:  $n = 78$ ,  $\mu = 18.0$  nm; aquatic vertebrates:  $n = 273$ ,  $\mu = 34.6$  nm; terrestrial invertebrates:  $n = 43$ ,  $\mu = 100.2$  nm; terrestrial vertebrates:  $n = 39$ ,  $\mu = 83.0$  nm. \* $p < 0.05$ . Analyses not controlled by phylogeny. (Online version in colour.)

evolutionary adaptation favours the use of environmentally matched opsins over an inter-generational time scale.

The results of our terrestrial versus aquatic models are congruent with the visual tuning hypothesis, which states that animal visual systems evolve to detect the light in their environments [23]. Terrestrial animals are exposed to a dynamic range of wavelengths of light that changes throughout the day, including both short- and long-wavelength light, as well as ultraviolet light in large forest gaps and open environments [25,26]. By contrast, aquatic animals, which we found to be less sensitive to long-wavelength and ultraviolet light, live in environments that are exposed to relatively less long-wavelength and ultraviolet light [24]. While our dataset did not contain large



**Figure 3.** Effect of habitat greenness on visual sensitivities. (a) Longest opsin: forest + intermediate:  $n = 14$ ,  $\mu = 547.1$  nm, s.d. = 17.71 nm; coastal:  $n = 40$ ,  $\mu = 297.3$  nm, s.d. = 72.42 nm; freshwater:  $n = 23$ ,  $\mu = 314.3$  nm, s.d. = 73.77 nm; open terrestrial:  $n = 22$ ,  $\mu = 534.1$  nm, s.d. = 49.09 nm. (b) Shortest opsin: forest + intermediate:  $n = 14$ ,  $\mu = 470.4$  nm, s.d. = 60.00 nm; coastal:  $n = 40$ ,  $\mu = 254.4$  nm, s.d. = 55.16 nm; freshwater:  $n = 23$ ,  $\mu = 261.1$  nm, s.d. = 56.52 nm; open terrestrial:  $n = 22$ ,  $\mu = 423.4$  nm, s.d. = 82.06 nm. (c) Opsin range: forest + intermediate:  $n = 14$ ,  $\mu = 76.63$  nm, s.d. = 72.61 nm; coastal:  $n = 40$ ,  $\mu = 742.88$  nm, s.d. = 70.15 nm; freshwater:  $n = 23$ ,  $\mu = 53.26$  nm, s.d. = 69.30 nm; open:  $n = 22$ ,  $\mu = 110.6$  nm, s.d. = 98.82 nm. \* $p < 0.05$ . Analyses controlled by phylogeny. (Online version in colour.)

numbers of aquatic-to-terrestrial transitions, it did contain aquatic-to-terrestrial habitat transitions in two animal phyla and encompasses transitions in both vertebrate and invertebrate taxa. Without phylogenetic controls, our coarse-grained analyses suggest that animals are likely to be maximally sensitive to wavelengths of light most often present in their environment and insensitive to wavelengths of light likely to be absent.

### (b) Canopy coverage may influence visual tuning

The results from our fine-grained habitat analyses that excluded generalists suggest that animals living in closed

**Table 1.** Effect of habitat greenness on longest  $\lambda_{\max}$ , shortest  $\lambda_{\max}$  and  $\lambda_{\max}$  range, with phylogenetic control. Numbers in bold are statistically significant.

habitats compared	$\lambda_{\max}$	s.e.	t-value	lower bound of confidence interval	upper bound of confidence interval	p-value
open versus coastal	longest	16.76	−14.13	−273.4	561.3	<b>&lt;2 × 10<sup>−16</sup></b>
open versus freshwater	longest	16.83	−11.67	−255.1	−211.3	<b>&lt;2 × 10<sup>−16</sup></b>
open versus closed + intermediate	longest	21.59	0.602	−29.47	−187.3	<b>&lt;2 × 10<sup>−16</sup></b>
coastal versus freshwater	longest	16.53	1.032	−16.38	46.185	0.304
coastal versus closed + intermediate	longest	19.61	12.74	216.7	284.16	<b>&lt;2 × 10<sup>−16</sup></b>
closed versus freshwater	longest	21.41	−0.602	−61.47	23.807	<b>&lt;2 × 10<sup>−16</sup></b>
open versus coastal	shortest	17.02	−9.934	−198.0	−136.8	<b>2.3 × 10<sup>−16</sup></b>
open versus freshwater	shortest	19.12	−8.492	−191.7	−128.0	<b>2.7 × 10<sup>−13</sup></b>
open versus closed + intermediate	shortest	21.92	2.144	2.180	89.627	<b>0.03456</b>
coastal versus freshwater	shortest	16.78	0.399	−30.83	35.106	0.691
coastal versus closed + intermediate	shortest	19.91	10.85	176.1	249.89	<b>&lt;2 × 10<sup>−16</sup></b>
closed versus freshwater	shortest	21.73	−9.635	−244.1	−172.5	<b>1.0 × 10<sup>−15</sup></b>
open versus coastal	range	28.33	−3.07	−143.1	−21.56	<b>0.0028</b>
open versus freshwater	range	32.72	−2.23	−133.4	−14.17	<b>0.0279</b>
open versus closed + intermediate	range	25.61	−1.32	−75.37	13.5	0.1905
coastal versus freshwater	range	21.68	0.641	−14.41	54.18	0.5228
coastal versus closed + intermediate	range	31.14	1.71	−1.917	104.5	0.0907
closed versus freshwater	range	35.17	−1.12	−94.61	39.09	0.2262

habitats see longer wavelengths of light than animals living in open habitats. This suggests the forest canopy, which admits mostly middle-wavelength light [25,26], influences terrestrial animals' visual tuning, a result consistent with studies performed in birds and nocturnal mammals [65,66]. The loss of this effect once generalists are considered may reflect the wide visual range required of animals that transition between open and forest habitats, or the relatively low sampling of forest and open habitat terrestrial animals.

Additionally, animals may choose to use light microhabitats which are suitable to their current visual physiology. Endler & Théry [18] observed that forest birds use areas in which they are most conspicuous to advertise to potential mates. Some species also modify their habitats to improve the visibility of their visual displays. For example, male golden-collared manakins clean the arenas they use to court females to improve their plumage's contrast against the arena background [67]. Arena cleaning also improves white-bearded manakins' ability to detect predators [68]. In such cases, evolution may be driving site preferences which match vision rather than driving vision to match site preferences, a complete reversal of the mechanism investigated in our study.

### (c) The ciliary/rhabdomeric opsin divergence may impact the wavelengths of light that animals can see

We found that invertebrates see a broader range of wavelengths of light than vertebrates. Invertebrates, which use rhabdomeric photoreceptors for vision, have opsins that are maximally sensitive to ultraviolet light [31,69–74]. By contrast, comparatively few vertebrates, which use ciliary photoreceptors for vision, have opsins that are maximally sensitive to UV light, although several species of birds and fish are sensitive to

ultraviolet light [40,75–77]. Additionally, many mammals have corneas that selectively filter UV, inhibiting their ability to see those wavelengths [78,79]. Both ciliary and rhabdomeric opsins are thought to have been present in the urbilaterian, the common ancestor of all modern animals save sponges, cnidarians, placozoans and ctenophores [55]. The emergence in chordates of ciliary opsins for vision rather than photoentrainment represents a singular event, one that may have also heralded differences in visual perception associated with reduced sensitivity to short wavelengths of light.

### (d) Phylogeny may mitigate the effect of habitat

In many of the analyses where we found phylogenetic signatures in our data, we did not recover effects of habitat on visual sensitivity. This may suggest that evolutionary history limits animals' ability to perform visual tuning, especially within coarse-grained habitats. Our findings differ from those of many studies looking at individual animal clades. For example, a 2018 survey found that fish living at depth were found to have reduced chromacy even after controlling for phylogeny [47]. Likewise, a historic study of cottoid fish in Lake Baikal found a correlation between lambda-max and habitat depth when not controlling for phylogeny [80]. Additionally, studies of marine mammals found that species that forage near the surface have visual pigments resembling those of terrestrial mammals [81]. By contrast, those that foraged at depth had visual pigments with amino acid substitutions that shifted the  $\lambda_{\max}$  towards shorter wavelengths [81]. The photoreceptors of nocturnally foraging terrestrial animals that live in forested habitats likewise have peak absorbances which match the peak flux of light in the night-time forest [66]. Bird species which live in forests have higher normalized expression of long-wave opsin genes compared to bird species which live in open habitats, and bird species native to open habitats

have higher normalized expression of ultraviolet-sensitive opsin genes compared to forest birds [65]. This opens a potential, additional route allowing visual tuning to exist without the need for changes to the wavelength of maximum sensitivity. However, our findings of limited spectral tuning in fine-grained habitats in terrestrial settings do correspond to those of a recent (2021) review of terrestrial and insect colour vision which suggests that there are not functional differences in the kinds of opsins expressed by insects [82]. That differences in range of  $\lambda_{\max}$  were maintained between open terrestrial and freshwater animals and between open terrestrial and coastal animals after phylogenetic control (table 1) suggests that there is at least some effect of habitat on visual sensitivity.

The effect of the c-opsin/ r-opsin divergence on vision is difficult to discern in a phylogenetic context since this transition happened once and maps on to the metazoan phylogenetic tree. However, both invertebrate and vertebrate visual pigments are structurally well-conserved, and changes in the polarity of specific amino acid residues leads to similar shifts in the wavelength of maximum sensitivity in both vertebrates and invertebrates [83]. Retinal is covalently bound to opsin via a Schiff base and the charges of the amino acid residues near the Schiff base influence the ability of retinal to change conformation and  $\lambda_{\max}$  of the associated opsin [84,85], which has been experimentally confirmed using directed mutagenesis [37,86,87]. Opsin sequence duplication followed by divergence has been observed in many taxa, especially among invertebrates, though electrophysiological investigation of the effects of these sequence divergences has been under-studied [50]. Thus, opsin evolutionary history such as mutation biases and duplications may account for the effect of phylogeny on visual ability in our analyses. Future research should consider whether there are inherent differences in the electronic charge of the binding pocket between ciliary and rhabdomic type opsins and should examine the physiological consequences of sequence divergence. Additionally, studies examining whether non-opsin means of visual tuning, including the differential absorption of light by screening pigments, differ between animals which use ciliary and rhabdomic opsins and which live in the same light environment may prove particularly illuminating.

### (e) Expanding invertebrate opsin data may offer new insights into spectral tuning

Our study incorporates the visual sensitivities of both invertebrates and vertebrates into its analyses. However, the

number of sighted aquatic vertebrate species, particularly ray-finned fishes, are relatively overrepresented, considering the number of species of sighted invertebrates and sighted terrestrial vertebrates that exist. Invertebrates, especially arthropods, have been found to exhibit striking diversity in the wavelengths of light they can best see [50,73,88]. Future studies focusing on documenting visual diversity among invertebrate species and including a greater number of phyla that have undergone aquatic to terrestrial transitions (Mollusca and Annelida, for example) may paint a fuller picture of visual adaptations across the Metazoa and broaden our understanding of constraints to visual tuning.

## 5. Conclusion

Here we used visual sensitivity data from nearly 450 animal species and four phyla to conduct a systematic survey of the effects of habitat light on the wavelengths of light animals are most sensitive to. We found that terrestrial animals and aquatic animals possess different ranges of spectral sensitivity from each other, but that evolutionary processes such as the c-opsin/ r-opsin transition may have limited chordates' ability to tune their opsins to blue light. Additionally, we only recover an effect of forest canopy cover on the spectral tuning of animals living in terrestrial habitats when excluding habitat generalists. Future research should consider whether inherent differences between chordate and non-chordate opsin amino acid sequences, or downstream neural signalling, are responsible for evolutionary limitations to visual tuning.

**Data accessibility.** Data pertaining to this study are available in the electronic supplementary material [89] or from Dryad Digital Repository [90]. Code pertaining to this study is available at GitHub repository: <https://github.com/mjos-murphy/opsin-evolutionary-ecology>.

**Authors' contributions.** M.J.M.: conceptualization, data curation, formal analysis, methodology, writing—original draft; E.L.W.: conceptualization, funding acquisition, methodology, writing—original draft.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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