Warming Strengthens Priority Effects Driven by an Ontogenetic Shift from Host to Predator

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abstract: Priority effects arise when species arrival order determines interaction outcomes. In many ecological systems, interacting species undergo ontogenetic shifts that reverse their roles as consumer and resource, making the consequences of arrival order inherently time dependent. Here, we examine how temperature alters priority effects using a host-parasite system where the tree hole mosquito *Aedes sierrensis* undergoes an ontogenetic shift from a vulnerable host to a predator of its parasite, *Lambornella clarki*. We hypothesized that the relative timing of mosquito hatching and parasite emergence would determine infection outcomes and that warming could either reduce or increase infection depending on whether mosquito development or parasite proliferation is more temperature sensitive. In microcosm experiments, we manipulated the mosquito larval stage (first vs. fourth instar) at parasite introduction across a 6°C–14°C temperature gradient, mimicking variation in arrival order and temperatures that might occur in their native habitats in California. Our results revealed a stark priority effect mediated by an ontogenetic role reversal: when parasites encountered fourth-instar larvae, they were rapidly consumed by the larvae, and infection was completely prevented. Conversely, when parasites encountered first-instar larvae, infection occurred, and parasitism rates increased significantly with increasing temperature. Warming strengthened the priority effect by disproportionately accelerating parasite proliferation relative to host development and defense, allowing the parasite to establish infection before the host reached a less susceptible stage. This finding highlights the potential for temperature to fundamentally alter community assembly by shifting the rate at which ontogenetic role reversals occur relative to the timing of species arrival.

Keywords: priority effects, host-parasite, predator-prey, stage structure, temperature dependence, mosquito.

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Introduction

The order of species arrival can have lasting effects on community structure and function (Chase 2003; Zou and Rudolf 2023). This phenomenon, known as priority effects, has been studied most intensively in competitive communities, where early-arriving species can preempt resources and exclude later colonists (Fukami 2015). However, priority effects can also play important roles in consumer-resource interactions such as predation and parasitism, which often unfold in temporally structured ways (Yang and Rudolf 2010; Hoverman et al. 2013; MacDonald and Brisson 2022; Stroud et al. 2024). In predator-prey and host-parasite systems, the relative timing of species' introductions can alter interaction outcomes, including the complete reversal of predator-prey roles (Choh et al. 2012). In a classic marine example, rock lobsters prey on whelks, but where whelks are established first at high densities, they can overwhelm and consume the lobsters, creating alternative stable community states (Barkai and McQuaid 1988; Sánchez-Garduño et al. 2014).

Priority effects can be particularly strong when species undergo distinct ontogenetic transitions that alter their ecological roles, so that the timing of arrival determines the developmental stage at which individuals interact (Rasmussen et al. 2014). Phenological differences in emergence or colonization timing that alter relative body size at first encounter can shift the balance between competitors, cannibals, or predators and prey and can produce reciprocal intraguild predation or role reversals (Fonseca et al. 2018; Sniegula et al. 2019; Raczyński et al. 2022). Intraguild predation arising from these stage-structured encounters is a context in which priority effects are often especially strong (Holt and Polis 1997). In pond and tree hole communities, for example, the identity and arrival timing of intraguild predators are known to strongly

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influence subsequent assemblage structure of other intraguild predators and prey (Fincke 1994, 1999; Blaustein and Margalit 1996; Padeffke and Suhling 2003). Host-parasite systems may also show similar historical contingencies when infectious stages are vulnerable to predation, which is known to depend on both predator and parasite size (Johnson et al. 2010; Orlofske et al. 2015). To date, however, most empirical work on priority effects in host-parasite systems has focused on the relative arrival timing of multiple parasite species, genotypes, or strains within hosts (Hoverman et al. 2013; MacDonald and Brisson 2022), rather than on the arrival order of hosts and parasites themselves.

The strength of stage-structured priority effects is likely to be temperature dependent. Temperature governs developmental rates, metabolic demands, and behavior in ectothermic organisms and can differentially affect species based on their thermal sensitivities (Angilletta 2009; Dell et al. 2014). For interacting competitors, warming is expected to amplify priority effects by accelerating the impact of early colonizers, increasing the likelihood of competitive exclusion when inferior competitors arrive late (Grainger et al. 2018; Vass et al. 2021; Dawson-Glass et al. 2025). In consumer-resource systems, however, predicting the effect of warming can be more complex. The outcome hinges on a thermal performance race between the interacting species and on which species arrives first to establish the priority effect. In a scenario where the consumer arrives first, the priority effect is driven by the consumer's ability to suppress the later-arriving resource (Olito and Fukami 2009). Warming should amplify the priority effect if it disproportionately benefits the consumer, for instance, by increasing rates of predation or parasitism more than the resource can compensate for (Öhlund et al. 2015; Cohen et al. 2020). Conversely, warming can dampen or even reverse a priority effect if it disproportionately benefits the resource, for instance, by allowing it to accelerate its development or growth to a less vulnerable stage (Pepi et al. 2023).

Furthermore, when the role of consumers and resources switches between species ontogenetically, temperature can interact with arrival order to affect which species consumes the other. Experimental studies show that warming can alter intraguild predation strength and shift competitive hierarchies in crabs (Rogers et al. 2018) and odonate larvae (Suhling and Suhling 2013; Frances and McCauley 2018; Stahl and Johansson 2024). Theory further predicts that temperature-dependent changes in growth and attack rates in stage-structured intraguild predation can cause abrupt switches between predator dominance, prey dominance, and coexistence (Thunell et al. 2021). However, this work has been conducted with synchronous introductions, and we still lack empirical tests of how warming modifies priority effects in systems with predator-prey role reversals. To understand the effects of warming on consumer-resource priority effects requires measuring how temperature changes the speed at which species undergo predator-prey role reversal, relative to the pace at which local communities assemble.

In this study, we examine temperature-dependent priority effects in a natural host-parasite and predator-prey system composed of the western tree hole mosquito (*Aedes sierrensis*) and its facultative ciliate parasite (*Lambornella clarki*). Larval mosquitoes consume microbial resources in tree hole water, including ciliates, whereas *Lambornella* can take on a free-living bacterivorous stage or a parasitic stage that infects mosquito larvae (Washburn et al. 1988). Both species exist in dormant stages in the dry season and emerge when tree holes fill with water, but the relative timing of mosquito hatching and *Lambornella* excystment can vary (Washburn et al. 1991*b*). This, combined with their dual roles as consumers and resources, creates a dynamic where stage-dependent priority effects are likely, as the timing of interaction can determine whether the ciliate becomes a parasite or prey, and whether the immature mosquito becomes a host or predator, in turn governing which species persists in a tree hole.

We hypothesized that the relative arrival time of the host and parasite would determine infection outcomes. Specifically, we predicted that early parasite arrival (or emergence from their dormant state) while the hosts remain at a vulnerable early developmental stage would lead to high infection rates, whereas later parasite arrival, when hosts are larger, would allow hosts to suppress the parasite via predation, resulting in low infection rates. We next asked how warming alters the strength of these priority effects. Because temperature can differentially affect host developmental rates and parasite proliferation (Ismail et al. 2024), warming could either shorten the period when hosts are vulnerable and hasten the onset of predation on free-living parasites, thereby reducing infection, or accelerate parasite growth enough to increase infection despite faster host development. To test these predictions, we conducted a factorial microcosm experiment manipulating mosquito developmental stage at parasite introduction (first vs. fourth instar) and temperature and a complementary microcosm experiment to quantify mosquito predation rates on free-living *Lambornella* across larval instars.

Methods

Study System

Aedes sierrensis and *Lambornella clarki* occupy water-filled tree holes across western North America from the

coast to montane areas (Arnell and Nielson 1972; Corliss and Coats 1976). Both species exist in a dormant state through the long dry summer season and become active when winter rains or melting snow flood their habitat (Washburn et al. 1991*b*). As a facultative parasite, *Lambornella* can exist in a free-living form that feeds on bacteria and a parasitic form that develops only when free-living cells are exposed to mosquito larvae or mosquito-conditioned water (Washburn et al. 1988). In response to these cues, free-living cells divide, and their daughter cells transform into invasive parasitic cells that encyst on the larval cuticle, invade mosquito larvae, proliferate internally, and are released upon host death (Washburn et al. 1991*b*). This facultative parasite life history strategy has been described as an evolutionary adaptation to escape stressful conditions like predation (Luong and Mathot 2019). *Lambornella* is the only ciliate parasite known to infect this mosquito species (Washburn and Anderson 1986). In coastal California, *Lambornella* and mosquito larvae are active almost exclusively during the wet season, and our previous work has shown that the peak of the infection response lies roughly between 10°C and 13°C in both lab observations (Ismail et al. 2024; Farner et al. 2026) and field surveys (Farner et al. 2026). *Lambornella* is thought to disperse when infected adult female mosquitoes introduce cysts or free-living cells into new tree holes during pseudo-oviposition (Egerter et al. 1986).

Mosquito and Parasite Source

The mosquito population used in the experiment was collected from a single uninfected tree hole in Jasper Ridge Biological Preserve (ʻOotchamin ʻOoyakma)—hereafter, JRBP(ʻOʻO)—located in the Santa Cruz Mountains of California (37.40736, −122.23756). Mosquitoes were collected as larvae, identified to species (Darsie and Ward 2005), reared to adulthood, and blood fed to produce eggs (detailed methods in Couper et al. 2024). Eggs were incubated at 21°C for 4 weeks and then 5°C for 6 weeks to mimic seasonal changes until being used in the experiment. Mosquitoes were hatched sequentially, either 1 day or 16 days before the experiment started. To hatch the eggs, we submerged them in a tray filled with 500 mL of distilled water, 300 mL of autoclaved tree hole water, and 12 mL of Brewer's yeast. From hatching onward, mosquitoes were kept at 10°C to match the average temperature of the wettest quarter—the season in which these species interact—at JRBP(ʻOʻO) as measured by WorldClim (Fick and Hijmans 2017). Mosquitoes were fed 0.1 mg of food per larva per day made of a finely ground mix of TetraMin fish flakes (48% by weight), guinea pig chow (48%), and liver powder (4%; Maïga 2017).

The *Lambornella* used in the experiment were collected from a nearby tree hole at JRBP(ʻOʻO). The *Lambornella* culture was isolated from a single infected mosquito in December 2022, which was crushed and put in 2 mL of autoclaved culturing media (made up of 1,000 mL of distilled water, one alfalfa pellet, and 0.38 g of Herptivite) and a barley seed (Fukami 2004). The culture was maintained at 21°C in 4-mL vials in the dark. Every 2 or 3 weeks half of the media was replenished. Four weeks before the experiment began the culture was moved to 10°C to prevent any temperature shock, and the media was doubled weekly.

Experiment 1: Priority Effects across Temperatures

We established microcosms in six-well Falcon plates to test for priority effects across five constant temperatures—6°C, 8°C, 10°C, 12°C, and 14°C—that were selected to reflect the range of seasonal temperatures experienced by mosquitoes and *Lambornella* at JRBP (ʻOʻO) during the wettest quarter, when ciliates and larval mosquitoes are active (for more details, see text S1 [available online]). At each temperature, all microcosms were inoculated with *Lambornella* and assigned to one of three arrival treatment groups ($n = 10$ replicates per treatment): (1) introduction of first-instar larvae, (2) introduction of fourth-instar larvae, or (3) a no-larvae control with mosquito-conditioned water. Each replicate included five mosquito larvae. For each temperature treatment, we used two separate incubators. Replicates 1–6 were placed in the first incubator assigned to that temperature, and replicates 7–10 were placed in the second incubator assigned to that temperature.

Microcosms contained 3 mL of *Lambornella* culture (100 cells/100 μL), 2 mL of mosquito-conditioned water, and a barley seed as a nutrient source, resulting in an initial concentration of 60 cells/100 μL. Previous studies have shown that this is a sufficient dose to cause infection (Ismail et al. 2024; Lyberger et al. 2024), and a pilot experiment confirmed that infection probability increases with dose (fig. S1; figs. S1–S4 are available online).

Microcosms were monitored daily for the first week and biweekly thereafter. We recorded (*a*) the density of free-living *Lambornella* (counted in 100-μL samples under ×40 magnification), (*b*) the number of larvae with parasitic cysts attached to their cuticle, (*c*) the number of infected larvae (with parasites inside the cuticle), (*d*) the intensity of these infections (the number of infectious cells inside the cuticle), and (*e*) larval mortality. The total number of cysts was also quantified but is not presented, as this metric was redundant with the number of larvae with cysts. After removing 100 μL for counting, each sample was replenished with an equal volume of fresh media.

Larvae were fed every other day at half the usual amount (0.05 mg/larva/day) to encourage grazing (Maïga 2017). The experiment's duration was temperature dependent, concluding when larvae in the first-instar treatment level began to pupate, which ranged from 21 days (14°C) to 42 days (8°C). The 6°C treatment level, in which no pupation occurred, was terminated at 56 days when free-living cells were no longer observed.

Experiment 2: Stage-Structured Feeding Trial

To determine the developmental stage at which mosquito larvae are capable of consuming *Lambornella*, we conducted a separate feeding trial using all larval stages. The rearing procedures for this experiment followed those described for experiment 1. To generate larvae at each of the four instar stages simultaneously, we staggered hatching times. Individuals were starved for at least 24 h before the experiment to standardize hunger levels and encourage feeding. For each instar ($n = 5$ per stage), we placed a single larva in a well of a Falcon plate containing 2 mL of *Lambornella* culture and 1 mL of tree hole water (total volume = 3 mL). The *Lambornella* culture used in this trial had an initial concentration of 85 cells/100 μL. Both the larvae and cultures were kept at 10°C both before and during this trial.

We checked each well at 3, 6, 12, 24, and 48 h after exposure for evidence of feeding (i.e., reduction in *Lambornella* cell density). Each larva was housed in an individual well (total = 25 units), and no food was added during the course of the trial. This short-term assay allowed us to assess whether the ability to graze on the free-living parasite varied by developmental stage.

Statistical Analysis

For experiment 1, we separately analyzed each response variable including free-living cell density, number of larvae with cysts, number and intensity of larval infections, and larval survival. Free-living cell densities across time were analyzed using a generalized linear mixed effects model (GLMM) with a generalized Poisson distribution, including fixed effects of temperature, instar, and their interaction. All models included a random intercept for tray nested within incubator to account for the experimental design unless otherwise noted. The proportion of larvae with cysts was analyzed at the time of peak cyst formation using a binomial GLMM with fixed effects of temperature (modeled as a quadratic polynomial to account for potentially nonlinear effects of temperature observed in previous work; Lyberger et al. 2024) and instar treatment (first or fourth). The proportion of larvae infected at the end of the experiment was analyzed using a binomial GLMM with temperature as a linear fixed effect, as the relationship appeared approximately linear. Infection intensity, measured as the total number of cells across infected larvae, was analyzed using a zero-inflated negative binomial model. In the analyses of infection and intensity, we analyzed only the first-instar treatment level because we observed zero infections in the fourth-instar treatment level. Larval survival was analyzed at the end of the experiment using a binomial GLMM including instar and temperature as fixed effects. Because mortality was nearly absent in the fourth-instar treatment, we additionally evaluated temperature-dependent mortality within the first-instar treatment using a binomial GLMM with linear and quadratic temperature terms. To better account for the temporal dynamics of larval mortality, we also analyzed survival using a discrete-time proportional hazards model. We constructed Kaplan-Meier-style survival curves and reported the resulting hazard ratios for temperature. For experiment 2, to measure grazing intensity, we analyzed the effects of larval instar stage and time on log-transformed free-living *Lambornella* cell counts using a linear mixed effects model with a random intercept to account for repeated measures. All analyses were conducted in R (ver. 4.1.1; R Core Team 2021), using the packages lme4 (Bates et al. 2015) for GLMMs and glmmTMB (Brooks et al. 2017) for the zero-inflated model, and fixed effects were tested using type III Wald χ^2 tests in the car package (Fox and Weisberg 2012). Model assumptions were evaluated using simulation-based residual diagnostics from the DHARMa package, including checks for overdispersion and zero inflation (Hartig and Hartig 2017). Statistical significance was assessed using likelihood ratio tests, with Bonferroni correction applied within predictor families to control for multiple testing.

Results

Experiment 1: Free-Living Cells

In the late-arrival treatment level, where *Lambornella* were introduced to fourth-instar larvae, free-living *Lambornella* densities declined rapidly across all temperatures (fig. 1). Densities dropped by more than 50% within 1 day, demonstrating strong suppression by larger larvae. In contrast, first-instar larvae suppressed *Lambornella* more gradually, with cell densities reaching half of the initial values only after roughly 10–20 days. This suppression occurred earlier at higher temperatures, likely because of accelerated larval development to predatory stages. Control treatment levels without larvae showed that *Lambornella* populations increased to peak densities at warmer temperatures (10°C, 12°C, and 14°C), whereas at colder

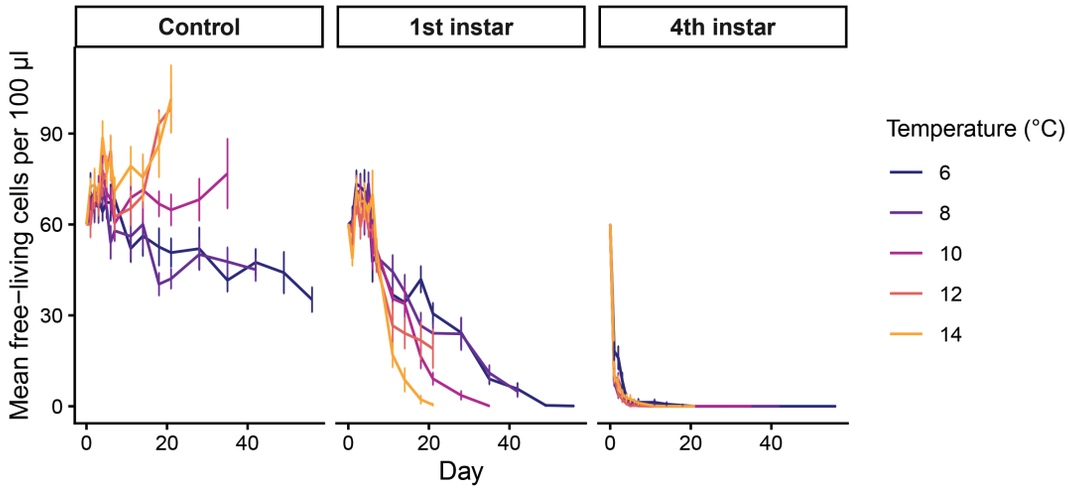


Figure 1: Plots show the density of free-living *Lambornella* over time (mean ± 1 SE) in experiment 1. Colors represent temperature treatments, and panels show arrival timing treatments. Fourth-instar *Aedes sierrensis* larvae reduced free-living *Lambornella* density immediately and more dramatically than first instars, which eventually reduced *Lambornella* density more strongly at higher temperatures.

temperatures (6°C and 8°C), densities declined slightly from initial concentrations. Our statistical model indicated significant effects of time and larval stage on free-living *Lambornella* density, with these effects varying across temperatures, as evidenced by significant interactions between time and temperature ($\chi^2_1 = 33.94$, $P < .001$), time and larval stage ($\chi^2_2 = 26.01$, $P < .001$), and time, temperature, and larval stage ($\chi^2_2 = 151.43$, $P < .001$).

Experiment 1: Parasitic Cysts and Infection

Both temperature and arrival treatment significantly affected the proportion of larvae with parasitic cysts. The number of larvae with parasitic cysts was significantly higher in the first-instar treatment level compared with the fourth-instar treatment level ($\chi^2_1 = 81.88$, $P < .001$). Quadratic effects of temperature indicated a nonlinear relationship, with intermediate temperatures yielding the highest proportion of larvae with cysts ($\chi^2_2 = 18.22$, $P < .001$; fig. 2*A*). The interaction between temperature and instar treatment was not significant and was dropped from our model.

No infections were observed in the fourth-instar treatment level, likely a result of the strong suppression of free-living *Lambornella*. For the first-instar treatment level, the infection rate averaged across all temperature treatments was 27%. Within the first-instar treatment level, we found a significant positive effect of temperature on infection rates ($\chi^2_1 = 14.12$, $P = .002$; fig. 2*B*) and infection intensities ($\chi^2_1 = 12.73$, $P < .001$; fig. S2).

Larval survival in this experiment was generally high (fig. 2*C*). Consistent with the lack of infection observed, nearly all larvae survived in the fourth-instar treatment level with the exception of three individuals in the 14°C treatment, equal to a 1% mortality rate. In contrast, we saw an average mortality rate of 11% in the first-instar treatment level. In the binomial GLMM including both instar treatments, mortality was significantly higher in the first-instar treatment than in the fourth-instar treatment ($\chi^2_1 = 13.26$, $P < .001$), whereas temperature was not significant ($\chi^2_1 = 0.28$, $P = .59$). Because mortality was nearly absent in the fourth-instar treatment, we then evaluated the shape of the temperature-mortality relationship within the first-instar treatment only. In this model, mortality was highest at intermediate temperatures, but the quadratic temperature effect was not statistically significant ($\chi^2_1 = 2.74$, $P = .10$). Consistent with these patterns, a Cox proportional hazards analysis of first-instar larvae showed no significant temperature effect on mortality risk (hazard ratios 1.5–4.8, all 95% confidence intervals overlapping; fig. S3). All statistically significant effects reported here remained significant after correction for multiple comparisons.

Experiment 2: Stage-Structured Feeding

We found that larval instar stage had a significant effect on grazing of free-living *Lambornella* ($\chi^2_4 = 34.98$, $P < .001$; fig. 3). Later instars consumed *Lambornella* more rapidly than earlier instars. Specifically, fourth instars reduced *Lambornella* density by an average of 71% after 24 h. Second and third instars reduced densities by 29% and 34%, respectively. In contrast, first instars had no measurable effect on *Lambornella* density, with a 1%

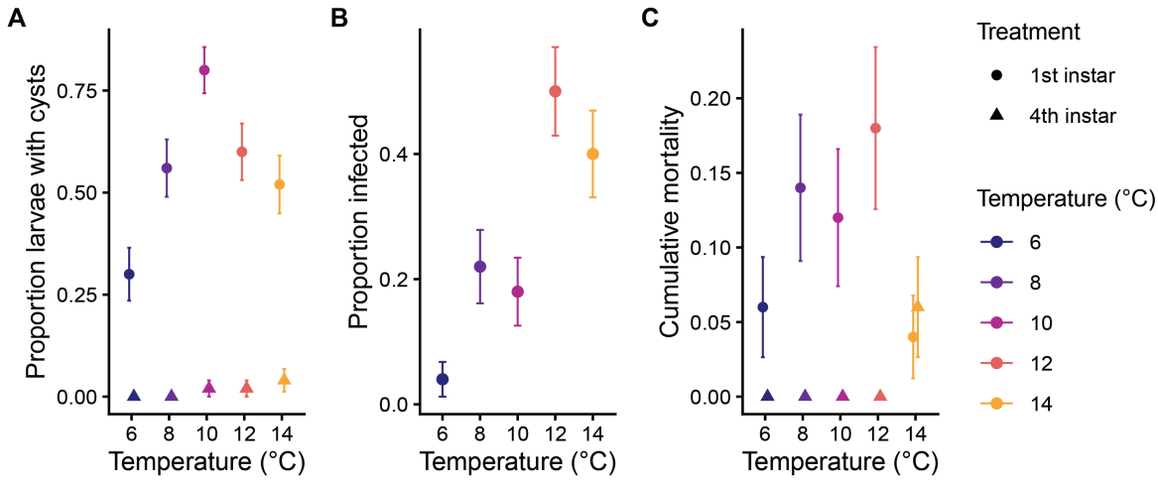


Figure 2: Plots show mean ± 1 SE for proportion of larvae with parasitic cysts (*A*), proportion of larvae infected (first-instar treatment level only, since no larvae were infected in the fourth-instar treatment level; *B*), and proportion of larvae that died from experiment 1 (*C*). Colors represent temperature treatments, and point shapes represent arrival timing treatments. Parasite cysts, infection, and resulting larval mortality of the mosquito *Aedes sierrensis* increased at intermediate and warm temperatures for larvae exposed to *Lambornella* as first instars, while no such effects were observed for fourth instars.

increase from initial densities, comparable to the no-larvae control (12% increase).

Discussion

Our study demonstrates that stage-specific priority effects, mediated by an ontogenetic shift from vulnerable host to effective predator, can be a strong determinant of infection outcomes in the *Aedes sierrensis–Lambornella clarki* system. The relative arrival (or emergence) timing of the mosquito larvae and their parasites was the primary driver of the interaction's outcome, shaping whether the ciliate population was suppressed or successfully established infections and, conversely, whether the mosquito population had high survival or infection-induced mortality. As we predicted, when the host had a significant developmental priority (fourth-instar larvae), they acted as predators, rapidly driving the free-living ciliates to low population densities and completely preventing infection (fig. 1). In contrast, when the parasite had the temporal

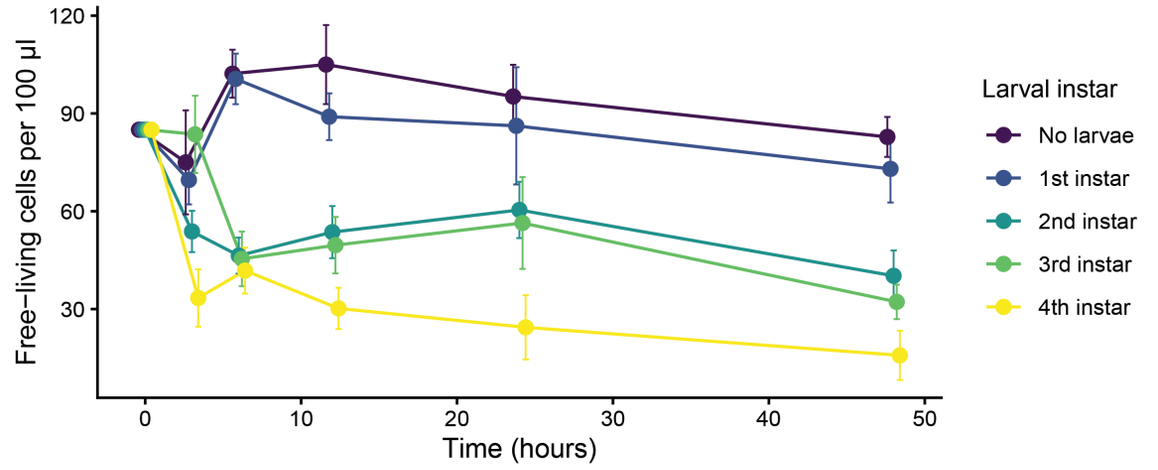


Figure 3: This plot shows the density of free-living *Lambornella* over time (mean ± 1 SE) in the four larval instar treatments from experiment 2, which was conducted at 10°C. Colors represent instar stage (first through fourth) of the mosquito *Aedes sierrensis* or *Lambornella* density in the absence of larval mosquitoes.

advantage of encountering the early host stage (first-instar larvae), they were able to establish infections, escaping predation and eventually killing some infected larvae (fig. 2). Experiment 2 confirmed that at 10°C only second, third, and fourth instars are capable grazers of free-living *Lambornella*, a finding consistent with a previous observation (Washburn et al. 1988), which suggests a sharp developmental threshold in predation on the parasite (fig. 3). In pilot experiments, we have found that at 10°C larvae transition from first to second instars at around 6 days, which roughly corresponds to the start of a decline in free-living cells in experiment 1 (see fig. S4 for all transition times between instars). This dynamic provides a clear example that demonstrates how priority effects can be powerful drivers in consumer-resource interactions.

We also found that temperature mediated the strength of these priority effects, in which warmer temperatures significantly amplified the priority effect of the parasite. While infection was only possible when parasites arrived before hosts developed into later instars, the rate of successful infection of larvae exposed as first instars rose substantially as temperatures increased (fig. 2*B*). This result occurred despite several key host advantages being enhanced at warmer temperatures. Specifically, higher temperatures accelerate the host's developmental rate toward larger, less susceptible instars (Washburn et al. 1988; Couper et al. 2024), which have higher predation rates on the parasite's free-living stage (fig. 3). Future studies testing the temperature sensitivity of this stage-dependent predation are needed to confirm the generality of this result. In addition, the host's immune capacity increases with temperature across the range tested in this experiment (Murdock et al. 2012; Farner et al. 2026). Ultimately, the thermal acceleration of the parasite's replication and invasion rates was enough to outweigh increases in the host developmental, immunological, and predatory defenses. However, our previous work shows that infection rates decline at temperatures above 14°C (Ismail et al. 2024; Lyberger et al. 2024), suggesting that the effect of temperature is nonlinear. As a result, at temperatures higher than tested here, the effect of warming may be reduced or even reversed.

Prior work on temperature-dependent intraguild predation suggests that the strengthening of priority effects we observed with warming may occur broadly in aquatic communities. In these communities, ontogenetic role reversals are widespread, where the young of many species begin as vulnerable planktivores but grow to become predators, sometimes preying on the young of their own former predators (Minto and Worm 2012; Nilsson et al. 2019). Warming can disproportionately benefit predators by increasing foraging efficiency more steeply than their prey's growth toward a size refuge (e.g., Twardochleb et al. 2020; Maszczyk et al. 2023), which would strengthen priority effects in intraguild predation systems. In one example, warming was found to shift the balance from invasive green crabs toward native blue crabs by increasing attack rates and favoring the intraguild predator at higher temperatures, which in a system with alternative states creates the potential for amplified priority effects (Rogers et al. 2018). In freshwater odonates, warming can create asymmetric predation when one species develops much faster at higher temperatures (Suhling et al. 2013) and can intensify intraguild predation overall (Frances and McCauley 2018). Across these examples, warming tends to increase predation by the species whose foraging and growth rates respond to temperature most strongly, which tightens the temporal window in which later-arriving, vulnerable stages can escape suppression. This temporal window is a critical feature determining how size-mediated priority effects structure communities (Rasmussen et al. 2014).

By contrast, warming can have weak, neutral, or negative effects when temperature does not favor the process that generates a given priority effect. Under conditions tested here, warming accelerated parasite proliferation and invasion more than host development, predation, and immune defense. This produced higher infection rates, thus strengthening the parasite-favored priority effect. At higher temperatures above 14°C, however, faster host development or improved defense could weaken the parasite-favored priority effect. In other cases, temperature may have little influence on priority effects, as reported in other consumer-resource contexts (e.g., Sniegula et al. 2019; Raczyński et al. 2022). For example, in odonate assemblages from Neotropical tree holes, temperature was not a strong predictor of species occupancy, despite strong priority effects among predators (Fincke 1999). Hatching phenology itself might be temperature dependent, but shifts in emergence do not always translate into size-mediated priority effects (Stahl and Johansson 2024). Theoretical work points to similar contingencies; in a stage-structured intraguild predation model, Thunell et al. (2021) found that warming can increase interspecific competition while reducing effective predation on their resource, moving the system away from parameter space in which priority effects occur. More broadly, this highlights that the strength and direction of priority effects emerge from the relative thermal sensitivities of interacting traits, not from temperature alone.

These experimentally demonstrated priority effects provide a potential explanation for the high degree of temporal and spatial variability in infection rates seen in natural tree hole communities (Egerter and Anderson 1985; Washburn and Anderson 1986; Farner et al. 2026). Several patterns observed in the field—where some tree

holes harbor infected mosquitoes one year but not the next or where infection appears late in a season—could be the result of these priority effects. Even subtle year-to-year or within-season variation in rainfall, flooding, and temperature may generate large enough phenological shifts in mosquito hatching, larval development, and *Lambornella* emergence to change whether ciliates encounter larvae during the vulnerable early-instar window or after larvae have developed into predators of the free-living ciliate. Many *Aedes* mosquitoes characteristically lay their eggs in successive bands above the waterline, meaning that different rainfall events can trigger different cohorts of mosquito eggs to hatch (Edgerly et al. 1993). Although little is known about the specific triggers of *Lambornella* transformation from desiccated resting cysts, it is likely similar to other ciliates and driven by environmental factors like flooding, temperature, and metabolites (Washburn et al. 1991*a*; Bracht et al. 2016). Such cue-driven shifts can alter trophic interactions when species differ in their sensitivity to temperature or precipitation (Thackeray et al. 2016), particularly when altered timing changes the stage or abundance of prey, predators, hosts, or parasites at encounter (Damien and Tougeron 2019).

The interplay between phenology and stage-dependent predation may be part of what generates the dynamic mosaic of infection prevalence seen across the landscape, in addition to dispersal events within the meta-population (Egerter and Anderson 1986). Under climate change, warmer winters may lead to larger outbreaks within infected tree holes in colder parts of the range and a potential shift northward in peak prevalence (Farner et al. 2026). Beyond these two main interacting species, early arrival or emergence of *Lambornella* could also have impacts on other microorganisms within the aquatic tree hole community. There is often a strong successional pattern among inhabiting microbes, and predation by mosquito larvae can alter this sequence (Norman and Walker 2019; Pascual-García and Bell 2020). In more complex tree hole systems, temperature-mediated priority effects may determine the outcome of competition between multiple invertebrate predators (Fincke 1994, 1999) or dictate infection dynamics across multiple co-occurring host species (Copeland and Craig 1992).

Understanding these temperature-dependent priority effects is relevant for other host-parasite systems with complex life cycles where infectious stages are vulnerable to predation (Johnson et al. 2010), such as trematode cercariae (Goedknegt et al. 2015) and the free-swimming zoospores of amphibian fungal pathogens (Kagami et al. 2007). In these systems, the net outcome of warming depends on a "thermal race" between trophic levels: if infective stages respond more strongly to warming than their predators, increasing temperature should widen the range of conditions that lead to successful infection. By contrast, if warming disproportionately accelerates the development, feeding rates, or immune responses of predators, this may greatly suppress these parasites. Because the free-living stages of many parasites occupy open water where they are exposed to diverse grazers, even small differences in phenology and thermal responses among hosts, parasites, and predators may tip these systems between states of high and low infection. More generally, as climate change continues to alter the phenology of interacting species, we can expect that even small shifts in arrival time may be amplified by warming whenever the biological mechanism required to secure a priority effect, such as infectious proliferation in a parasite or resource preemption in a predator, disproportionately benefits the early-arriving species before the opponent can reach a less vulnerable stage.

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Statement of Authorship

All authors conceived of the idea, K.L. ran the experiment, conducted the analysis, and wrote the first draft. All authors contributed to writing and revisions. T.F. and E.A.M. provided supervision.

Data and Code Availability

All data and code have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.q573n5twk; Lyberger et al. 2026).

Literature Cited

Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford.

Arnell, J. H., and L. T. Nielsen. 1972. Mosquito studies (Diptera, Culicidae). XXVII. The varipalpus group of *Aedes* (Ochlerotatus). Contributions of the American Entomological Institute. American Entomological Institute, Ann Arbor, MI.

Barkai, A., and C. McQuaid. 1988. Predator-prey role reversal in a marine benthic ecosystem. Science 242:62–64.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. Journal of Animal Ecology 65:77–84.

Bracht, J. R., E. M. Ferraro, and K. A. Bracht. 2016. How do cysts know when to hatch? the role of ecological communication in awakening latent life. Pages 97–119 *in* G. Witzany and M. Nowacki, eds. Biocommunication of ciliates. Springer, Cham.

Brooks, M. E., K. Kristensen, K. J. Van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9:378–400.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

Choh, Y., M. Ignacio, M. W. Sabelis, and A. Janssen. 2012. Predator-prey role reversals, juvenile experience and adult antipredator behaviour. Scientific Reports 2:728.

Cohen, J. M., E. L. Sauer, O. Santiago, S. Spencer and J. R. Rohr. 2020. Divergent impacts of warming weather on wildlife disease risk across climates. Science 370:eabb1702.

Copeland, R. S., and G. B. Craig Jr. 1992. Interspecific competition, parasitism, and predation affect development of *Aedes hendersoni* and *A. triseriatus* (Diptera: Culicidae) in artificial treeholes. Annals of the Entomological Society of America 85:154–163.

Corliss, J. O., and D. W. Coats. 1976. A new cuticular cyst-producing tetrahymenid ciliate, *Lambornella clarki* n. sp., and the current status of ciliatosis in culicine mosquitoes. Transactions of the American Microscopical Society 95:725–739.

Couper, L. I., J. E. Farner, K. P. Lyberger, A. S. Lee, and E. A. Mordecai. 2024. Mosquito thermal tolerance is remarkably constrained across a large climatic range. Proceedings of the Royal Society B 291:20232457.

Damien, M., and K. Tougeron. 2019. Prey-predator phenological mismatch under climate change. Current Opinion in Insect Science 35:60–68.

Darsie, R. J., and R. A. Ward. 2005. Identification and geographical distribution of the mosquitoes of North America, north of Mexico. University Press of Florida, Gainesville.

Dawson-Glass, E., R. Schiafo, S. E. Kuebbing, and K. L. Stuble. 2025. Warming-induced changes in seasonal priority effects drive shifts in community composition. Ecology 106:e4504.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

Edgerly, J. S., M. S. Willey, and T. P. Livdahl. 1993. The community ecology of *Aedes* egg hatching: implications for a mosquito invasion. Ecological Entomology 18:123–128.

Egerter, D. E. and J. R. Anderson. 1985. Infection of the western treehole mosquito, *Aedes sierrensis* (Diptera: Culicidae), with *Lambornella clarki* (Ciliophora: Tetrahymenidae). Journal of Invertebrate Pathology 46:296–304.

Egerter, D. E., J. R. Anderson, and J. O. Washburn. 1986. Dispersal of the parasitic ciliate *Lambornella clarki*: implications for ciliates in the biological control of mosquitoes. Proceedings of the National Academy of Sciences of the USA 83:7335–7339.

Farner, J. E., K. P. Lyberger, L. I. Couper, M. Cruz-Loya, and E. A. Mordecai. 2026. Nonlinear effects of temperature on mosquito parasite infection across a large geographic climate gradient. Ecology 107:e70307.

Fick, S. E., and R. J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Fincke, O. M., 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia 100:118–127.

———. 1999. Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority. Ecological Entomology 24:13–23.

Fonseca, M. M., A. Pallini, E. Lima, and A. Janssen. 2018. Ontogenetic stage-specific reciprocal intraguild predation. Oecologia 188:743–751.

Fox, J., S. Weisberg, D. Adler, D. Bates, G. Baud-Bovy, S. Ellison, D. Firth, et al. 2012. Package car. R Foundation for Statistical Computing, Vienna.

Frances, D. N., and S. J. McCauley. 2018. Warming drives higher rates of prey consumption and increases rates of intraguild predation. Oecologia 187:585–596.

Fukami, T. 2004. Assembly history interacts with ecosystem size to influence species diversity. Ecology 85:3234–3242.

———. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Systematics 46:1–23.

Goedknegt, M. A., J. E. Welsh, J. Drent, and D. W. Thieltges. 2015. Climate change and parasite transmission: how temperature affects parasite infectivity via predation on infective stages. Ecosphere 6:1–9.

Grainger, T. N., A. I. Rego, and B. Gilbert. 2018. Temperature-dependent species interactions shape priority effects and the persistence of unequal competitors. American Naturalist 191: 197–209.

Hartig, F., and M. F. Hartig. 2017. Package DHARMa. R package. https://CRAN.R-project.org/package=DHARMa.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745–764.

Hoverman, J. T., B. J. Hoye, and P. T. Johnson. 2013. Does timing matter? how priority effects influence the outcome of parasite interactions within hosts. Oecologia 173:1471–1480.

Ismail, S., J. Farner, L. Couper, E. Mordecai, and K. Lyberger. 2024. Temperature and intraspecific variation affect host-parasite interactions. Oecologia 204:389–399.

Johnson, P. T., A. Dobson, K. D. Lafferty, D. J. Marcogliese, J. Memmott, S. A. Orlofske, R. Poulin, and D. W. Thieltges. 2010. When parasites become prey: ecological and epidemiological significance of eating parasites. Trends in Ecology and Evolution 25:362–371.

Kagami, M., E. von Elert, B. W. Ibelings, A. de Bruin, and E. Van Donk. 2007. The parasitic chytrid, *Zygorhizidium*, facilitates the growth of the cladoceran zooplankter, *Daphnia*, in cultures of the inedible alga, *Asterionella*. Proceedings of the Royal Society B 274:1561–1566.

Luong, L. T., and K. J. Mathot. 2019. Facultative parasites as evolutionary stepping-stones towards parasitic lifestyles. Biology Letters 15:20190058.

Lyberger, K., J. Farner, L. Couper, and E. A. Mordecai. 2024. A mosquito parasite is locally adapted to its host but not temperature. American Naturalist 204:121–132.

Lyberger, K., J. Farner, E. A. Mordecai, and T. Fukami. 2026. Data from: Warming strengthens priority effects driven by an ontogenetic shift from host to predator. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.q573n5twk.

MacDonald, H., and D. Brisson. 2022. Host phenology regulates parasite-host demographic cycles and eco-evolutionary feedbacks. Ecology and Evolution 12:e8658.

Maïga H. 2017. Guidelines for routine colony maintenance of *Aedes* mosquito species. FAO-IAEA, Vienna. https://www.iaea.org/resources/manual/guidelines-for-routine-colony-maintenance-of-aedes-mosquito-species-version-10.

Maszczyk, P., W. Wilczynski, Z. M. Gliwicz, K. Leniowski, M. L. Zebrowski, J. S. Lee, and E. Babkiewicz. 2023. Mechanisms of increasing predation by planktivorous fish with rising temperature may explain the temperature–body size relationships in zooplankton. Frontiers in Ecology and Evolution 11:1187404.

Minto, C., and B. Worm. 2012. Interactions between small pelagic fish and young cod across the North Atlantic. Ecology 93:2139–2154.

Murdock, C. C., K. P. Paaijmans, A. S. Bell, J. G. King, J. F. Hillyer, A. F. Read, and M. B. Thomas. 2012. Complex effects of temperature on mosquito immune function. Proceedings of the Royal Society B 279:3357–3366.

Nilsson, J., H. Flink, and P. Tibblin. 2019. Predator-prey role reversal may impair the recovery of declining pike populations. Journal of Animal Ecology 88:927–939.

Norman, B. C., and E. D. Walker. 2019. Succession of bacteria and fungi in leaf litter of tree hole habitats: responses of diversity to mosquito larvae. Aquatic Microbial Ecology 83:237–250.

Öhlund, G., P. Hedström, S. Norman, C. L. Hein, and G. Englund. 2015. Temperature dependence of predation depends on the relative performance of predators and prey. Proceedings of the Royal Society B 282:20142254.

Olito, C., and T. Fukami. 2009. Long-term effects of predator arrival timing on prey community succession. American Naturalist 173:354–362.

Orlofske, S. A., R. C. Jadin, and P. T. Johnson. 2015. It's a predator-eat-parasite world: how characteristics of predator, parasite and environment affect consumption. Oecologia 178:537–547.

Padeffke, T., and F. Suhling. 2003. Temporal priority and intraguild predation in temporary waters: an experimental study using Namibian desert dragonflies. Ecological Entomology 28:340–347.

Pascual-García, A., and T. Bell. 2020. Community-level signatures of ecological succession in natural bacterial communities. Nature Communications 11:2386.

Pepi, A., T. Hayes, and K. Lyberger. 2023. Thermal asymmetries influence effects of warming on stage and size-dependent predator-prey interactions. Theoretical Ecology 16:105–115.

Raczyński, M., R. Stoks, and S. Sniegula. 2022. Warming and predation risk only weakly shape size-mediated priority effects in a cannibalistic damselfly. Scientific Reports 12:17324.

Rasmussen, N. L., B. G. Van Allen, and V. H. Rudolf. 2014. Linking phenological shifts to species interactions through size-mediated priority effects. Journal of Animal Ecology 83:1206–1215.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Rogers, T. L., T. C. Gouhier, and D. L. Kimbro. 2018. Temperature dependency of intraguild predation between native and invasive crabs. Ecology 99:885–895.

Sánchez-Garduño, F., P. Miramontes, and T. T. Marquez-Lago. 2014. Role reversal in a predator-prey interaction. Royal Society Open Science 1:140186.

Sniegula, S., M. J. Golab, and F. Johansson. 2019. Size-mediated priority and temperature effects on intra-cohort competition and cannibalism in a damselfly. Journal of Animal Ecology 88:637–648.

Stahl, L., and F. Johansson. 2024. Effects of temperature and resource level on interspecific interactions in two species of *Odonata* larvae. Ecology and Evolution 14:e11502.

Suhling, I. D. A., and F. Suhling. 2013. Thermal adaptation affects interactions between a range-expanding and a native odonate species. Freshwater Biology 58:705–714.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245.

Thunell, V., M. Lindmark, M. Huss, and A. Gårdmark. 2021. Effects of warming on intraguild predator communities with ontogenetic diet shifts. American Naturalist 198:706–718.

Twardochleb, L. A., T. C. Treakle, and P. L. Zarnetske. 2020. Foraging strategy mediates ectotherm predator-prey responses to climate warming. Ecology 101:e03146.

Stroud, J. T., B. M. Delory, E. M. Barnes, J. M. Chase, L. De Meester, J. Dieskau, T. N. Grainger, et al. 2024. Priority effects transcend scales and disciplines in biology. Trends in Ecology and Evolution 39:677–688.

Vass, M., A. J. Székely, E. S. Lindström, O. A. Osman, and S. Langenheder. 2021. Warming mediates the resistance of aquatic bacteria to invasion during community coalescence. Molecular Ecology 30:1345–1356.

Washburn, J. O., and J. R. Anderson. 1986. Distribution of *Lambornella clarki* (Ciliophora: Tetrahymenidae) and other mosquito parasites in California treeholes. Journal of Invertebrate Pathology 48:296–309.

Washburn, J. O., J. R. Anderson, and D. R. Mercer. 1991*a*. Parasitism of newly-hatched *Aedes sierrensis* (Diptera: Culicidae) larvae by *Lambornella clarki* (Ciliophora: Tetrahymenidae) following habitat flooding. Journal of Invertebrate Pathology 58:67–74.

Washburn, J. O., M. E. Gross, D. R. Mercer, and J. R. Anderson. 1988. Predator-induced trophic shift of a free-living ciliate: parasitism of mosquito larvae by their prey. Science 240:1193–1195.

Washburn, J. O., D. R. Mercer, and J. R. Anderson. 1991*b*. Regulatory role of parasites: impact on host population shifts with resource availability. Science 253:185–188.

Yang, L. H., and E. V. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 13:1–10.

Zou, H. X., and V. H. Rudolf. 2023. Bridging theory and experiments of priority effects. Trends in Ecology and Evolution 38:1203–1216.

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