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Does the thermal mismatch hypothesis predict disease outcomes in different morphs of a terrestrial salamander?

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Abstract

Many aspects of ectotherm physiology are temperature-dependent. The immune system of temperate-dwelling ectothermic host species is no exception and their immune function is often downregulated in cold temperatures. Likewise, species of ectothermic pathogens experience temperature-mediated effects on rates of transmission and/or virulence. Although seemingly straightforward, predicting the outcomes of ectothermic host–pathogen interactions is quite challenging. A recent hypothesis termed the thermal mismatch hypothesis posits that cool-adapted host species should be most susceptible to pathogen infection during warm temperature periods whereas warm-adapted host species should be most susceptible to pathogens during periods of cool temperatures. We explore this hypothesis using two ecologically and physiologically differentiated color morphs of the Eastern Red-backed Salamander (*Plethodon cinereus*) and a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*; hereafter "*Bd*") using a fully factorial laboratory experiment. At cool temperatures, unstriped salamanders (i.e., those that are tolerant of warm temperatures) had a significantly higher probability of *Bd* infection compared with cool-tolerant striped salamanders, consistent with the thermal mismatch hypothesis. However, we found no support for this hypothesis when salamanders were exposed to *Bd* at warm temperatures: the probability of *Bd* infection in the cool-tolerant striped salamanders was nearly identical in both cool and warm temperatures, opposite the predictions of the thermal mismatch hypothesis. Our results are most consistent with the fact that *Bd* grows poorly at warm temperatures. Alternatively, our data could indicate that the two color morphs do not differ in their tolerance to warm temperatures but that striped salamanders are more tolerant to cool temperatures than unstriped salamanders.

KEYWORDS

amphibian, *Batrachochytrium dendrobatidis*, chytridiomycosis, color polymorphism, fungal pathogen, temperature

Matthew D. Venesky and Joseph DeMarchi contributed equally and have shared first authorship

1 | INTRODUCTION

Temperature affects all levels of biological organization. At the organismal level, environmental variation in temperature affects physiological processes because biochemical reactions, cellular membranes, and even organ function are temperature-sensitive (Klein et al., 2017; Pieau & Dorizzi, 2004; Wright & Cooper, 1981). These constrain organismal physiological performance between critical thermal limits (i.e., a minimum and maximum body temperature that grants minimum values of performance) and performance is optimized at a species-specific body temperature (Angilletta et al., 2002; Lutterschmidt & Hutchison, 1997). An organism's optimal performance breadth represents the range of temperatures over which physiological performance is above some arbitrary percentage of the optimal thermal performance (Angilletta et al., 2002). These effects of temperature scale up to higher levels of biological organization and can limit population growth rates (Savage et al., 2004), constrain the distribution of species (Kellermann et al., 2012; Woodword, 1987), and influence species-interactions and the structure of ecological communities (Grigaltchik et al., 2012; Srinivasan et al., 2018; Zacher et al., 2019).

Ectothermic host–pathogen interactions are ideal systems to study the effects of temperature on species-interactions because ectotherms cannot maintain their body temperature with their own metabolism. From the perspective of the host, cellular and humoral components of the ectotherm immune system rely on temperature-sensitive molecules, enzymes, and cells. For instance, although a lipopolysaccharide (LPS) injection stimulated the phagocytic activity of wall lizards (*Hemidactylus flaviviridis*) across a temperature range of 15–37°C, the percentage of increase in phagocytic activity in LPS-injected lizards relative to lizards from the sham treatment was highest at 25°C and no different at 7°C (Mondal & Rai, 2001). This pattern of immune-activity is consistent with physiological performance curves (Angilletta et al., 2002) and the general features of this type of temperature-dependent response are observed in many ectotherm host species (Ferguson et al., 2018). From the perspective of the pathogen, temperature is known to affect many pathogen traits, including growth rates (Verant et al., 2012), transmission rates (Mordecai et al., 2013), and expression of genes associated with virulence (Huang et al., 2019). Not surprisingly, temperature is often implicated in mediating host–parasite interactions and there are known associations between temperature and disease outbreaks across numerous host–pathogen systems (reviewed in Altizer et al., 2013).

The fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) is an emerging infectious disease of amphibians that infects the skin of adult amphibians and causes the disease chytridiomycosis (reviewed in Kilpatrick et al., 2010). *Bd* grows well in culture between 4°C and 25°C (Piotrowski et al., 2004) and at the high end of this spectrum (23°C), the *Bd* lifecycle is faster and results in more, and larger, zoospores than when *Bd* is grown at 4°C (Voyles et al., 2012). However, the duration of *Bd* zoospore activity is longer at 4°C compared with 23°C, possibly indicating that zoospores in cold environments could have a high encounter rate with amphibian hosts despite producing fewer total zoospores (Voyles et al., 2012). As such, *Bd* is typically considered a cool-adapted pathogen. Amphibian immune responses, as with other physiological processes, are temperature dependent and many amphibians have reduced immunocompetence under cold conditions (Rollins-Smith, 2017). Because early field studies associated outbreaks of chytridiomycosis with cool environmental temperatures (e.g., Kriger & Hero, 2007) and some species of amphibian can clear *Bd* infections when placed in warm temperatures (Chatfield & Richards-Zawacki, 2011; McMahon et al., 2014), it is generally thought that chytridiomycosis outbreaks occur only in cool temperatures. However, this is not always the case (Bosch et al., 2007) and the association between cool temperatures and chytridiomycosis outbreaks oversimplifies the context-dependent effects of temperature on amphibians and *Bd* in nature (Venesky et al., 2014).

A recent hypothesis, termed the thermal mismatch hypothesis, addresses the inconsistencies in how temperature affects the outcome of host–parasite interactions, including between amphibians and *Bd* (Cohen et al., 2017). Because parasites are relatively smaller and generally have broader thermal performance breadths than their hosts, they can acclimate to new temperatures faster than hosts (Martiny et al., 2006). Thus, when host–parasite interactions occur within both species' thermal performance breadths, hosts should be susceptible to parasites when a performance gap exists between parasites and hosts at a given temperature. Disease outbreaks should occur when this performance gap is significantly high (Cohen et al., 2017). Operationally, this suggests that cool-adapted host species should be most susceptible to pathogen infection during warm temperature periods whereas warm-adapted host species should be most susceptible to pathogens during periods of cool temperatures (Cohen et al., 2017). This hypothesis has been supported in laboratory experiments using amphibians and *Bd* (Cohen et al., 2017; Sauer et al., 2018) and these findings were supported in a recent meta-analysis (Sauer et al., 2020). Despite the generality of thermal mismatch hypothesis, factors such as geographic location, habitat specialization, and host life stage can each affect the strength and outcome of thermal mismatches on host–parasite interactions (Cohen et al., 2019).

We explore the thermal mismatch hypothesis using two ecologically and physiologically differentiated color morphs of the Eastern Red-backed Salamander (*Plethodon cinereus*) and *Bd*. Individuals of *P. cinereus* are common throughout eastern North America and Canada (Petranka, 1998) and they actively seek temperatures of 16–18°C (Feder & Pough, 1975). Red-backed salamanders exhibit color polymorphism and have two common phenotypes: a striped morph with a red dorsal band that extends from the head or neck to the tail (striped), and an unstriped morph that is uniformly black (unstriped). Early studies examined subsets of the geographic range of *P. cinereus* [e.g., Michigan (Test, 1952) and Connecticut (Lotter & Scott, 1977)] and found that frequencies of the striped morph decreased with increasing temperatures. More recent studies have incorporated larger portions of the geographic range (Gibbs & Karraker, 2006; Moore &

Ouellet, 2015), and the largest study to date, encompassing nearly 240,000 individual *P. cinereus* over the entirety of the range (1170 localities), found that the frequency of striped salamanders was positively correlated with forest cover only in warmer regions (Cosentino et al., 2017). These results suggest that striped salamanders have some intolerance to warmer climates. At our study site, unstriped salamanders retreat from the surface of the forest floor with decreasing temperatures in autumn, suggesting that the unstriped morph may be intolerant to cooler temperatures (Anthony et al., 2008). The preferred temperatures, assessed by patterns of seasonal activity, of the two color phenotypes differ at our site by 1.5°C with the striped morph preferring cooler temperatures (Anthony et al., 2008).

Given the above, we assumed that salamanders in our study had opposite temperature tolerances at the end points of our experimental temperatures. Following the thermal mismatch hypothesis, we predicted that unstriped salamanders (i.e., the "warm tolerant" morph) should have relatively high *Bd* infections (i.e., poor resistance) at cool temperatures but that striped salamanders (the "cool tolerant" morph) should have relatively low *Bd* infections (i.e., high resistance) at cool temperatures. If the color morphs do not differ in their performance at either cool or warm temperatures, we should see no difference in *Bd* infections at those temperatures.

2 | METHODS

2.1 | Salamander collection and husbandry

All *P. cinereus* were collected (ODNR permit # 92-112) by hand from a private property (41°13'37.2"N, 81°31'17.2" W) in Summit County, OH on September 30 and October 1, 2016. Only adult salamanders (SVL > 34 mm; Anthony & Pfingsten, 2013) were collected. Before any experimentation, salamanders were housed individually in vented plastic containers (13.7 × 11.4 × 6.4 cm) on natural leaf litter at John Carroll University (University Heights, OH) under a natural photoperiod (15:9 L:D, synched to sunrise and sundown for the dates that the experiment was run) at 16.5°C. Individuals of *P. cinereus* were fed wingless fruit flies twice per week (approximately 25 *Drosophila melanogaster* per feeding) and the leaf litter bedding was changed as needed.

2.2 | Experimental design

Our experiment utilized a 2 × 2 x 2 fully factorial design to test how striped and unstriped individuals of *P. cinereus* respond to the main and interactive effects of temperature (cool and warm) and pathogen exposure (*Bd*-exposed and nonexposed). To accomplish this, we randomly assigned 122 (striped $N = 64$; unstriped $N = 58$) adult *P. cinereus* to either a warm or cool temperature treatment and then randomly assigned each salamander to a pathogen exposure treatment. The resulting eight experimental treatments had 14–16 replicates (we caught fewer unstriped salamanders than striped salamanders which resulted in fewer replicates in each treatment group that used unstriped salamanders). On July 16, 2017, we created the first of our four temporal blocks and transferred approximately ¼ of the salamanders from each of the eight treatments to their designated temperature treatment. We continued this process each day until July 19, 2017, on which the remaining group of salamanders (approximately ¼) were placed in their designated temperature treatment. Before being placed in their temperature treatment, we transferred each salamander to an identical sized vented plastic container and used a non-bleached paper towel soaked with 13 ml of natural spring water as the substrate.

To avoid spatial pseudoreplication between the temperature treatments, all of the individual plastic containers were placed in a single room at approximately 16°C. We used terrarium heating pads (24 Watt 20 × 46 cm Zilla©) to raise the temperatures of individual containers in the warm treatment. To prevent the buildup of water condensation on the inside lid of the container due to evaporation from the paper towel, we lifted the containers from the heating pad and gently tapped the container on a table twice each day. This effectively prevented the buildup of water on the lid of the salamander container and kept the bedding moist throughout the experiment. We also gently tapped the containers with salamanders from the cool treatment in a similar manner so that salamanders from both temperature groups experienced similar effects of container movement. Heating pads radiate heat which caused two unexpected effects in our temperature treatments. First, we used a randomized block design within the room and some containers with salamanders from a "cool" treatment were placed adjacent to a heating pad and thus experienced temperatures slightly warmer than ambient room temperature. In addition to this, salamanders were able to position themselves vertically within the chamber and thus could avoid direct contact with the heating pad. Collectively, these factors resulted in two temperature gradients being produced rather than two different absolute temperatures (cool: 16.3–19.5°C; warm: 20.0–25.6°C). Although we will continue to refer to the temperature treatments as "cool" or "warm," we used the actual temperature of each salamander (using an Extech® Infrared Thermometer with emissivity set to 0.95; Cohen et al., 2017; Rowley & Alford, 2007) as a continuous predictor in each of the statistical models rather than the categorical descriptors of the temperature treatment. The salamanders were acclimated to their respective temperature treatments for 6 days before being exposed to *Bd* or a sham exposure.

2.3 | *Bd* exposure

The *Bd* isolate used in the experiment (JEL 660) was grown in the laboratory in 1% tryptone broth at 4°C before the experiment and plated on 1% tryptone agar for this experiment. Plates of *Bd* were acclimated to each temperature treatment for approximately 24 h (Cohen et al., 2017) to minimize differential temperature acclimation effects (Raffel et al., 2013). To harvest *Bd* zoospores, we flooded

numerous agar plates with spring water for 30 min and collected the zoospores that were released into the water. Each salamander assigned to the *Bd*-exposure treatment from temporal blocks A, C, and D was given an inoculum that contained 1.6×10^6 *Bd* zoospores per experimental block (salamanders in block B were given 1.0×10^6 *Bd* zoospores) by directly pipetting the inoculum onto each salamander. Salamanders from the control treatment received a sham exposure that contained water from agar plates that did not contain any *Bd*. Bedding was changed 48 h after inoculation. Throughout the experiment, all equipment that came into contact with *Bd* or *Bd*-exposed salamanders was soaked in 10% bleach to kill *Bd* (Johnson & Speare, 2003).

2.4 | Swabbing, DNA extractions, and qPCR

Bd infection on salamanders was measured by swabbing each salamander on Day 7 and Day 14 postexposure by passing a sterile swab (Medical Wire & Equipment; MW 113) across the dorsal surface of each salamander, including the tail, a total of 15 times. The DNA extractions and qPCR analyses followed the methods of Boyle et al. (2004) and modified by Hyatt et al. (2007). Test samples were run singly instead of triplicate to control costs, as recommended by Kriger et al. (2006). We added TaqMan® Exogenous Internal Positive Control (Exo IPC) Reagents (Applied Biosystems) to every reaction well to assess inhibition of the PCR reaction (Hyatt et al., 2007). The Exo IPC system uses a standardized concentration of an artificial DNA sequence that is added to each reaction well with its own set of primers and a separate fluorescent probe. The strength of this reaction is used to assess overall reaction inhibition. Extractions were diluted 1:100 and processed in an Applied Biosystems Step One Real-time PCR system. We considered infection intensity as the number of *Bd* zoospore equivalents per sample. The number of zoospore equivalents per swab was calculated by multiplying the values generated by the qPCR assay by 80, which accounts for the fact that only a portion of the extracted DNA from each swab was amplified in our qPCR analysis and that the extracted DNA was diluted during the qPCR preparation. Each swab sample was run against a standard curve of seven serially diluted plasmid samples (Pisces Molecular; Kirshtein et al., 2007), each of which contains the rDNA ITS region of *Bd*. The minimum R^2 value for a standard curve was >0.992 (mean $R^2 = 0.996$). We considered a sample *Bd* positive when zoospore equivalents were ≥1.

2.5 | Statistical analyses

We used the "lm" function in R statistical software (ver. 4.0.5; R Core Team, 2017) to conduct a linear model to test whether the application of the two experimental temperature treatments (cold, warm) resulted in different salamander temperatures on Day 7 and Day 14. Statistical significance ($p < 0.05$) was assessed using the "ANOVA" function in the "car" package in R.

There are three parameters frequently used to quantify pathogen infection: prevalence, infection intensity, and infection abundance. Upon exposure to a pathogen, individual hosts will become either infected or remain noninfected (and the percentage of hosts exposed to a pathogen that become infected is termed "prevalence"). Hosts that become infected carry a pathogen burden (termed "infection intensity"). Infection abundance unifies the parameters of prevalence and infection intensity because it measures the number of pathogens found in all hosts that were exposed to a pathogen, including the zero values of the hosts that were exposed to, but not infected with, a pathogen. Because plethodontid salamanders are relatively resistant to *Bd* (Fonner et al., 2017; Hess et al., 2015) and many of our salamanders had an infection value of "0" (see Section 3), we had limited statistical power to analyze infection intensity. As such, we analyzed *Bd* abundance (i.e., the number of *Bd* zoospore equivalents of the salamanders exposed to *Bd*, including those whose value was "0") using a zero-inflated negative binomial statistical model (using the "glmmADMB" function in the "glmmADMB" package in R). This statistical model considers the response variable a function of a binomial process (uninfected vs. infected) and a count process (negative-binomial distributed infection intensity), consistent with the metric of infection abundance. We trimmed the nonexposed salamanders from the data set and conducted separate statistical analyses on the Day 7 and Day 14 swabs. In each statistical model, we tested for the main effects of the categorical predictors color (striped, unstriped), sex (female, male), and temporal block (A, B, C, or D) on *Bd* abundance. We also included the salamander temperature recorded on each swab date as a continuous predictor in the statistical models. In each statistical model, we also tested for a color by temperature interaction. Statistical significance ($p < 0.05$) was assessed using the "ANOVA" function in the "car" package in R. We used the "logi.hist.plot" function in the "popbio" package in R to create Figure 2.

3 | RESULTS

3.1 | Differences in temperature

Our experimental design successfully created environments that differed in their temperature (Day 7: $F_{1,120} = 711.95$, $p < 0.001$; Day 14: $F_{1,120} = 720.66$, $p < 0.001$). Although the mean temperature of salamanders between the two treatments differed, there was considerable variation within each temperature treatment (Figure 1), justifying our use of the actual temperature of each salamander as a continuous statistical predictor instead of the categorical predictors "cold" or "warm."

3.2 | *Bd* infection

Infection prevalence and infection intensity decreased through time. 47.5% of salamanders exposed to *Bd* were infected on Day 7 (mean

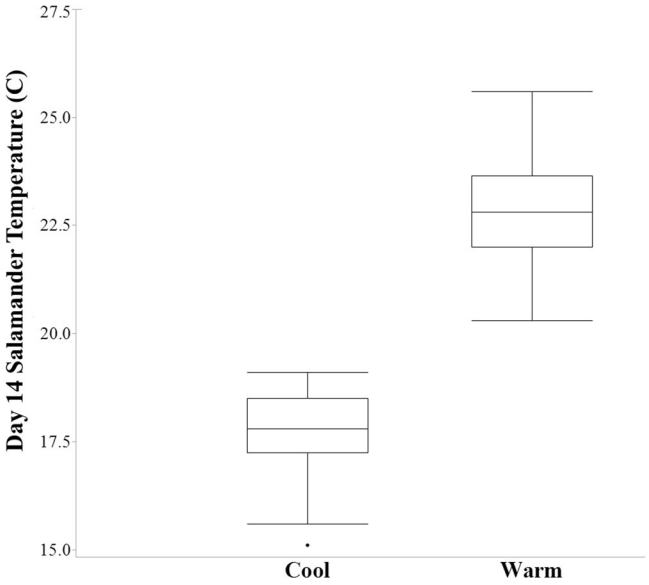

FIGURE 1 Recorded differences in actual temperatures of individual salamanders of *Plethodon cinereus* maintained in the cool and warm temperature treatments on Day 14 of the experiment

TABLE 1 Summary statistics for the two zero-inflated negative binomial statistical models conducted. Each statistical model had similar categorical (color morphology, sex, experimental block) and continuous (recorded salamander temperature) predictor variables but were conducted on *Batrachochytrium dendrobatidis* (*Bd*) data collected from Day 7 or Day 14 swabs

	df	χ^2 value	*p* value
Day 7 *Bd* abundance			
Color	1	0.090	0.764
Day 7 salamander temperature	1	0.965	0.326
Sex	1	0.138	0.710
Experimental block	3	0.695	0.874
Color × Day 7 temperature	1	.0244	0.622
Day 14 *Bd* abundance			
Color	**1**	**8.712**	**0.003**
Day 14 salamander temperature	1	1.187	0.276
Sex	**1**	**17.930**	**<0.001**
Experimental block	3	0.634	0.889
Color × Day 14 temperature	**1**	**4.595**	**0.032**

Note: Variables in bold indicate significant ($p < 0.05$) effects.

intensity of 714.88) and 23.0% were infected on Day 14 (mean intensity of 504.63). We did not find any main or interactive effects of any response variable on Day 7 *Bd* infection abundance (Table 1). However, we found significant main effects of color, sex, and an interaction between color and temperature on Day 14 *Bd* abundance (Table 1). On average, unstriped salamanders carried a 6.5-fold higher *Bd* abundance compared with striped salamanders (mean abundance of 273.15 and 42.08, respectively). Although salamander temperature alone did not predict *Bd* abundance, we found a significant interaction between color morph and temperature on *Bd* abundance measured on Day 14 (Table 1). In the cold temperature treatment, striped salamanders carried an average infection abundance of 69.77 whereas unstriped salamanders had an infection abundance of 373.26 (±SE 48.88 and 220.03, respectively). In the warm temperature treatment, average *Bd* infection abundance on striped salamanders was 14.38 and was 165.90 on unstriped salamanders (±SE 11.67 and 156.94, respectively). This color by temperature interaction can be visualized by differences in the probability of infection at different temperatures: the probability of infection for unstriped salamanders is high at cool temperatures and decreases as the temperature increases whereas striped salamanders maintain a relatively low, and constant, probability of infection across all measured temperatures (Figure 2).

4 | DISCUSSION

The thermal mismatch hypothesis states that cool-adapted host species should be most susceptible to pathogen infection at warm temperatures whereas warm-adapted host species should be most susceptible to pathogens during periods of cool temperatures (Cohen et al., 2017). We used this hypothesis to make predictions on how temperature might differentially affect two ecologically and physiologically differentiated morphs of the Eastern Red-backed Salamander (Anthony et al., 2008; Davis & Milanovich, 2010 Lotter & Scott, 1977; Petruzzi et al., 2006). At cool temperatures, unstriped salamanders (i.e., those that are tolerant of warm temperatures) had a significantly higher probability of *Bd* infection compared with cool-tolerant striped salamanders (Figure 2). In addition to this, the average *Bd* infection abundance on unstriped salamanders was approximately 2× higher when they were raised in cold temperatures compared with when raised in warm temperatures, consistent with the thermal mismatch hypothesis. This result is also similar to *Bd* infection patterns of *Atelopus zeteki*, a species of anuran that lives in high-elevation locations and is tolerant to cold temperatures: individuals of this species carry significantly higher *Bd* infections at warm temperatures compared with cool temperatures, even though *Bd* grows poorly in warm temperatures (Cohen et al., 2017). Outside of the amphibian-*Bd* system, individuals of *D. melanogaster* collected from tropical subpopulations in Africa (i.e., warm tolerant) have poorer resistance to pathogenic bacteria at cool temperatures compared with cold-tolerant flies from temperate subpopulations in North America (Lazzaro et al., 2008), a pattern that is consistent with the predictions of the thermal mismatch hypothesis.

Despite the growing consensus that thermal mismatches increase host susceptibility to pathogens (Cohen et al., 2020), the mechanism(s) that drive this pattern are not well studied. Many studies that measure immune parameters of ectotherms in cold temperatures do so under the context of overwintering and the results of these studies clearly demonstrate that immune

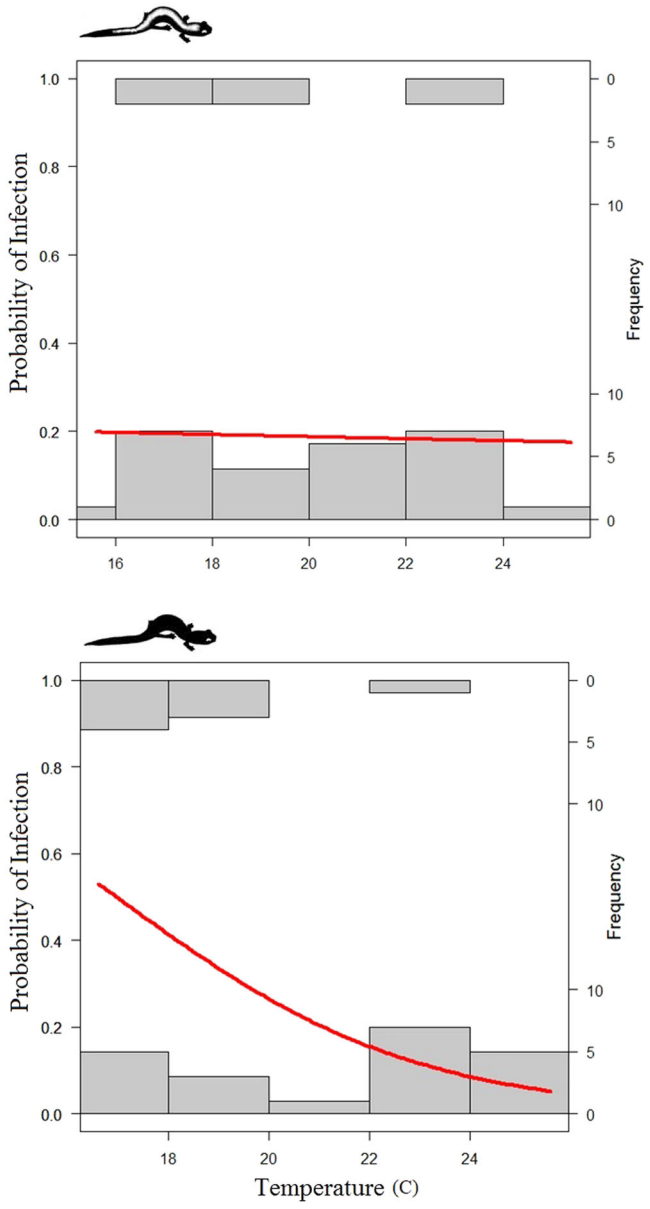

FIGURE 2 A visualization of the significant temperature by color morph interaction on *Bd* abundance measured on Day 14 of the experiment. Each line represents the fitted logistic regression curve showing the probability of infection with *Batrachochytrium dendrobatidis* (0 = noninfected, 1 = infected) on the left *y*-axis. The histograms indicate the frequency of salamanders of *Plethodon cinereus* that were infected (top values of the right *y*-axis) and those that were not infected (bottom values on the right *y*-axis) observed across the recorded salamander temperatures on Day 14 of the experiment. The top panel presents data for striped salamanders and the bottom panel presents data for the unstriped salamanders. The probability of infection for unstriped salamanders is high at cool temperatures and decreases as the temperature increases whereas striped salamanders maintain a relatively low, and constant, probability of infection across all measured temperatures

performance is downregulated in overwintering ectotherms (reviewed in Ferguson et al., 2018; Rollins-Smith, 2020). This is thought to occur because of the direct effects of temperature on biochemical reactions and the fact that individuals that overwinter experience reductions in food availability and thus have different energy budgets (Ferguson et al., 2018). This context, however, is very different than exploring pathogen resistance in species, or morphs, that prefer cool temperatures. The lack of published studies on specific immune defenses of cool-tolerant ectotherms, coupled with the fact that we did not measure immune activity of the salamanders, makes it difficult to speculate about why striped salamanders do not appear to experience immune suppression at cool temperatures but unstriped salamanders do. More research is needed to elucidate how cool-tolerant ectotherms can achieve higher pathogen resistance in cool temperatures relative to warm temperatures so that we can make clear predictions about when thermal mismatches will, or will not, lead to increased host susceptibility to pathogens.

Even though our results at cool exposure temperatures were consistent with the thermal mismatch hypothesis, we found no support for this hypothesis in salamanders exposed to *Bd* at warm temperatures. The probability of *Bd* infection in striped salamanders (i.e., the cool-tolerant color morph) was nearly identical in both cool and warm temperatures (Figure 2) and the *Bd* infection abundance actually decreased by approximately four-fold on striped salamanders when raised in warm temperatures compared with cold temperatures, opposite the predictions of the thermal mismatch hypothesis. Instead of supporting the thermal mismatch hypothesis, this particular finding corroborates previous work demonstrating that *Bd* does not grow well in warm temperatures (Piotrowski et al., 2004; Voyles et al., 2012) and that striped salamanders are more resistant to *Bd* than unstriped salamanders (Venesky et al., 2015). Recently, Neely et al. (2020) tested the thermal mismatch hypothesis using *Bd* and host species of tropical frogs that have different thermal tolerances. Although their patterns of *Bd*-induced mortality were consistent with those of the thermal mismatch hypothesis, all three species had lower *Bd* infections when exposed at warm experimental temperatures compared with cool experimental temperatures (Neely et al., 2020), a result that was consistent with our infection data. Although our results and those of Neely et al. (2020) lend credence to the thermal mismatch hypothesis, they both identify contexts in which this hypothesis is not fully supported. One likely explanation for why our results and those of Neely et al. (2020) did not fully support the thermal mismatch hypothesis is that we did not produce enough thermal variation in our experimental design. The difference between the highest and lowest amphibian temperature measured in our experiment was 9.3°C and the difference between the highest and lowest environmental temperature in Neely et al. (2020) was 10 C; most of the amphibian species used in Cohen et al. (2017) experienced an 18°C difference between the lowest and highest experimental temperature. If an increase in the warm treatment were to cause an increase in *Bd* infection abundance (or *Bd*-induced mortality) in the cool-tolerant striped salamanders, our results would fully support the thermal mismatch hypothesis. Likewise, the addition of a lower experimental temperature and a concomitant reduction of *Bd* infection abundance in striped salamanders would also fully support the thermal mismatch hypothesis.

An alternative explanation for why our results did not support the thermal mismatch hypothesis at warm temperatures is because striped salamanders might not be adverse to the warm temperatures (i.e., 20.0–25.6°C) that we used in our experiment. We assumed that salamanders in our study had opposite temperature tolerances at the end points of our temperature extremes because the striped morph of *P. cinereus* appears to be less tolerant of higher temperatures across the geographic range of this species (Cosentino et al., 2017) and the unstriped morph retreats from the surface earlier in the autumn at our study site, suggesting an intolerance to cooler conditions (Anthony et al., 2008). However, differences in surface activity might not match thermal performance at different temperatures. If the temperatures that the striped salamanders experienced in our warm temperature treatment did not cause any negative physiological changes, there would be no reason to expect an effect of temperature on *Bd* abundance for salamanders in the warm temperature treatment. Despite known physiological differences between the color morphs of *P. cinereus* at 10°C, Petruzzi et al. (2006) found that striped and unstriped salamanders did not differ in their maintenance metabolic rate (MMR) at 20°C. However, it is inappropriate to extend this interpretation to temperatures beyond those used in Petruzzi et al. (2006) and the average temperature in our "warm" treatment was 3°C higher than the highest temperature used in Petruzzi et al. (2006) and the salamanders in our "warm" treatment regularly had measured temperatures that measured >25°C. Moreover, one of the difficulties in drawing conclusions about temperature tolerance and color morphology in *P. cinereus* stems from the large geographic range (Petranka, 1998) and resulting genetic diversity of the species (Radomski et al., 2020). Studies that are limited to one or a few populations may find relationships that do not hold in other parts of the geographic range (Hantak et al., 2020). For example, Moreno (1989) used salamanders from the Northern Clade (sensu Radomski et al., 2020) to show that the SMR of the unstriped morph was lower than that of the striped morph at 15°C. However, salamanders from the Ohio Clade (sensu Radomski et al., 2020) did not differ in MMR at that same temperature (Petruzzi et al., 2006). Future studies that directly measure physiological performance of salamanders collected across their entire geographic range and using a large gradient of temperatures are needed to further assess the degree at which the color morphs are physiological differentiated.

It is important to note that although increases in temperature seem to decrease *Bd* risk in this host species, increases in global temperatures are predicted to have complex and nonlinear effects on organisms and ecosystems. Concluding that increased temperature will have a net-positive effect on this species, and potentially other amphibian hosts, oversimplifies climate–disease relationships. The long-term consequences of increased temperatures on terrestrial plethodontid salamanders include negative physiological effects such as increased levels of circulating stress hormones (Novarro et al., 2018) and increases in resting metabolic rate (Homyack et al., 2010). Warming temperatures are also expected to contribute to the degradation of critical microhabitat on the forest floor (Milanovich et al., 2010; Whitfield et al., 2007), resulting in increased rates of dehydration (Spotila, 1972), reduced activity periods (Riddell & Sears, 2015; Riddell et al., 2018), and concomitant loss of foraging opportunities (Feder & Londos, 1984; Lyons et al., 2016). Additionally, the interactive effects of warming and the presence of invasive earthworms are predicted to cause decreases in native plant diversity, increases in litter decomposition rates, and soil drying in temperate forests (Eisenhauer et al., 2012). As warmer, drier conditions continue to facilitate earthworm invasions, we would expect these factors to exert strong negative effects on terrestrial dwelling, lungless salamanders (Brunges et al., 2020). Evidence suggests that nonnative earthworms consume leaf litter microhabitat that houses salamander fDprey at very rapid rates and that these invaders are negatively associated with juvenile and male red-backed salamanders in the field (Ziemba et al., 2015, 2016).

In summary, we found mixed support for the thermal mismatch hypothesis. In cool temperatures, cool-tolerant striped salamanders had lower metrics of disease (i.e., probability and frequency of infection as well as *Bd* abundance) than did warm-tolerant unstriped salamanders. If temperature alone were driving disease outcomes in this species and if their patterns of seasonal activity truly indicate different thermal preferences, we would have observed high rates of infection in both color morphs of this species at cool temperatures. In warm temperatures, all of the measured metrics of *Bd* infection were low on both color morphs. At warm temperatures, our results are most consistent with the fact that *Bd* grows poorly at warm temperatures and do not support the predictions of the thermal mismatch hypothesis.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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