The visual ecology of selective predation: Are unhealthy hosts less stealthy hosts?

Authors: Nina Wale*, Rebecca C. Fuller, Sönke Johnsen, McKenna L. Turrill, Meghan. A. Duffy

*Corresponding author: Departments of Microbiology & Molecular Genetics and Integrative Biology, Program in Ecology, Evolution and Behavior, 567 Wilson Road, East Lansing, Michigan State University, MI, USA. walenina@msu.edu

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Abstract

Predators can strongly influence disease transmission and evolution, particularly when they prey selectively on infected hosts. Although selective predation has been observed in numerous systems, why predators select infected prey remains poorly understood. Here, we use a model of predator vision to test a longstanding hypothesis as to the mechanistic basis of selective predation in a *Daphnia*-microparasite system, which serves as a model for the ecology and evolution of infectious diseases. Bluegill sunfish feed selectively on *Daphnia* with a variety of parasites, particularly in water uncolored by dissolved organic carbon. The leading hypothesis for selective predation in this system is that infection-induced changes in the appearance of *Daphnia* render them more visible to bluegill. Rigorously evaluating this hypothesis requires that we quantify the effect of infection on the visibility of prey from the predator's perspective, rather than our own. Using a model of the bluegill visual system, we show that the three common parasites, *Metschnikowia bicuspidata*, *Pasteuria ramosa* and *Spirobacillus cienkowskii*, increase the opacity of *Daphnia*, rendering infected *Daphnia* darker against a background of downwelling light. As a result of this increased brightness contrast, bluegill can see infected *Daphnia* at greater distances than uninfected *Daphnia* – between 19-33% further, depending on the parasite. *Pasteuria* and *Spirobacillus* also increase the chromatic contrast of *Daphnia*. Contrary to expectations, the visibility *Daphnia* was not strongly impacted by water color in our model. Our work generates hypotheses about which parasites are most likely affected by selective predation in this important model system and establishes visual models as a valuable tool for understanding ecological interactions that impact disease transmission.

1 Introduction

When predators preferentially consume sick prey over healthy prey, a phenomenon called 'selective predation', they can substantially alter parasite transmission and evolution (Choo et al., 2003, Holt and Roy, 2007, Kisdi et al., 2013, Morozov and Adamson, 2011, Packer et al., 2003, Williams and Day, 2001). For example, when parasites need to be consumed to be transmitted (i.e., they are trophically transmitted), selective predation can promote parasite transmission; in contrast, when predators remove infectious hosts from the host population it can depress transmission and, as a consequence, alter parasite prevalence and host density (Choo et al., 2003, Packer et al., 2003). Given the strong impacts of selective predation on parasite and host fitness, we expect there to be strong selection on the traits of infected hosts that cause predators to preferentially consume them. However, in many systems, it is unclear what these traits are or by how much they increase the probability that a host will be consumed. As a result, our ability to predict when selective predation will occur, or forecast its effects on the ecological and evolutionary dynamics of infectious diseases, remains limited.

One reason predators might selectively prey on infected hosts is because infection-induced changes in the appearance of prey (which we refer to as visible symptoms) make them easier to detect. Parasites often induce changes in their hosts' appearance – altering their body condition (Sánchez et al., 2018), size (Hall et al., 2007), shape (Roy, 1993), and color (Jones et al., 2016, Thünken et al., 2019, Wale et al., 2019, Williams and Cory, 1994, Zhou et al., 2016) – and it has been hypothesized that trophically transmitted parasites manipulate their hosts so as to increase their chances of consumption (Thünken et al., 2019).

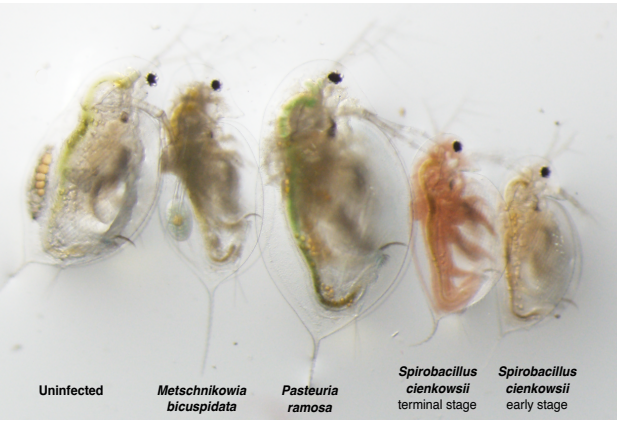

Figure 1: Parasites of *Daphnia* dramatically change their host's appearance. Infection with a variety of parasites (as labelled) induce distinctive symptoms in *Daphnia dentifera* and increase the likelihood of selective predation by bluegill sunfish (Duffy and Hall, 2008, Duffy et al., 2005). The symptoms of *Spirobacillus* infection change dramatically with infection stage.

We cannot rely on our own perception to assess whether visible symptoms impact a predator's ability to detect prey (and hence mediate selective predation), however, because humans and animals have different visual systems and therefore see objects differently. The human visual system differs from that of many animals in the number and spectral sensitivity of the photoreceptors it has. For example, humans have three photoreceptors whereas birds have four, one of which is sensitive to UV light; as a result, birds 'see' in the UV and may perceive objects very differently than humans (Olsson et al., 2018). These differences between human and animal visual systems can be even greater in environments where light behaves differently than it does on land, such as in

aquatic and foggy habitats (Cronin et al., 2014). The field of visual ecology has revealed that, because of these mismatches between human and animal visual systems, humans can overestimate the importance of visual signals that mediate ecological interactions—or, conversely, completely overlook them (Eaton, 2005, Matz et al., 2006). For this reason, we must take a 'predator's eye view' as we seek to understand if, and by how much, visible symptoms of infection alter interactions between predators and prey.

Here, we use a visual model to quantitatively examine the impact of visible symptoms on the perceptibility of infected hosts in a zooplankton-parasite system where predation is widespread, selective and has important epidemiological effects. *Daphnia* are transparent prey of visually hunting fish like bluegill sunfish (*Lepomis macrochirus*) and are host to a wide variety of parasites (Duffy et al., 2005, Mittelbach, 1984); these parasites directly influence host mortality and also increase their vulnerability to predation by bluegill (Duffy et al., 2019, Duffy and Hall, 2008, Duffy et al., 2005, Johnson et al., 2006). Selective predation by bluegill on infected *Daphnia* could be a consequence of a variety of symptoms, including changes in motility and behavior, increased size, reduced transparency, and changes in color (Fig. 1). Reduced transparency, in particular, is thought to be an important driver of selective predation and an experimental study demonstrated that the selectivity of bluegill changed with the intensity of infection (i.e., the amount of bacteria in the hemolymph that could obstruct light penetrating the host body) (Johnson et al., 2006). This study also showed that the selectivity of bluegill for infected *Daphnia* was abrogated by high concentrations of dissolved organic carbon (DOC), which alters water color (Johnson et al., 2006), further supporting the notion that visual traits mediate selective predation in this system and suggesting that environmental variation may play a role in mediating the size of its effect.

Here, we find that the reduction in transparency that occurs with infection dramatically increases the brightness contrast of *Daphnia* against their watery background and thus increases the distance at which bluegill can see *Daphnia* infected by a variety of pathogens, as compared to healthy hosts. The extent to which infection changes the brightness and color contrast of *Daphnia* varies across parasites, with the bacterium *Spirobacillus cienkowskii* having the largest impacts. Intriguingly, our model suggests that variation in water color plays a limited role in mediating selective predation in this system. Overall, our findings lend strong support to the hypothesis that selective predation by bluegill is driven by increased opacity of *Daphnia*.

2 Methods

2.1 Approach

The extent to which an object contrasts with its background determines whether it is detectable to a viewer (e.g., dark blue ink is easier to see on white paper than on black). Therefore, quantifying the contrast of an object (or target, as we shall refer to it hereafter) is the central goal of any analysis aimed at understanding how detectable a target is.

There are two ways that a target can contrast with the background—by how bright it is (brightness or achromatic contrast) and by how different it is in color (chromatic contrast) (Fig. 2AI). The target's contrast is first determined by the inherent light properties of the target and its background: how much light, and of what spectrum, does the target reflect back to the viewer's eye and how different is this light from the background? The second determinant is a function of the viewer—does the viewer have a visual system capable of detecting the contrast between the target and the background? To quantify the contrast of a target with its

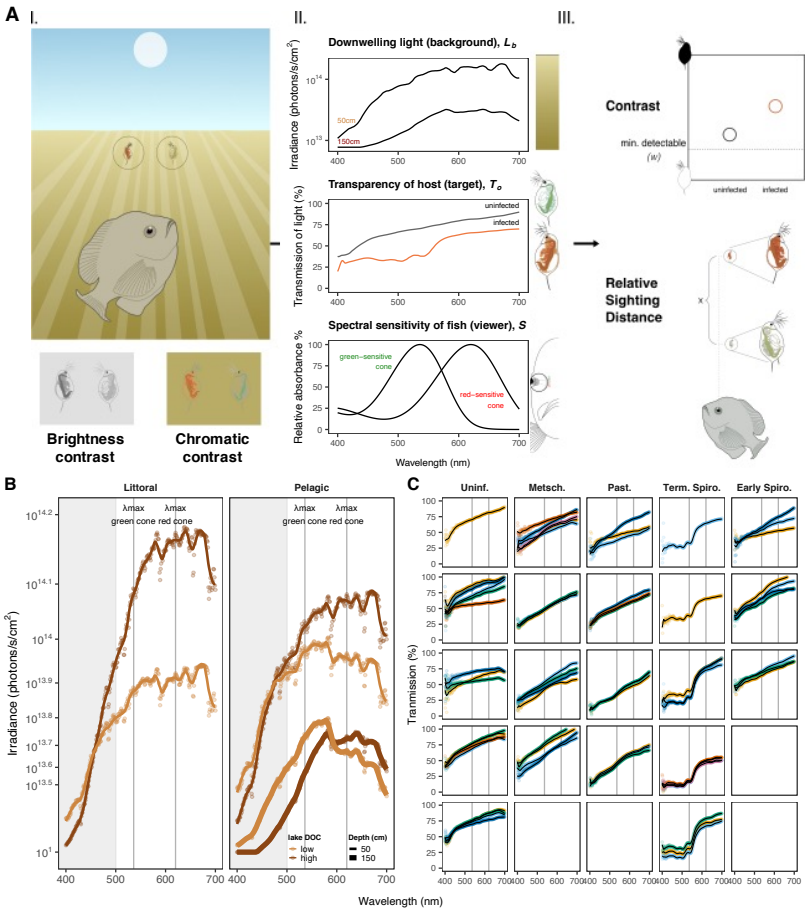

Figure 2: A visual ecology approach to understanding the impact of visual symptoms on predation. A i. To characterize how readily bluegill predators can see *Daphnia* when they are looking up at them, we quantified the brightness and chromatic contrast of *Daphnia* with the downwelling light. **ii.** To achieve this, we used spectroradiometry to measure the spectra of downwelling light in different lake environments (top panel—data displayed are those from the pelagic region of the high DOC Lake; see B), the transmittance of light through *Daphnia* tissues (middle—spectra displayed are of an uninfected and a terminal-stage *Spirobacillus*-infected host; see C). Data from (Hawryshyn et al., 1988) was used to calculate the spectral sensitivity of the bluegill's two cones (bottom). **iii.** To quantify the brightness & chromatic contrast of *Daphnia*, we input these data into a model of bluegill vision (Section 2.3) that accounts for the bluegill's capacity to detect the contrast between two stimuli, as determined by the contrast threshold (ω). From this model we also calculate how much further an infected vs. uninfected animal is detectable to a bluegill (the relative sighting distance). **B** The irradiance of downwelling light in the environment. The irradiance of downwelling light in the littoral (left) and pelagic (right) regions of two lakes that differ in DOC concentration. Raw data are given by points; smoothed data, as used in the analysis, by the line. Shaded area indicates the part of the spectrum most absorbed by DOC. **C** The spectra of light transmitted by uninfected and infected *Daphnia*. *Daphnia* were infected with *Metschnikowia* (Metsch.), *Pasteuria* (Past.) or *Spirobacillus* (Term. Spiro, Early Spiro). *Spirobacillus*-infected animals change dramatically in color as the infection progresses from the early to the terminal (Term.) stage (see Fig. 1). Each panel contains data from a single individual; raw data from each technical replicate is plotted in different colors with the smoothed spectra indicated by the line. In **B & C** the vertical lines indicate the wavelength of light to which the green-sensitive and red-sensitive cones of the bluegill are most sensitive (i.e. their λ_{max})

background in the eyes of a specific viewer, we thus need to combine information about the light properties of the target, background and viewer; this is what visual systems models do.

Here, we use the model of Johnsen and Widder (1998) to understand if and how the changes in opacity and color associated with infection in *Daphnia* alter their brightness and chromatic contrast in the eyes of a bluegill sunfish. This model integrates data on (a) the downwelling light that serves as the background against which *Daphnia* are seen, in the eyes of a bluegill looking up (Fig. 2, AII, top), (b) the capacity of downwelling light to transmit through uninfected and infected *Daphnia* (i.e., the transparency of *Daphnia*, Fig. 2, AII, middle), (c) the capability of fish to detect the light coming from the background and the *Daphnia* (Fig. 2, AII, bottom), (d) the contrast threshold of the fish's visual system—the minimum difference between two objects that an organism can detect (ω)—which determines whether the fish can detect the contrast between the *Daphnia* and their background (Fig. 2, AIII). With this model we can estimate whether, in a particular body of water, infected *Daphnia* are differentially detectable from uninfected *Daphnia* (Fig. 2, III), so that bluegill might selectively prey upon them.

2.2 Data

2.2.1 The background: downwelling light

We quantified light conditions in two lakes, North and Gosling (Livingston County, Michigan USA), which harbor both bluegill and our focal parasites. The two lakes differ vary in their content of dissolved organic carbon (DOC), which strongly absorbs UV, short- ('blue') and mid- ('green') wavelength light and hence shifts the appearance of lakes toward a yellow or brown color (Wetzel, 2001) . Relative to a set of 15 study lakes in the region around the University of Michigan (Rogalski and Duffy (2020), M.A. Duffy unpublished data), Gosling and North lake contain relatively high (~13mg/L) and low (~5mg/L) concentrations of DOC, respectively; we hereafter refer to them as the 'high DOC' and 'low DOC' lakes. We quantified light conditions in two locations (pelagic and littoral) in each of these lakes.

In August 2018, we measured downwelling irradiance using a spectroradiometer (Ocean Optics S2000) connected to a patch cord (Ocean Optics QP400 -2 UV-VIS), which was in turn connected to a cosine corrector (Ocean Optics CC-3 DA). Bluegill feed nearly continuously during the day in the epilimnion of the water column (Keast and Welsh, 1968, Werner and Hall, 1988) and can often be seen feeding in the shallows of these lakes. We thus measured downwelling light in the upper part of the water column—at a depth of 50cm in the littoral zone and at 50cm & 150cm in the pelagic zone. Due to the vertical migration of *Daphnia*, which rise around dusk and descend around dawn (Lampert, 2011), it is often thought that bluegill consume *Daphnia* only during dusk and/dawn periods, though Keast and Welsh (1968) found equivalent numbers of Cladocera in the stomachs of

bluegill in the mid-afternoon (3–5.30PM) and early morning (5–9AM), with peak stomach fullness occurring at 3pm. To minimize the variance between light measurements between lakes and depths caused by the changing in the direction and intensity of light as the sun was setting, we made our measurements between 3–6pm.

We acknowledge that measures of radiance, rather than irradiance, are normally used in models of visual systems. Our use of irradiance should not significantly impact our conclusions, however, because the shape of the spectra of downwelling irradiance and radiance (and so the relative sighting distance, see eq. **??**) at shallow depths is very similar (Jerlov, 1976).

2.2.2 The target: infected and uninfected *Daphnia*

We focused on three parasites that are common in Michigan lakes and that induce visible symptoms in *Daphnia*: the fungal parasite, *Metschnikowia bicuspidata*, and the bacterial parasites, *Spirobacillus cienkowskii* and *Pasteuria ramosa* (hereafter, referred to by genus name only). In lakes, bluegill sunfish selectively prey upon *Metschnikowia*- and *Spirobacillus*-infected hosts; in an environment with equal numbers of infected and uninfected *Daphnia*, the rate of predation on infected hosts is estimated to be nine (in the case of *Metschnikowia*) or three (in the case of *Spirobacillus*) times greater, as compared to uninfected *Daphnia*) (Duffy and Hall, 2008). However, since these data were collected at different times and in different lakes, it is not possible at present to directly compare the extent to which these two parasites increase the risk of predation. To our knowledge, no one has quantified selective predation upon *Pasteuria*-infected hosts.

To measure the inherent capacity of *Daphnia* to transmit light of different wavelengths, we measured light transmission through the thorax of uninfected *Daphnia dentifera* and *Daphnia dentifera* infected with our focal parasites (Table S1), using the aforementioned spectrophotometer connected to the trinocular port of a compound light microscope (Olympus BX53) via a patch cord and SMA connector. Animals were illuminated using the microscope's light and observed under 20x magnification. Given this, our estimates of contrast are best interpreted as estimates of the *Daphnia*'s inherent contrast (i.e., when it is close to the bluegill's eye).

The infected *Daphnia* subjects we used were experimentally infected as part of long-term efforts to maintain the three focal parasites in culture in the lab. Different clones of *Daphnia* are used to maintain these parasites (see Table S1). We used uninfected animals of the L6D9 clone, which are used to maintain *Spirobacillus* infections, as the uninfected subjects in this experiment. Therefore, our data do not account for any baseline between-clone differences in the appearance of the *Daphnia* in the different infection treatments that could be perceived by a bluegill; no differences are perceptible to human eyes.

2.2.3 The viewer: the bluegill visual system

Bluegill sunfish are dichromats with color vision (Hawryshyn et al., 1988, Hurst, 1953). They have two photoreceptors: a single cone that maximally absorbs light at a wavelength of 536 nanometers ('green-sensitive' or mid wavelength sensitive (MWS) cone) and a double cone that maximally absorbs light at a wavelength of 620 nanometers ('red-sensitive' or long wavelength sensitive (LWS) cone) (Hawryshyn et al., 1988, Northmore et al., 2007) (Fig. 1**bii.**). With this visual system, bluegill can discriminate between both the brightness (achromatic contrast) and hue (chromatic contrast).

A key parameter of the visual system models used herein is the contrast threshold of the cones, which determines the minimum difference between two objects that an organisms can detect (ω). This parameter is inversely proportional to the signal to noise ratio of the photoreceptor used to see the object in question (Vorobyev et al., 2001, Vorobyev and Osorio, 1998). We use Northmore et al. (2007)'s estimate of the brightness contrast threshold—0.03, which means the minimum difference in the brightness of two objects that a bluegill could detect is 3%—to calculate brightness contrast and relative sighting distance; we refer to it as ω_b (eqs. 4, 7). We use Hawryshyn et al. (1988)'s estimates (0.003 & 0.007 for the MWS and LWS cones respectively) to calculate chromatic contrast (eqs. 5), and refer to them as ω_{mws} and ω_{lws}, respectively. See Supplementary Information for justification.

2.3 Model

To investigate how infection alters the detectability of an infected vs. an uninfected *Daphnia* by a bluegill sunfish, we adapt the model of Johnsen and Widder (1998).

2.3.1 Inherent contrast

The detectability of an object underwater is primarily determined by the extent to which it is brighter or darker than its background (Johnsen, 2014). This quantity is the inherent achromatic contrast ('inherent contrast', hereafter). The inherent contrast of an object o, against a large background b, in the context of a particular visual system is defined by the Weber contrast:

$$C_o = \frac{Q_{o,p} - Q_{b,p}}{Q_{b,p}} = \frac{Q_{o,p}}{Q_{b,p}} - 1 \tag{1}$$

where Q is the quantum catch of a particular photoreceptor p (i.e. a cone) of the viewer (Johnsen, 2014). The quantum catch is defined as

$$Q \propto \int_{min}^{max} L(\lambda)S(\lambda)d\lambda \tag{2}$$

where L is the spectrum of the illuminating light and S is the spectral sensitivity of the photoreceptor at wavelength λ (i.e. the degree to which it absorbs light of said wavelength).

Daphnia are partially transparent animals. We define transparency (T) as a value between 0 (completely opaque) and 1 (completely transparent). When perceived from below, the light hitting the front on an animal and being reflected back to the viewer is scant. Hence, in this context, the contrast of an animal is determined by the extent to which the light that is illuminating the animal from above (downwelling light) can penetrate through it. The inherent contrast of a *Daphnia* being seen from below (its contrast at zero distance) is thus calculated per eq. 1, where Q_o is defined as

$$Q_o \propto \int_{min}^{max} L(\lambda)S(\lambda)T_o d\lambda \tag{3}$$

As such, C_o spans from 0, where the *Daphnia* completely matches the bright, downwelling light and -1, where it appears as a completely opaque silhouette against it.

To implement this model, we estimated the spectral sensitivity S of the cones from their wavelengths of maximal absorption (Section 2.2.3) according to the model of Govardovskii et al. (2000), using the `pavo` package in R (Maia et al., 2019), and integrated over the wavelengths from 400nm–700nm, which encompasses the spectral sensitivity of the bluegill visual system. The irradiance of downwelling light was used as L.

2.3.2 Brightness & chromatic contrast from a 'bluegill-eye's' view

Whether a target is detectable to a particular viewer is determined by the viewer's capacity to detect the target's inherent contrast. This capacity is determined by the properties of the viewer's photoreceptors. The brightness contrast of a *Daphnia* as perceived by a bluegill is thus given by:

$$\Delta S = \frac{|C_o|}{\omega_b} \tag{4}$$

Whereas, for chromatic contrast it is

$$\Delta S = \sqrt{\frac{(\Delta q_{lws} - \Delta q_{mws})^2}{\omega_{lws}^2 + \omega_{mws}^2}} \tag{5}$$

where ω_{lws} and ω_{ws} are the contrast thresholds of the bluegill's green-sensitive (MWS) and red-sensitive (LWS) photoreceptor(s) (Siddiqi et al., 2004, Vorobyev and Osorio, 1998) and

$$\Delta q = log(|Q_o|) - log(|Q_b|) \tag{6}$$

where the subscripts denote that the quantum catches of *Daphnia* and of the downwelling light. The quantum catches of the different cones were normalized to 1 for this analysis of chromatic contrast.

Contrasts are expressed in units of just noticeable differences (JNDs). A target is detectable if it contrasts with its background by 1 JND or more (Olsson et al., 2018) i.e. 1 JND is the discriminability threshold. Whether two stimuli that are >1 JND different from their background are differentially conspicuous to the viewer remains a matter of debate (Fleishman et al., 2016, Santiago et al., 2020). Recent experiments suggest that the relative conspicuousness of two targets with suprathreshold chromatic contrasts (JND >1) does increase with the difference in their JNDs (Fleishman et al., 2016, Santiago et al., 2020). However, Santiago et al. (2020) found that ability of fish to discriminate between targets saturates as the targets' contrast with the background increases, suggesting that two objects that contrast greatly with their background e.g. by >20 JNDS may not be discriminable. Since the contrast thresholds we use to calculate chromatic contrast are an order of magnitude smaller than those used to calculate brightness contrast, our estimates of chromatic contrast are much greater than our estimates brightness contrast. In light of the aforementioned debate, and because differences between these threshold estimates likely stem from the different methodologies used to estimate them (Douglas and Hawryshyn, 1990), we encourage the reader to be cautious in their interpretation of the absolute size of the chromatic contrasts but rather focus on the relative difference between treatments.

2.3.3 Relative Sighting Distance

To set the measurements of brightness contrast of infected vs. uninfected *Daphnia* in further biological context, we used the estimates of inherent contrast to calculate the relative sighting distance of infected, i, vs. uninfected, u, *Daphnia*. This is given by

$$R_{sight} = \frac{ln(\frac{|C_i|}{\omega_b})}{ln(\frac{|C_u|}{\omega_b})} \tag{7}$$

(see Supplementary Material for derivation).

2.4 Statistical Analysis

Statistical analysis was performed using R, version 4.0.4. We employed mixed effects models to analyze the brightness and chromatic contrast of *Daphnia* using the `lmer` and `nlme` packages, respectively. To control for individual variation between *Daphnia*, experimental individual was included as a random effect. The fit of models was verified by visual inspection of residuals. In the analysis of chromatic contrast, we found that the residuals varied systematically with treatment. We thus used the `nlme` package to analyze chromatic contrast, since it

permitted us to specify treatment as a variance covariant following Zuur et al. (2009). For further discussion of the choice of random effects structure and model assumptions see Supplementary Material.

We built a full model that included the environmental parameters—depth, lake, and zone of the lake (pelagic vs. littoral)—and infection treatment as main effects. We included an infection treatment by lake interaction to investigate whether the effect of infection on the perceptibility of *Daphnia* changed with lake environment (per Johnson et al. (2006)). Because depth greatly alters light environment (Fig. 2B)—and hence potentially contrast—we also included a treatment by depth interaction.

To obtain a final model, which included only significant explanatory variables, we sequentially dropped insignificant terms using either Kenward-Roger's F-test or likelihood ratio tests, for models of brightness and chromatic contrast, respectively. If a model term was insignificant but improved the AIC of the model it was retained. To investigate whether the contrast of *Daphnia* harboring each parasite was different from uninfected animals, we performed posthoc comparisons using the `emmeans` package. P-values were corrected using the Dunnet adjustment for multiple comparisons.

3 Results

Brightness contrast To a bluegill looking up at the water's surface, *Daphnia* appear as dark silhouettes against the background of bright downwelling light (Fig. 3A; JND > 1). *Daphnia* contrast less with their background in the high DOC lake and in deeper water (brightness contrast *lake* $F_{1,379} = 6.7$, $p = 0.01$; brightness contrast *depth* $F_{1,379} = 9$, $p < 0.01$) but the effect of these environmental parameters is small (estimated reduction in contrast in the higher DOC lake = 0.5 JND, 0.12-0.85 95% CI; with depth = 0.6 JND, 0.2-0.99% CI) The contrast of *Daphnia* was unaffected by lake zone (i.e., pelagic vs. littoral; brightness contrast, *location* $F_{1,378} = 1.5$, $p = 0.2$).

Against a background of downwelling light, infected *Daphnia* appear darker than uninfected animals (Fig. 3A, brightness contrast, *treatment* $F_{4,16} = 14$, $p < 0.001$). As a result, bluegill are predicted to detect infected *Daphnia* at farther distances than healthy *Daphnia* (Fig. 3B). How much further away a bluegill can detect an infected *Daphnia*, as compared to a healthy conspecific, is dependent on the infection's cause: the sighting distance of terminal-stage *Spirobacillus*-infected animals is 33% (on average, 95% CI = 30-38%) greater than healthy animals, while the sighting distance of *Metschnikowia* animals is 19% (on average, 95% CI = 15-25%) higher than healthy conspecifics. The great disadvantage of *Spirobacillus* infection, in terms of perceptibility to predators, only appears at the terminal-stage of infection, however. *Daphnia* with early-stage *Spirobacillus* infection contrast with their background no more than healthy animals (post-hoc analysis of brightness contrast, $p = 0.5$).

Contrary to expectations, the effect of infection on brightness contrast (and hence sighting distance) is not different in lakes that vary in DOC (brightness contrast, *treatment*lake* $F_{4, 370} = 0.09$, $p = 0.98$). However, a power analysis indicated that we had a limited ability to detect an impact of lake on the contrast of animals in different infection treatments (e.g., the probability of detecting a 1 JND change in the contrast of terminal-stage *Spirobacillus*-infected animals with lake was only 42%.)

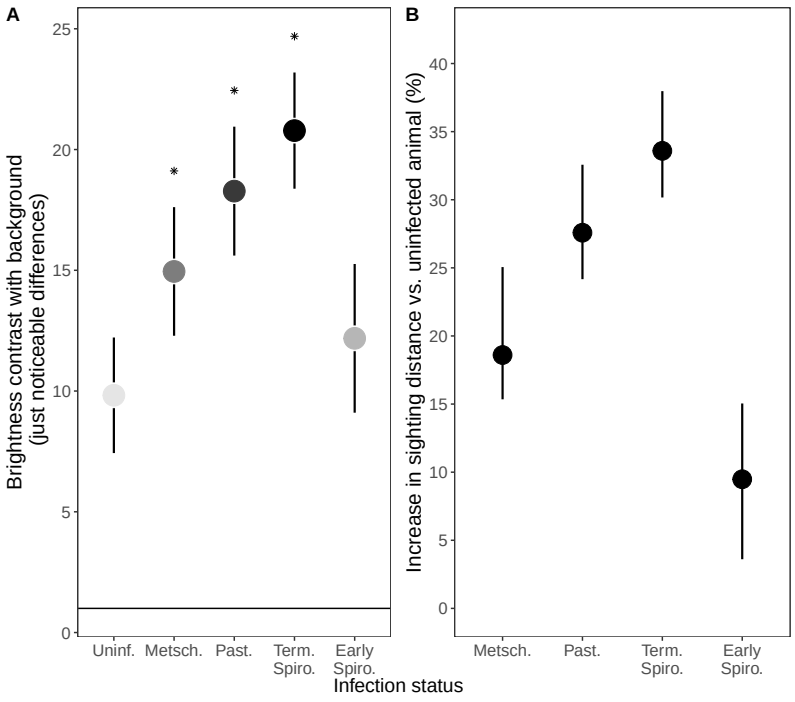

Figure 3: Infection increases the detectability of *Daphnia* by bluegill sunfish by increasing their brightness contrast with the background downwelling light. The **A** brightness contrast and **B** relative sighting distance of uninfected *Daphnia* and *Daphnia* infected with *Metschnikowia* (Metsch.), *Pasteuria* (Past.) and at the terminal- and early- stages of *Spirobacillus* infection (Term. Spiro. and Early Spiro., respectively). **A** Horizontal line indicates 1 JND: the smallest difference in brightness contrast that a bluegill can detect. Points and error bars represent means and 95% confidence intervals as estimated from the final statistical model of brightness contrast. Point fill indicates the appearance of *Daphnia* in the eyes of the bluegill, as estimated from a statistical model of inherent contrast (eqs. 1–3). Stars indicate where the brightness contrast of *Daphnia* is significantly greater than that of uninfected *Daphnia*. **B** The relative sighting distance of infected *Daphnia* as compared to an uninfected *Daphnia*. Points and error bars represent means & 95% confidence intervals, as estimated by the resampling procedure described in the Supplementary Material.

Chromatic contrast *Daphnia* are a different color than the water in which they live (Fig. 4, chromatic contrast JND >1). Infection further increases the chromatic contrast of *Daphnia* with their background, particularly in bright, shallow water (Fig. 4; chromatic contrast, *treatment*depth* $\chi^2_4 = 14$, $p = 0.01$).

The effect of different parasites on the chromatic contrast of *Daphnia* was generally consistent with their effect on brightness contrast. The exception was that animals infected with *Metschnikowia* did not chromatically contrast with the background any more than uninfected hosts. The remaining findings were consistent with the brightness contrast findings. *Pasteuria*-infected and terminal-stage *Spirobacillus*-infected *Daphnia* have a higher chromatic contrast than healthy animals (posthoc comparisons: *Pasteuria* $p = 0.03$, *Spirobacillus* $p < 0.001$; Fig. 4). Although *Spirobacillus*-infected animals at the terminal stage of infection contrast greatly with the downwelling light (Fig. 4), early-stage *Spirobacillus*-infected animals do not differ from healthy animals in terms of their chromatic contrast (post-hoc comparison with uninfected animals, early-stage *Spirobacillus* $p = 0.7$; Fig.

4). Finally, the effect of infection on the chromatic contrast of *Daphnia* did not change in different lake (i.e., DOC) environments (chromatic contrast, *treatment*lake* χ^2_4 = 2.8, p = 0.6).

4 Discussion

Selective predation by fish on infected *Daphnia* has been repeatedly demonstrated (Duffy and Hall, 2008, Duffy et al., 2005, Johnson et al., 2006) and can strongly influence epidemiological dynamics (Duffy and Hall, 2008, Duffy et al., 2005), but why predators select infected hosts had not been rigorously examined. Our model confirms the hypothesis that parasites increase the visibility of *Daphnia* to bluegill predators by decreasing their transparency and, in the case of *Pasteuria* and terminal-stage *Spirobacillus* infection, changing their color.

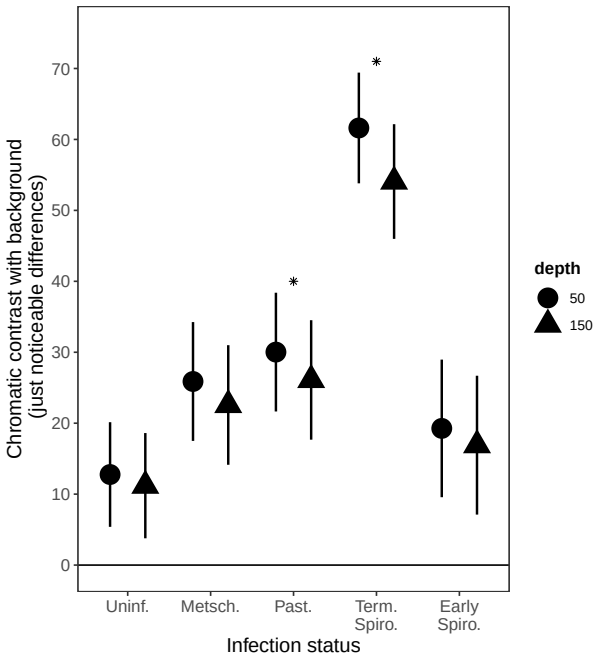

Figure 4: Terminal *Spirobacillus* and *Pasteuria* infections increases the chromatic contrast of *Daphnia*, particularly in shallow water. The horizontal line indicates the smallest difference in chromatic contrast that a bluegill can detect. Points and error bars represent means & 95% confidence intervals as estimated from the final statistical model. Stars indicate treatments in which the chromatic contrast of *Daphnia* is significantly greater than that of uninfected *Daphnia* in both lake environments. Depth given in units of centimeters.

These changes in appearance are of such magnitude as to drive significant differences in the rate at which infected and uninfected animals are consumed (i.e., selective predation). We estimate that infection-induced changes in brightness contrast increase the sighting distance of *Daphnia* by 19-30%, relative to uninfected conspecifics, depending on the infection. Accordingly, given that the rate at which fish encounter *Daphnia* is proportional to the square of their sighting distance (Aksnes and Giske, 1993), fish could consume 40-75% more infected *Daphnia* than uninfected *Daphnia* in a given period. It is more difficult to interpret the changes in chromatic contrast that occur with infection but, since bluegill preferentially feed on 'red' objects over 'green' objects, even when they are equally bright (Hurst, 1953), it is likely that this symptom also contributes to the selectivity of bluegill for infected animals.

While infections universally increase the visibility of *Daphnia*, some infections do so more than others. The different extent to which parasites change the brightness and chromatic contrast of *Daphnia* can be explained

by their differential impact on the wavelengths of light to which bluegill are sensitive. Freshwater fish like bluegill are thought to perceive brightness using the green-sensitive cone. The tissues of infected *Daphnia* obstructed the penetration of light in the spectral region absorbed by this cone (Fig. 2C), presumably because they were filled with parasites. Thus the *Daphnia* are 'silhouetted' against the bright downwelling light (Fig. 3A). On the other hand, bluegill perceive the hue (and hence chromatic contrast) of objects by comparing the amount of light captured by the green-sensitive and red-sensitive cones. So it is the *difference* in the amount of light received by each cone that maximizes chromatic contrast. The spectrum of light transmitted by *Spirobacillus*-infected hosts (and some *Pasteuria*-infected hosts) changes rapidly in the spectral region that separates the peak absorbance of the bluegill's cones (as indicated by the grey vertical lines in Fig. 2C). Thus the chromatic contrast of *Spirobacillus*-infected hosts is large as compared to uninfected and *Metschnikowia*-infected hosts, which transmit light in a relatively constant manner in this region of the spectrum. Our finding that environmental variables have a negligible impact on the relative visibility of infected vs. uninfected *Daphnia* to bluegill can similarly be explained by looking at the features of the bluegill visual system. DOC absorbs UV, short- ('blue') and mid ('green') light (300-500nm) (Wetzel, 2001) but at the shallow depths we investigated, the effect of DOC is most apparent in the blue part of the spectrum (Fig. 2B: shaded region). Neither of the bluegill's photoreceptors is particularly sensitive to light of this wavelength, so any change in the amount of light in this region will have had a limited impact on our estimates of *Daphnia*'s contrast and hence perceptibility.

Why then did Johnson et al. (2006) observe that the selectivity of bluegill sunfish for infected hosts changed with DOC, whereas our model predicts that it should not? The first explanation is that Johnson et al. (2006) used juvenile bluegill sunfish in their experiments, whereas our model focuses on the adult visual system. Unlike adults, juvenile bluegill have a visual system sensitive to (changes in) short-wavelength and UV light, and hence to changes in DOC. Uninfected *Daphnia* scatter and reflect UV light and also absorb UV-A light (Leech and Johnsen, 2006, White et al., 2005) and so are expected to contrast with UV light; how this contrast changes with infection is unknown. Nonetheless, if juvenile fish use a UV-A sensitive cone to detect and select *Daphnia*, the concentration of DOC in water could change their foraging behavior and hence selectivity for infected *Daphnia*. That said, Leech and Johnsen (2006) found UV light had no effect on the foraging behavior of juvenile bluegill and theory suggests that temperate, freshwater fish should not use short wavelength light to forage because its intensity in their habitat changes so markedly and frequently (Lythgoe, 1975). A second explanation for the discrepancy between our findings and those of Johnson et al. (2006) is that our model does not fully account for the impact of DOC on the sighting distance of *Daphnia*. The absolute sighting distance of an object is affected by several properties of the underwater light environment, including the spectra of light and the rate at which it attenuates with distance,

which determine the "color" and "amount" of light that reaches the viewer's eye, respectively (Johnsen, 2014). Since we were interested in the detectability of infected *Daphnia* relative to uninfected conspecifics and did not possess attenuation information, we used a model of relative sighting distance here (eq. 7). DOC changes both the color and attenuation rate of light underwater (and therefore the absolute and relative sighting distance of an object) (Wetzel, 2001), however, and its effect on light attenuation could particularly impact bluegill feeding. For example, the rate at which bluegill feed on zooplankton decreases in the light limited environment induced by high DOC (Weidel et al., 2017) and even the much-vaunted preference of bluegill for large size prey is abrogated in low light conditions induced by turbid water (Vinyard and O'brien, 1976). It may be that the absolute sighting distance is so limited in high-DOC environments that relative changes in the sighting distance of infected vs. uninfected animals have little impact on feeding rates. Lastly, and relatedly, it is thought that in conditions of low light, bluegill may switch to hunting via lateral line sensing (Vinyard and O'brien, 1976). Such a change could be measured in a behavioral experiment Johnson et al. (2006) but not by a visual model.

Indeed, our model has several assumptions that could limit its capacity to predict the behavior of bluegill in the wild. We used measurements of the transmission of light through the *Daphnia* thorax in our model. Thus, we implicitly assume that the entire *Daphnia* transmits light the same way that the thorax does, despite there being substantial spatial variation in the distribution of symptoms in infected hosts (Fig. 1). Given that freshwater fish can select *Daphnia* according to the size of the eye (Branstrator and Holl, 2000, Zaret and Kerfoot, 1975) and the presence or absence of eggs (Johnson et al., 2006), it is not unreasonable to assume that the distribution of symptoms within a host might impact predator selectivity. Second, for technical reasons, we modeled a very specific hunting scenario, where the bluegill is looking up at the *Daphnia*, whereas bluegill also hunt while horizontally oriented with the prey in front of them (Spotte, 2007, Williamson and Keast, 1988). In this scenario, *Daphnia* would be observed against a background of sidewelling rather than downwelling light, which has a different spectrum, reduced intensity, and is subject to absorption and scattering by particulate matter on its way to the bluegill eye (Johnsen, 2014, Lythgoe, 1975). Though transparent *Daphnia* contrast less with their background in this scenario (Loew and Lythgoe, 1978, White et al., 2005) it is difficult to intuit the (relative) impact of infection on *Daphnia's* perceptibility in this orientation. Unfortunately, modeling *Daphnia* in this situation is fraught with assumptions and would require a considerable amount of data that we were unable to collect.

Our model, combined with the observations of Johnson et al. (2006), suggests that the visible symptoms of infection contribute to selective predation. This presents a quandary: these *Daphnia* parasites are obligate killers (Ebert (2005), Wale & Duffy *unpublished data*) that survive poorly in the bluegill gut (Duffy et al., 2019, 2005), so the fitness costs of inducing symptoms that increase the detectability of hosts could be substantial. Why then

do these parasites induce such symptoms? Let's assume that phenotypes are in the control of the parasite (as we believe they are in the case of *Spirobacillus* (Bresciani et al., 2018)). The first hypothesis is it is merely a constraint of the system's biology—*Daphnia* are transparent, so occupying their hemolymph will naturally come at the cost of making them opaque. The second is that the production of symptoms puts parasites at risk of predation but that it is a risk worth taking. Were parasites to grow slower, reducing the symptoms they induce and hence the probability of their hosts being eaten, this could come at a disadvantage in terms of within-host competition with other parasite strains/species (de Roode et al., 2005) and surviving the *Daphnia* immune system (assuming a threshold model of immunity (Grossman and Paul, 1992)). Under this hypothesis, we would expect the frequency of "risky" symptoms to increase as the abundance of predators in the environment decreases. Intriguingly, *Pasteuria* strains induce a red color in their hosts in rock pools in Finland where fish predators are absent (D. Ebert, personal communication), and, conversely, in some lakes, terminal *Spirobacillus* infections tend to be white rather than red (Duffy & Wale *unpublished data*). Alternatively, selection might favor parasites that balance the benefits of symptoms with the risks, by limiting the production of predation-increasing symptoms to a small period of the infection, as in the case of at least *Spirobacillus*.

Our study provides proof of principle that visual ecology can help disease ecologists to better understand the ecological implications of visual symptoms of infection and hence their evolution. Visual models can be used to test and generate hypotheses about the impact of infection on ecological interactions that would be difficult to investigate empirically. For example, in order to examine the selectivity of bluegill for *Daphnia* infected with different parasites in different environments empirically, epidemics of the different parasite species would have to occur simultaneously in a variety of lakes (a rare, if nonexistent, event). Our model, by contrast, provides a quantitative hypothesis of how important selective predation might be in determining epidemic dynamics of these different parasites across a range of habitats. The tools and principles of visual ecology could be used to illuminate how organismal traits that mediate disease transmission in other parasite-host systems, such as those where parasites complete their life cycle by being trophically transmitted between multiple host species. Such parasites must reach a definitive host in order to reproduce and so incur a substantial cost if their intermediate host is consumed by a predator other than their definitive host (Mouritsen and Poulin, 2003). Visual ecologists have discovered that organisms can take advantage of the differences in the visual systems of different organisms to direct signals exclusively to a desired recipient (Cummings et al., 2003). This raises an intriguing question: do trophically transmitted parasites exploit differences among predator visual systems to ensure that they reach the 'right host', for example by inducing symptoms in their intermediate host that are visible to their definitive host, but not other predators? This example and the model herein, demonstrate that integrating visual ecology

and disease ecology could advance our understanding of the impact of symptoms on ecological interactions and thence disease transmission.

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6 Author contributions

NW, RCF, MT and MAD designed the study. NW, RCF and MT collected the data. NW analyzed the data, partially using code written by RCF. SJ wrote the original model, helped to implement it and interpret the results. NW and MAD wrote the manuscript. SJ and RCF provided comments on the manuscript.

7 Data accessibility statement

We affirm that we will make the data collected for this article publicly available via Dryad, upon this artice's acceptance.

References

Aksnes, D. L. and Giske, J. (1993). A theoretical model of aquatic visual feeding. *Ecological Modelling*, 67(2-4):233–250.

Branstrator, D. K. and Holl, C. M. (2000). Planktivory by bluegill (*Lepomis macrochirus*) on *Leptodora kindti* in a small North American lake. *Hydrobiologia*, 437(1-3):101–106.

Bresciani, L., Lemos, L. N., Wale, N., Lin, J. Y., Strauss, A. T., Duffy, M. A., and Rodrigues, J. L. M. (2018). Draft genome sequence of "*Candidatus* Spirobacillus cienkowskii," a pathogen of freshwater *Daphnia* species, reconstructed from hemolymph metagenomic reads. *Microbiology Resource Announcements*, 7(22).

Choo, K., Williams, P. D., and Day, T. (2003). Host mortality, predation and the evolution of parasite virulence. *Ecology Letters*, 6(4):310–315.

Cronin, T. W., Johnsen, S. J., Marshall, N. J., and Warrant, Eric, J. (2014). Vision in Attenuating Media. In *Visual Ecology*, pages 202–242. Princeton University Press.

Cummings, M. E., Rosenthal, G. G., and Ryan, M. J. (2003). A private ultraviolet channel in visual communication. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1518):897–904.

de Roode, J. C., Pansini, R., Cheesman, S. J., Helinski, M. E. H., Huijben, S., Wargo, A. R., Bell, A. S., Chan, B. H. K., Walliker, D., and Read, A. F. (2005). Virulence and competitive ability in genetically diverse malaria infections. *Proceedings of the National Academy of Sciences of the United States of America*, 102(21):7624 – 7628.

Douglas, R. H. and Hawryshyn, C. W. (1990). Behavioural studies of fish vision: an analysis of visual capabilities. In *The Visual System of Fish*, chapter 11, pages 373 – 418. Chapman and Hall.

Duffy, M. A., Cáceres, C. E., and Hall, S. R. (2019). Healthy herds or predator spreaders? Insights from the plankton into how predators suppress and spread disease. In Wilson, K., Fenton, A., and Tompkins, t. D., editors, *Wildlife Disease Ecology: Linking Theory to Data and Application*, pages 458–479. Cambridge University Press.

Duffy, M. A. and Hall, S. R. (2008). Selective predation and rapid evolution can jointly dampen effects of virulent parasites on Daphnia populations. *The American Naturalist*, 171(4):499 – 510.

Duffy, M. A., Hall, S. R., Tessier, A. J., and Huebner, M. (2005). Selective predators and their parasitized prey: Are epidemics in zooplankton under top-down control? *Limnology and Oceanography*, 50(2):412–420.

Eaton, M. D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *Proceedings of the National Academy of Sciences*, 102(31):10942–10946.

Ebert, D. (2005). *Ecology, Epidemiology, and Evolution of Parasitism in Daphnia*. National Center for Biotechnology Information. National Center for Biotechnology Information.

Fleishman, L. J., Perez, C. W., Yeo, A. I., Cummings, K. J., Dick, S., and Almonte, E. (2016). Perceptual distance between colored stimuli in the lizard Anolis sagrei: comparing visual system models to empirical results. *Behavioral Ecology and Sociobiology*, 70(4):541–555.

Govardovskii, V. I., Fyhrquist, N., Reuter, T., Kuzmin, D. G., and Donner, K. (2000). In search of the visual pigment template. *Visual Neuroscience*, 17(4):509–528.

Grossman, Z. and Paul, W. E. (1992). Adaptive cellular interactions in the immune system: the tunable activation threshold and the significance of subthreshold responses. *Proceedings of the National Academy of Sciences*, 89(21):10365–10369.

Hall, S. R., Becker, C., and Cáceres, C. E. (2007). Parasitic castration: a perspective from a model of dynamic energy budgets. *Integrative and Comparative Biology*, 47(2):295 – 309.

Hawryshyn, C. W., Arnold, M. G., and McFarland, W. N. (1988). Aspects of color vision in bluegill sunfish (*Lepomis macrochirus*): ecological and evolutionary relevance. *Journal of Comparative Physiology A*, 164(1):107 – 116.

Holt, R. D. and Roy, M. (2007). Predation can increase the prevalence of infectious disease. *The American Naturalist*, 169(5):690 – 699.

Hurst, P. M. (1953). Color discrimination in the bluegill sunfish. *Journal of Comparative and Physiological Psychology*, 46(6):442–445.

Jerlov, N. (1976). *Marine Optics*. Elsevier Oceanography Series. Elsevier, New York.

Johnsen, S. (2014). Hide and seek in the open sea: pelagic camouflage and visual countermeasures. *Annual Review of Marine Science*, 6(1):369 – 392.

Johnsen, S. and Widder, E. A. (1998). Transparency and visibility of gelatinous zooplankton from the Northwestern Atlantic and Gulf of Mexico. *American Naturalist*, 195:337 – 348.

Johnson, P. T. J., Stanton, D. E., Preu, E. R., Forshay, K. J., and Carpenter, S. R. (2006). Dining on disease: how interactions between infection and environment affect predation risk. *Ecology*, 87(8):1973 – 1980.

494 Jones, R. S., Fenton, A., and Speed, M. P. (2016). “Parasite-induced aposematism” protects entomopathogenic
495 nematode parasites against invertebrate enemies. *Behavioral Ecology*.

496 Keast, A. and Welsh, L. (1968). Daily feeding periodicities, food uptake rates, and dietary changes with hour of
497 day in some lake fishes. *Journal of the Fisheries Research Board of Canada*, 25(6):1133–1144.

498 Kisdi, E., Geritz, S. A. H., and Boldin, B. (2013). Evolution of pathogen virulence under selective predation: a
499 construction method to find eco-evolutionary cycles. *Journal of Theoretical Biology*, 339:140 – 150.

500 Lampert, W. (2011). Diel Vertical Migration (DVM). In *Daphnia: Development of a Model Organism in Ecology
501 and Evolution*, Excellence in Ecology. International Ecology Institute.

502 Leech, D. M. and Johnsen, S. (2006). Ultraviolet vision and foraging in juvenile bluegill (Lepomis macrochirus).
503 *Canadian Journal of Fisheries and Aquatic Sciences*, 63(10):2183–2190.

504 Loew, E. R. and Lythgoe, J. N. (1978). The ecology of cone pigments in teleost fishes. *Vision Research*,
505 18(6):715–722.

506 Lythgoe, J. N. (1975). Problems of seeing colors under water. In *Vision in Fishes*, volume 1 of *NATO Advanced
507 Study Institutes Series (Series A: Life Sciences)*, pages 619–634. Springer.

508 Maia, R., Gruson, H., Endler, J. A., and White, T. E. (2019). `pavo 2`: New tools for the spectral and spatial
509 analysis of colour in r. *Methods in Ecology and Evolution*, 10(7):1097 – 1107.

510 Matz, M. V., Marshall, N. J., and Vorobyev, M. (2006). Are corals colorful? *Photochemistry and Photobiology*,
511 82(2):345.

512 Mittelbach, G. G. (1984). Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*,
513 65(2):499–513.

514 Morozov, A. Y. and Adamson, M. W. (2011). Evolution of virulence driven by predator–prey interaction: possible
515 consequences for population dynamics. *Journal of Theoretical Biology*, 276(1):181 – 191.

516 Mouritsen, K. N. and Poulin, R. (2003). Parasite-induced trophic facilitation exploited by a non-host predator: a
517 manipulator’s nightmare. *International Journal for Parasitology*, 33(10):1043–1050.

518 Northmore, D. P. M., Oh, D.-J., and Celenza, M. A. (2007). Acuity and contrast sensitivity of the bluegill sunfish
519 and how they change during optic nerve regeneration. *Visual Neuroscience*, 24(3):319–331.

Olsson, P., Lind, O., and Kelber, A. (2018). Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. *Behavioral Ecology*, 29(2):273 – 282.

Packer, C., Holt, R. D., Hudson, P. J., Lafferty, K. D., and Dobson, A. P. (2003). Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecology Letters*, 6(9):797–802.

Rogalski, M. A. and Duffy, M. A. (2020). Local adaptation of a parasite to solar radiation impacts disease transmission potential, spore yield, and host fecundity. *Evolution*.

Roy, B. A. (1993). Floral mimicry by a plant pathogen. *Nature*, 362(6415):56 – 58.

Santiago, C., Green, N. F., Hamilton, N., Endler, J. A., Osorio, D. C., Marshall, N. J., and Cheney, K. L. (2020). Does conspicuousness scale linearly with colour distance? A test using reef fish. *Proceedings of the Royal Society B*, 287(1935):20201456.

Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M., and Summers, K. (2004). Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology*, 207(14):2471–2485.

Spotte, S. (2007). *Bluegill*. American Fisheries Society.

Sánchez, C. A., Becker, D. J., Teitelbaum, C. S., Barriga, P., Brown, L. M., Majewska, A. A., Hall, R. J., and Altizer, S. (2018). On the relationship between body condition and parasite infection in wildlife: a review and meta-analysis. *Ecology Letters*, 21(12):1869–1884.

Thünken, T., Baldauf, S. A., Bersau, N., Frommen, J. G., and Bakker, T. C. M. (2019). Parasite-induced colour alteration of intermediate hosts increases ingestion by suitable final host species. *Behaviour*, pages 1–20.

Vinyard, G. L. and O'brien, W. J. (1976). Effects of Light and Turbidity on the Reactive Distance of Bluegill (Lepomis macrochirus). *Journal of the Fisheries Research Board of Canada*, 33(12):2845–2849.

Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S. B., and Menzel, R. (2001). Colour thresholds and receptor noise: behaviour and physiology compared. *Vision Research*, 41(5):639–653.

Vorobyev, M. and Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B: Biological Sciences*, 265(1394):351 – 358.

Wale, N., Turrill, M. L., and Duffy, M. A. (2019). A colorful killer: *Daphnia* infected with the bacterium *Spirobacillus cienkowskii* exhibit unexpected color variation. *Ecology*, 100(3).

Weidel, B. C., Baglini, K., Jones, S. E., Kelly, P. T., Solomon, C. T., and Zwart, J. A. (2017). Light climate and dissolved organic carbon concentration influence species-specific changes in fish zooplanktivory. *Inland Waters*, 7(2):210–217.

Werner, E. E. and Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology*, 69(5):1352–1366.

Wetzel, R. G. (2001). Light in Inland Waters. In *Limnology*, chapter 5, pages 49 – 69. Elsevier.

White, E. M., Church, S. C., Willoughby, L. J., Hudson, S. J., and PARTRIDGE, J. C. (2005). Spectral irradiance and foraging efficiency in the guppy, Poecilia reticulata. *Animal Behaviour*, 69(3):519 – 527.

Williams, P. D. and Day, T. (2001). Interactions between sources of mortality and the evolution of parasite virulence. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 268(1483):2331 – 2337.

Williams, T. and Cory, J. S. (1994). Proposals for a new classification of iridescent viruses. *The Journal of General Virology*, 75 (Pt 6)(6):1291 – 1301.

Williamson, M. and Keast, A. (1988). Retinal structure relative to feeding in the rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*). *Canadian Journal of Zoology*, 66(12):2840–2846.

Zaret, T. M. and Kerfoot, W. C. (1975). Fish predation on *Bosmina longirostris*: Body-size selection versus visibility selection. *Ecology*, 56(1):232–237.

Zhou, W., Li, J., Chen, J., Liu, X., Xiang, T., Zhang, L., and Wan, Y. (2016). The red pigment prodigiosin is not an essential virulence factor in entomopathogenic *Serratia marcescens*. *Journal of invertebrate pathology*, 136:92 – 94.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). Dealing with Heterogeneity. In *Mixed effects models and extensions in ecology with R*, pages 71 – 100. Springer.