

Appendix A: Experiments

Detailed methods for larvae temperature experiments

Experimental methodology

Source of Ostertagia gruehneri eggs

Two adult female reindeer housed at the Wildlife Research Station, Faculty of Veterinary Medicine, University of Calgary, were experimentally infected with *O. gruehneri* third stage larvae (L3) sourced from the Bathurst caribou herd, Northwest Territories and Nunavut, Canada (Hoar 2012). Fresh fecal samples were collected from the infected reindeer and refrigerated at approximately 4°C. No more than 24 hours later, *O. gruehneri* eggs were isolated from the fecal samples following the methods outlined in Hoar *et al.* (2012).

Data Collection

Following the isolation of *O. gruehneri* eggs from reindeer feces, forty Petri dishes of 3 cm diameter were seeded with approximately 50 eggs each. These Petri dishes were then distributed into incubators with 100% relative humidity and set at 5, 10, 15, 20, 25, 30, 35, and 40°C, respectively, thus yielding five replicate cohorts for each temperature trial. Larval food (250 µl; Hubert and Kerboeuf, 1984) was added to each Petri dish on the same day at least one egg had hatched in all of the five replicates of a given temperature trial. Initially, each replicate was examined daily at room temperature (~10-15 minutes per replicate) using a Leica L2 dissecting microscope at 20-25x magnification, when the numbers of live individuals in each stage of development (eggs, L1, L2, L3) were recorded. Larvae that were moving were hereby considered to be alive, whereas immobile larvae were considered to be dead. Eggs were considered dead when a breakdown of internal structure was noted or when the entire egg turned black. Examination of all replicates within a given temperature treatment was reduced to every three days once a minimum of one L3 was observed in each of the five replicates. The only exception to this sampling protocol was the 5°C treatment where, due to the slower development rate at this temperature, replicates were examined every three days from the beginning of the trial. At each sampling occasion, egg and larval counts were performed three times for every replicate

dish to minimize the effect of potential observer error in detecting eggs and larvae, in correctly identifying the developmental stages of larvae, and in correctly assessing larval survival. Replicates continued to be examined until no live larvae or eggs were observed, or for a maximum of 120 days (a conservative estimate of the number of days with mean temperatures $>0^{\circ}\text{C}$ in the Canadian low Arctic).

Model development

To extract development and mortality rates from the cohort data, we begin by describing a cohort model that tracks individuals through the pre-infective (egg, L1, L2) and infective (L3) life stages. As we are primarily interested in the appearance of the infective L3, the model considers a simplified life cycle where eggs, L1 and L2 are pooled into a “pre-infective” class (subscript 0), and larvae in the L3 stage constitute the “infective” class (subscript 3). The model specifies the expected number of individuals in the pre-infective and infective classes as a function of time and temperature, and is specifically designed to account for variability in development rates among individuals as well as for any mortality that may occur between the start of the experiment at time $t_0 = 0$ and a given sampling day t .

We first determine the probability that an individual in experimental treatment i experiencing rearing temperature T_i is alive on day t but has not yet developed to the infective L3 stage. Régnière and Powell (2003) argue that in many cases the actual development time of an individual at temperature T , $t^*(T)$, will have a log-normal distribution with a mean that equals the cohort mean, $\tau(T)$. From this, it follows that development times to the infective stage are log-normally distributed:

$$t^*(T) \sim \text{logN}\left(-\frac{\sigma^2}{2} - \log(\rho_0(T)), \sigma^2\right), \quad (\text{A1})$$

where the cohort mean development rate, $\rho_0(T) = 1/\tau(T)$, is the inverse of the cohort mean development time, σ is the scale parameter of the log-normal distribution, and $-\sigma^2/2$ is a correction to the mean of the lognormal so the expected development time is $1/\rho_0(T)$ (Hilborn

52 and Mangel 1997). Given a starting cohort of N_0 eggs, the expected number of live, pre-infective
 53 individuals on sampling day t is

$$L_0(t, T_i) = N_0 \overbrace{\exp(-\mu_0(T_i) t)}^{\text{not yet dead}} \underbrace{\left(1 - \Phi \left[\frac{\overbrace{\left(\ln(t \rho_0(T_i)) + \frac{\sigma^2}{2} \right)}^{\text{probability developed}}}{\sigma} \right] \right)}_{\text{not yet developed}} \quad (\text{A2})$$

54 where $\mu_0(T_i)$ is the per capita mortality rate of pre-infectives (eggs, L1, and L2) at temperature
 55 T_i and Φ is the cumulative distribution function of the standard normal distribution. To calculate
 56 the expected number of larvae in the L3 stage on day t , we first need to account for the fact that
 57 – due to the variability in development times – different individuals will start this life stage at
 58 different times. The expected number of individuals that start the L3 stage exactly at time t ,
 59 $L_{3,\text{start}}(t, T_i)$, can be obtained from the probability density function of the lognormal
 60 development distribution, discounted for any mortality occurring in the pre-infective stage:

$$L_{3,\text{start}}(t, T_i) = \frac{N_0}{t \sqrt{2 \pi \sigma^2}} \exp \left[-\frac{\left(\ln(t \rho_0(T_i)) + \frac{\sigma^2}{2} \right)^2}{2 \sigma^2} - \mu_0(T_i) t \right] \quad (\text{A3})$$

61 The expected number of larvae in the infective L3 stage on sampling day t is obtained by
 62 integrating over all larvae that have reached the L3 stage before day t while discounting for any
 63 mortality that has occurred since these larvae started the L3 stage:

$$L_3(t, T_i) = \int_0^t L_{3,\text{start}}(t', T_i) \exp(-\mu_3(T_i)(t - t')) dt' \quad (\text{A4})$$

64 where $\mu_3(T_i)$ is the per capita mortality rate of infectious L3 at temperature T_i .

Metabolic Theory of Ecology relationships

We assessed up to four different sub-models for the temperature dependencies of $\mu_0(T)$, $\mu_3(T)$, and $\rho_0(T)$: (1) no relationship among parameters at different temperatures, (2) constant parameter value across temperatures, (3) an Arrhenius relationship that describes increasing development and mortality rates with temperature (McCoy and Gillooly 2008), or (4) a Sharpe-Schoolfield relationship that builds on the Arrhenius relationship to include the possibility of upper and/or lower temperature thresholds (Schoolfield et al. 1981; Molnár et al. 2013).

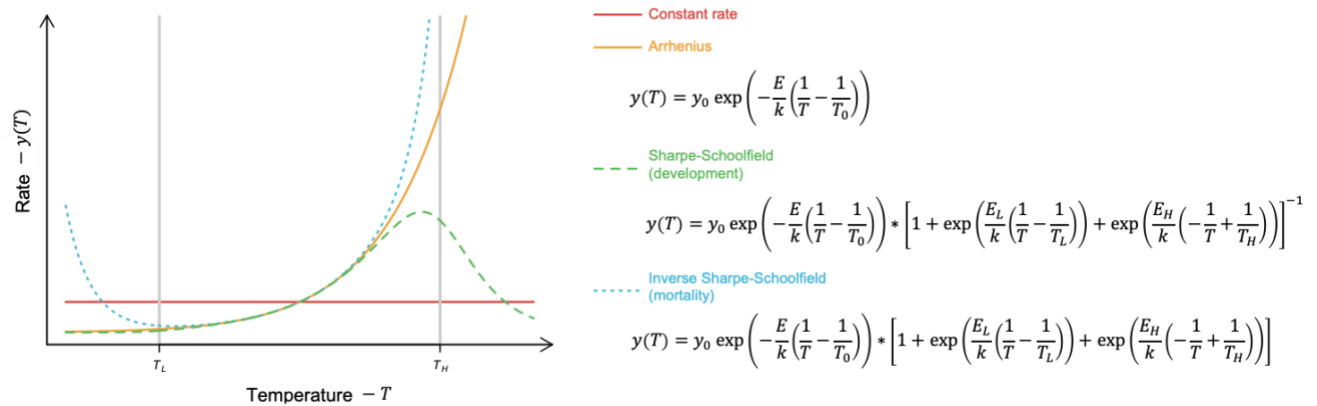


Figure A1. Illustration of the possible MTE relationships for mortality and development parameters (written generally as $y(T)$), with corresponding equations on the right. The vertical grey lines indicate the lower and upper temperature thresholds in the Sharpe-Schoolfield relationships (green and blue dashed lines). The inverse Sharpe-Schoolfield relationship is tailored to the mortality rate, which tends to increase at extreme values. Parameters are described in Table A1, and $k = 8.62 \times 10^{-5}$ eV K⁻¹ is Boltzmann's Constant.

As described in the main text, testing all possible combinations of five MTE relationships (constant, Arrhenius, and Sharpe-Schoolfield with lower, upper, or both thresholds) for the three parameters ($n = 3^5 = 243$ models) was not practically feasible due to the computation time involved, and also would have increased the chance of spurious significant results. We chose nine models to test based on initial parameter estimates and limitations of the data (Table A2). Notably, this suite of 9 models does not include the Sharpe-Schoolfield model with a

lower temperature threshold, since the lower bound of temperatures tested in experiments was 5 °C, which is well above the lower thermal limits of this parasite. We encountered convergence issues when trying to estimate an upper thermal bound for L3 because of low survival to this stage at high temperatures, but include results for one of those models from which the estimates were applied in the population modelling.

Parameter estimation

We fit the cohort model, incorporating temperature-dependent parameters $\mu_0(T)$, $\rho_0(T)$, and $\mu_3(T)$ in a Bayesian framework that could accommodate a hierarchical structure accounting for potential variability in parameters among replicates, latent variables, as well as the triplicate counts at each sampling occasion. We included a random effect for replicate (i.e., petri dish) on the parameters $\mu_0(T_i)$, $\rho_0(T_i)$, $\mu_3(T_i)$, and σ within each temperature trial i . Specifically, the parameter for replicate k was drawn from a log-normal distribution, e.g., $\mu_{0,i,k} \sim \text{logN}(\text{mean log} = \log(\mu_0(T_i)), \text{sd} = 0.05)$. We initially tried to estimate the standard deviation among replicates as a free parameter, but could not achieve convergence in that case and so we assumed the standard deviation to have a fixed value of 0.05 which is relatively small but nonetheless allowed the flexibility to capture observed differences in survival and mortality among replicates (Figure A2).

Due to counting error, the initial number of eggs in each petri dish was not known and so it was treated as a latent variable to be estimated for each temperature, i , and replicate, k , with prior distribution $N_{0,i,k} \sim \text{logNormal}(\log(50) - 0.3^2/2, 0.3)$, with an expected value of 50 eggs.

The likelihood of the pre-infective and infective counts from day 0 to day 120 was calculated assuming Poisson count error for the triplicate observations, with an expected count equal to the prediction from the cohort model for the given day, temperature, and replicate.

We used the MCMC software JAGS (Plummer 2003), and implemented the fitting via R (R Core Team 2021) using the packages rjags (Plummer 2019) and dclone (Sólymos 2010). R code for

the analysis is available at https://github.com/sjpeacock/OsterBou_pop. An example of a model function for Model 3 from Table 2 is provided below on pages 7-8.

We applied relatively uninformative priors on all MTE parameters, but constrained to biologically reasonable values (Table A1).

Table A1. The priors on MTE hyperparameters used in the Bayesian parameter estimation (see Figure A1 for equations).*

Hyperparameter	Description	Units	Prior distribution
γ_0	Parameter value at standardization temperature $T_0 = 15^\circ\text{C}$	d^{-1} (mortality rate) or d (development time)	$\text{log-normal}(\log(0.5), 1)$
E	Activation energy	eV	$\text{log-normal}(\log(0.65), 0.5)$
E_H	Upper inactivation energy	eV	$\text{log-normal}(\log(3.25), 1)$
T_H	Upper temperature threshold	$^\circ\text{C}$	$\text{normal}(23, 3)$

* We report all temperatures in $^\circ\text{C}$ for ease of interpretation, with the conversion to K occurring in the model code.

In total, we had 2,520 unique sampling instances (i.e., temperature, petri dish, and day combinations) with triplicate counts and two larval stages, yielding 15,120 data points. Due to the large amount of data, the hierarchical (non-independent) structure of both the data and the model, and the complexity of the model, we were concerned about overfitting. Thus, we evaluated models by holding out one of the five replicates when estimating parameters, using the remaining four replicates as the training data, and then calculating how well the fitted model predicted the hold-out replicate (i.e., the likelihood of the hold-out data given the model fitted to the training data). This was repeated using each of the five replicates as the hold-out data, and then taking the average likelihood over the five hold-out replicates. We took the model with the lowest average negative log-likelihood among the validation sets as the best

128 model and re-fitted that model to the entire dataset to yield the best parameter estimates for
129 inference and prediction.

```

130 #####
131 # Model 3: A A SSU
132 #####
133 model3 <- function(){
134     #-----
135     # Parameter models
136     # Note: variance in prior distributions specified as precision = sd^-2
137     #-----
138     # For each parameter (u0, u1, rho), draw base value (a) and activation
139     # energy (E)
140     for(j in 1:3){
141         a[j] ~ dlnorm(log(0.5), pow(1, -2))
142         E[j] ~ dlnorm(log(0.65), pow(0.5, -2))
143     }
144     # Set upper threshold to zero for the two Arrhenius relationships
145     for(j in 1:2){
146         Eh[j] <- 0
147         Th[j] <- 0
148     }
149     # Draw upper thresholds for the SS relationship of u1
150     Eh[3] ~ dlnorm(log(3.25), pow(1, -2))
151     Th[3] ~ dnorm(23, pow(3, -2))
152     # Calculate temperature-specific mean parameter value
153     for(i in 1:nT){ # for each temperature treatment
154         for(j in 1:2){ # for the two Arrhenius relationships (u0, u1)
155             p.mean[i,j] <- a[j]*exp(-E[j]/(8.62*10^-5)*(1/(T.obs[i]+273.15)-1/(15+273.15))))
156
157             # For the SS relationships (rho)
158             p.mean[i,3] <- a[3]*exp(-E[3]/(8.62*10^-5)*(1/(T.obs[i]+273.15)-1/(15+273.15)))*(1+exp(Eh[3]/(8.62*10^-
159 5)*(-1/(T.obs[i]+273.15)+1/(Th[3]+273.15))))^(-1)
160         }
161
162         # Sigma - constant across temperature; no metabolic theory underpinning
163         sigma.log ~ dnorm(0, 0.01)
164         for(i in 1:nT){p.mean[i,4] <- exp(sigma.log)}
165
166         # Draw random model parameters (u0, u1, rho, sigma) for each temp and replicate
167         for(i in 1:nT){ # for each temperature
168             for(k in 1:nk){ # for each replicate
169                 for(j in 1:4){ # for each parameter
170                     p.rep[i,j,k] ~ dlnorm(log(p.mean[i,j]), sigp^(-2))}}
171
172             # Draw starting number of eggs in each temp and replicate
173             for(i in 1:nT){ # for each temperature
174                 for(k in 1:nk){ # for each replicate
175                     N0[i,k] ~ dlnorm(log(50)-1/2*(sigN0^2), 1/(sigN0^2))}}
176
177             #-----
178             # Process model
179             #-----
180             for(i in 1:nT){ # for each temperature
181                 for(k in 1:nk){ # for each replicate
182
183                     # Pre-infectives
184                     for(j in 1:nt){
185                         N[i,1,j,k]<-N0[i,k]*exp(-p.rep[i,1,k]*t[j])*(1-
186 phi((log(t[j])*p.rep[i,3,k])+p.rep[i,4,k]^2/2)/p.rep[i,4,k]))
187                     }

```

```

188
189         # Infectives that develop at time "jj"
190         for(j in 1:nt){
191             N1_start[i,j,k]<-N0[i,k]/(t[j]*sqrt(2*3.141593*p.rep[i,4,k]^2))*exp(-
192 1/(2*p.rep[i,4,k]^2)*(log(t[j]*p.rep[i,3,k])+p.rep[i,4,k]^2/2)^2-p.rep[i,1,k]*t[j])
193         }
194         # ...and survive to time j
195         for(j in 1:nt){
196             for(jj in 1:j){
197                 N1_surv[i,j,k,jj]<-N1_start[i,jj,k]*exp(-p.rep[i,2,k]*(t[j]-t[jj]))
198             }
199             # Summed from 1:j
200             N[i,2,j,k]<-sum(N1_surv[i,j,k,1:j]*dt)
201         } #end j
202     }}
203
204     #-----
205     # Data model
206     #-----
207     # n_obs[i,j,k,l,s] is the observed number of larvae alive in
208     # temperature i, time j, replicate k, count l, and stage s
209
210     for(i in 1:nT){ #for each temperature
211         for(k in 1:nk){ # for each replicate
212             for(l in 1:3){ # for each of three counts
213
214                 # Likelihood of initial number of eggs
215                 n_obs[i,1,k,l,1] ~ dpois(N0[i,k])
216
217                 # Likelihood of preinfective and infective stages
218                 # at each timestep
219                 for(s in 1:2){ # for each stage
220                     for(j in 2:nt_obs[i,k]){ # for each timestep
221                         n_obs[i,j,k,l,s] ~ dpois(max(10^-10, N[i,s,ind[i,j,k],k]))
222                     }
223                 }
224             } # end model

```

Supplemental results

Table A2. Model comparison statistics for the MTE models fit to experimental data of *O. gruehneri* larval mortality and development at seven temperature treatments from 5 – 35 °C. The negative log-likelihoods of the training data (four replicates) and of the validation data (one replicate) were averaged across the five different hold-out replicates, and the overall negative log-likelihood is from the given model fitted to all five replicates (which is why it is a larger number than the sum of the other two values).

Model #	μ_0^1	μ_3	ρ_0	np ²	Negative log-likelihood			AIC
					mean	mean		
					training	validation	overall	
model1	I	I	I	22	15675.2	4396.5	20962.9	41970
model5³	A	C	SSU	8	17495.7	4475.8	22663.3	45343
model3	A	A	SSU	9	17520.9	4486.1	22689.1	45396
model7	SSU	A	SSU	11	17519.8	4487.7	22687.1	45396
model10 ⁴	A	SSU	SSU	11	17507.7	4503.1	22777.6	45577
model4	A	C	A	6	19344	4897.4	25148.1	50308
model6	SSU	A	A	9	19370.1	4909.4	25187.7	50393
model2	A	A	A	7	19370.6	4909.6	25189.1	50392
model8	SSU	C	A	8	67626.2	11350.8	25143.3	50303
model9	SSU	C	SSU	10	69712.8	19447.9	440627.6	881275

1. Temperature relationships considered were: I = parameter estimated independently at each temperature ($n = 7$ parameters); C = constant parameter value across temperature ($n = 1$ hyperparameter); A = Arrhenius relationship ($n = 2$ hyperparameters), SSU = Sharpe-Schoolfield relationship with an upper thermal bound ($n = 4$ hyperparameters).

2. The number of (hyper)parameters in the model. For each model, the standard deviation in the log-normal distribution of development times, σ , was also estimated.

3. Model5 in bold was the best-fit MTE model, with the lowest average validation NLL.

4. There were some convergence issues for this model, see Table A5.

Table A3. Parameter estimates¹ for pre-infective and infective mortality and pre-infective development of *O. gruehneri* larvae, estimated separately for each of seven temperature treatments from 5 – 35 °C.

Temperature	μ_0	μ_3	ρ_0
5 °C	0.017 (0.016, 0.019)	0.011 (0.008, 0.014)	0.012 (0.012, 0.013)
10 °C	0.024 (0.023, 0.026)	0.046 (0.042, 0.049)	0.023 (0.022, 0.024)
15 °C	0.103 (0.097, 0.109)	0.024 (0.020, 0.028)	0.021 (0.020, 0.023)
20 °C	0.102 (0.095, 0.110)	0.018 (0.016, 0.019)	0.059 (0.056, 0.063)
25 °C	0.307 (0.288, 0.327)	0.008 (0.006, 0.010)	0.077 (0.072, 0.083)
30 °C	0.469 (0.436, 0.504)	0.072 (0.049, 0.099)	0.086 (0.077, 0.095)
35 °C	0.456 (0.425, 0.489)	1.739 (0.080, 51.570) ²	0.007 (0.001, 0.042) ²

1. The estimate for σ was 0.441 (0.425, 0.457).

2. Estimates in red did not converge, likely because there were no infective larvae counted in any replicate at 35 °C.

Table A4. Hyperparameter estimates¹ for MTE relationships describing pre-infective and infective mortality and pre-infective development of *O. gruehneri* larvae across seven temperatures (Table S2).

Hyperparameter	Parameter		
	μ_0	μ_1	ρ
y_0	0.068 (0.066, 0.070)	0.022 (0.021, 0.023)	0.032 (0.031, 0.033)
E	0.884 (0.865, 0.902)		0.686 (0.659, 0.713)
E_H			7.957 (3.781, 13.390)
T_H			30.568 (30.202, 31.170)

1. The estimate for σ was 0.436 (0.421, 0.451).

Estimation of lower temperature thresholds for population modelling

As described in the main text, we were unable to estimate freezing survival of pre-infective and infective larvae from experiments because the minimum temperature tested was 5 °C. We therefore estimated lower thresholds on mortality parameters by fixing other hyperparameters in the Sharpe-Schoolfield relationship according to their estimated values in Table A5, and estimated just the lower inactivation energy (E_L) and lower temperature threshold (T_L) using data on freezing survival of *Marshallagia marshalli* larvae reported in Figure 3 of Aleuy et al. (2020). Specifically, we fit exponential curves to the mean survival over time of eggs, L1, and L3 at -9 °C and -20 °C, yielding the mortality rates for *M. marshalli* at each of those temperatures (Figure A2). We then estimated the two unknown parameters in the Sharpe-Schoolfield relationship for pre-infective and infective stages from these two points for L1 and L3, respectively, assuming a log-normal error distribution (Figure A3, Table A5). We used the mortality rates for L1, rather than eggs, to estimate the lower bounds for the pre-infective larvae because *M. marshalli* eggs are less sensitive to freezing and thus not the limiting stage determining lower thermal tolerance (Figure A2).

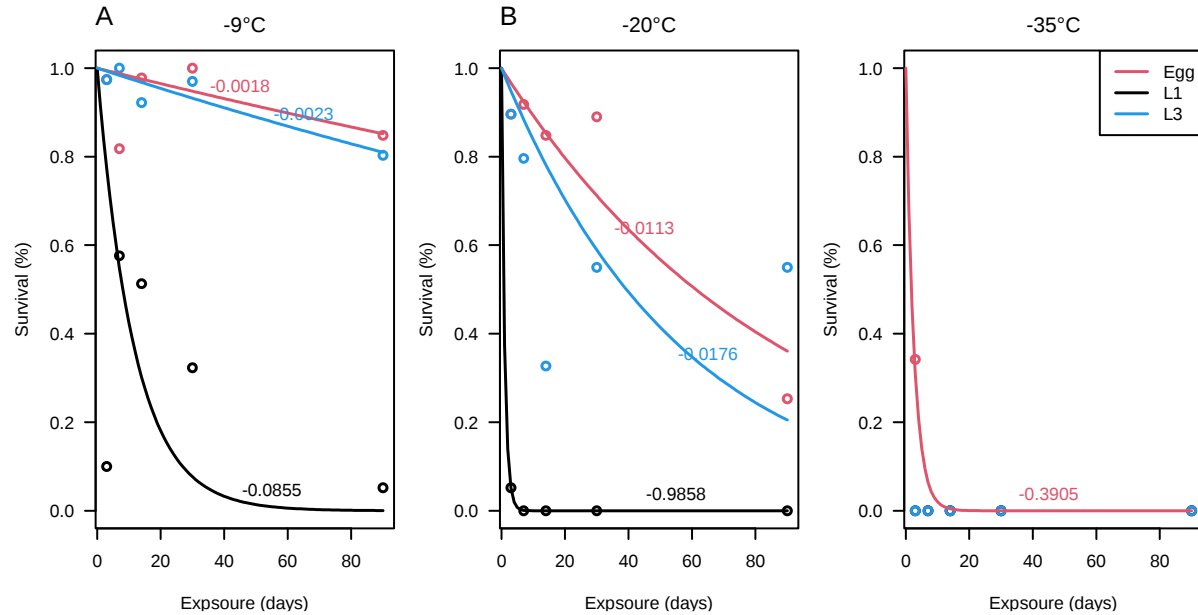


Figure A2. The proportion of eggs, L1, and L3 stages of *Marshallagia marshalli* surviving over 80 days at (A) -9 °C, (B) -20 °C, (C) -35 °C, taken from Aleuy et al. (2020). The solid lines are the fitted exponential curves, with the estimated mean mortality rates indicated on the figure.

Table A5. Hyperparameters **assumed in population modelling** for MTE relationships describing pre-infective and infective mortality and pre-infective development of *O. gruehneri*.¹

Hyperparameter	Parameter		
	μ_0	μ_3	ρ_0
y_0	0.068 (0.066, 0.070)	0.0211 (0.020, 0.022)	0.032 (0.031, 0.033)
E	0.884 (0.865, 0.902)	0.208 (0.171, 0.246)	0.686 (0.659, 0.713)
E_H		3.554 (3.217, 3.970) ²	7.957 (3.781, 13.390)
T_H		27.6 (26.7, 28.3) ²	30.568 (30.202, 31.170)
E_L	-3.358 (-4.279, -2.406)	-19.318 (-20.596, -18.084)	
T_L	2.928 (2.759, 3.088)	3.409 (1.961, 5.136)	

1. Hyperparameters in red were estimated from data on *Marshallagia marshalli* from Aleuy et al. (2020).
 Hyperparameters in blue were estimated from Model 10. Note that the hyperparameters for μ_0 and ρ_0 were not significantly different between Model 5 and Model 10 (Table A2).
 2. Parameters showed some convergence issues with $\hat{R} > 1.1$.

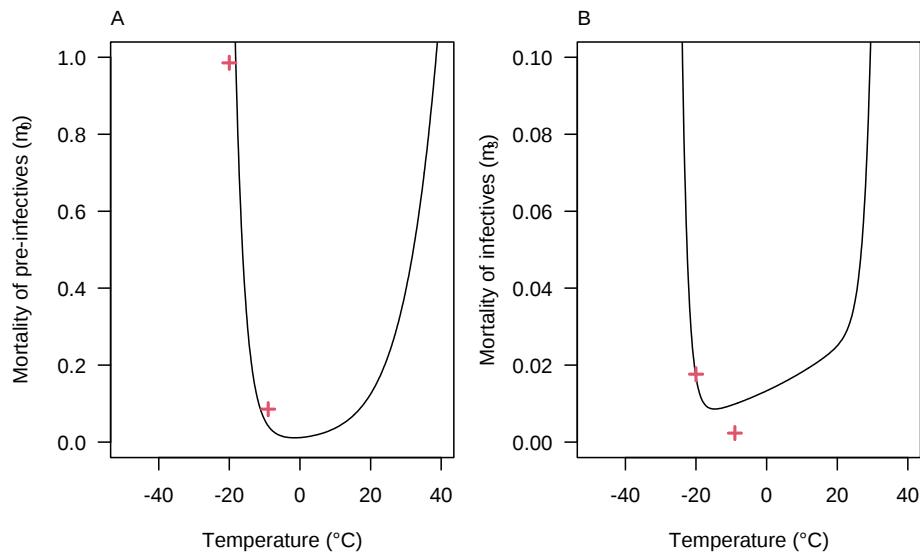


Figure A3. Full MTE curves for the mortality rates (d⁻¹) of (A) pre-infective stage and (B) infective stage larvae, including lower thermal bounds estimated from *M. marshalli* data (red points).

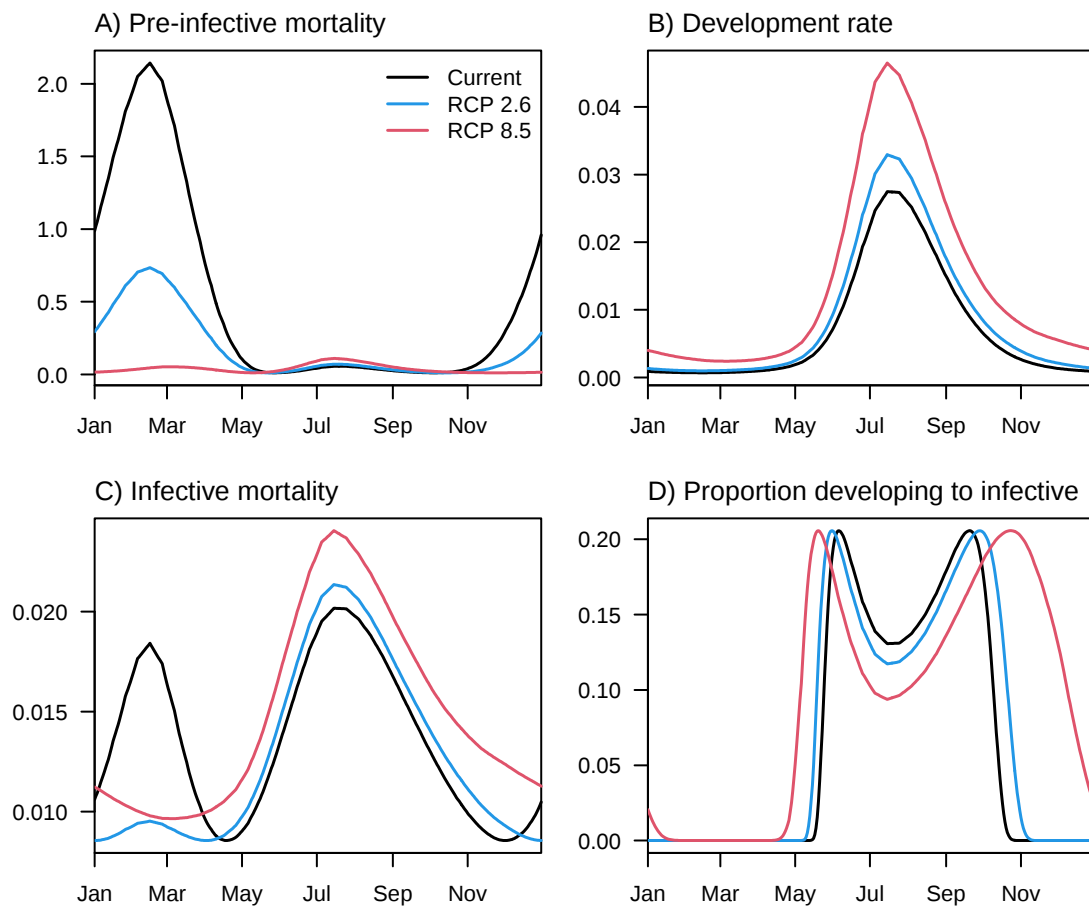
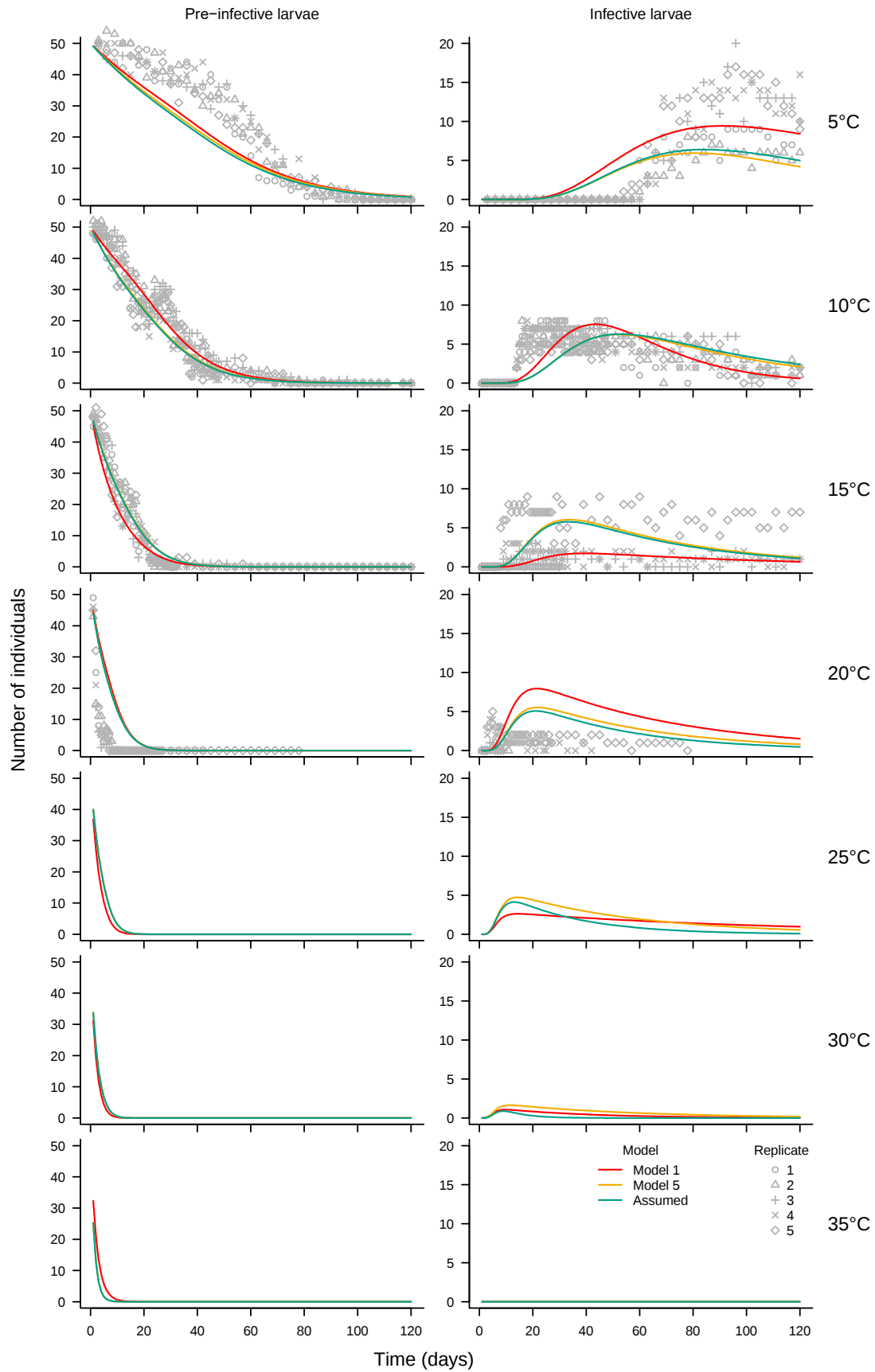
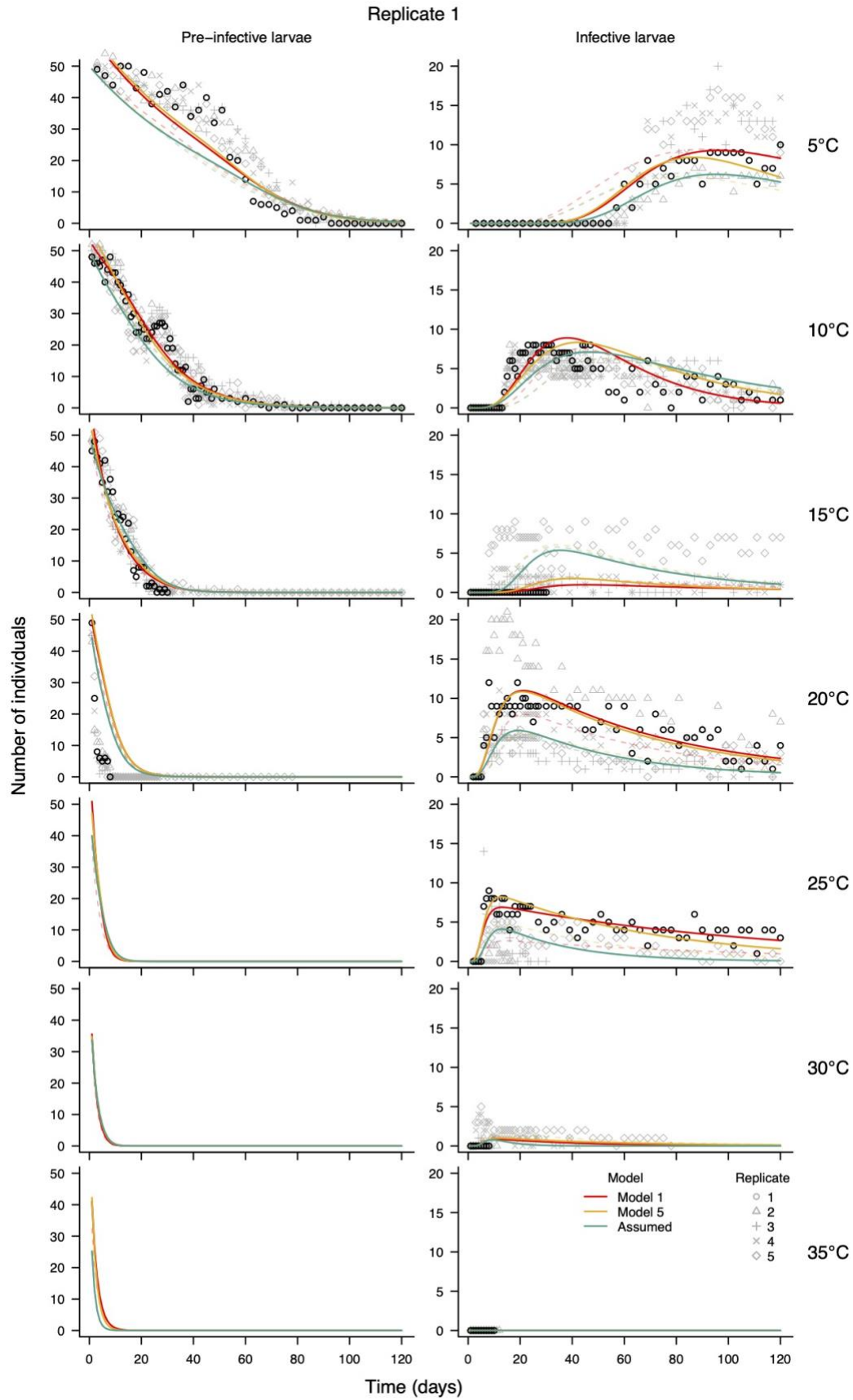
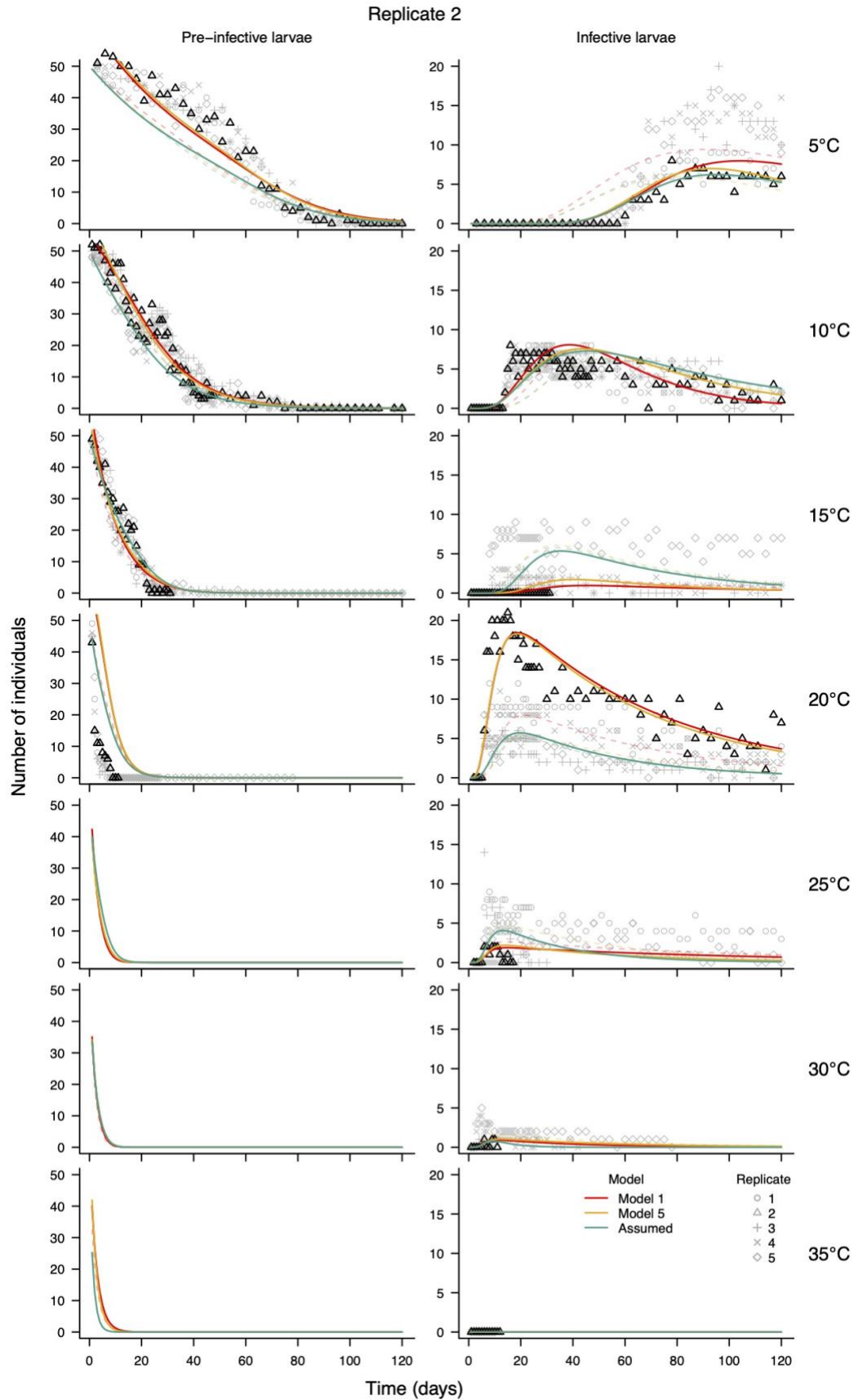


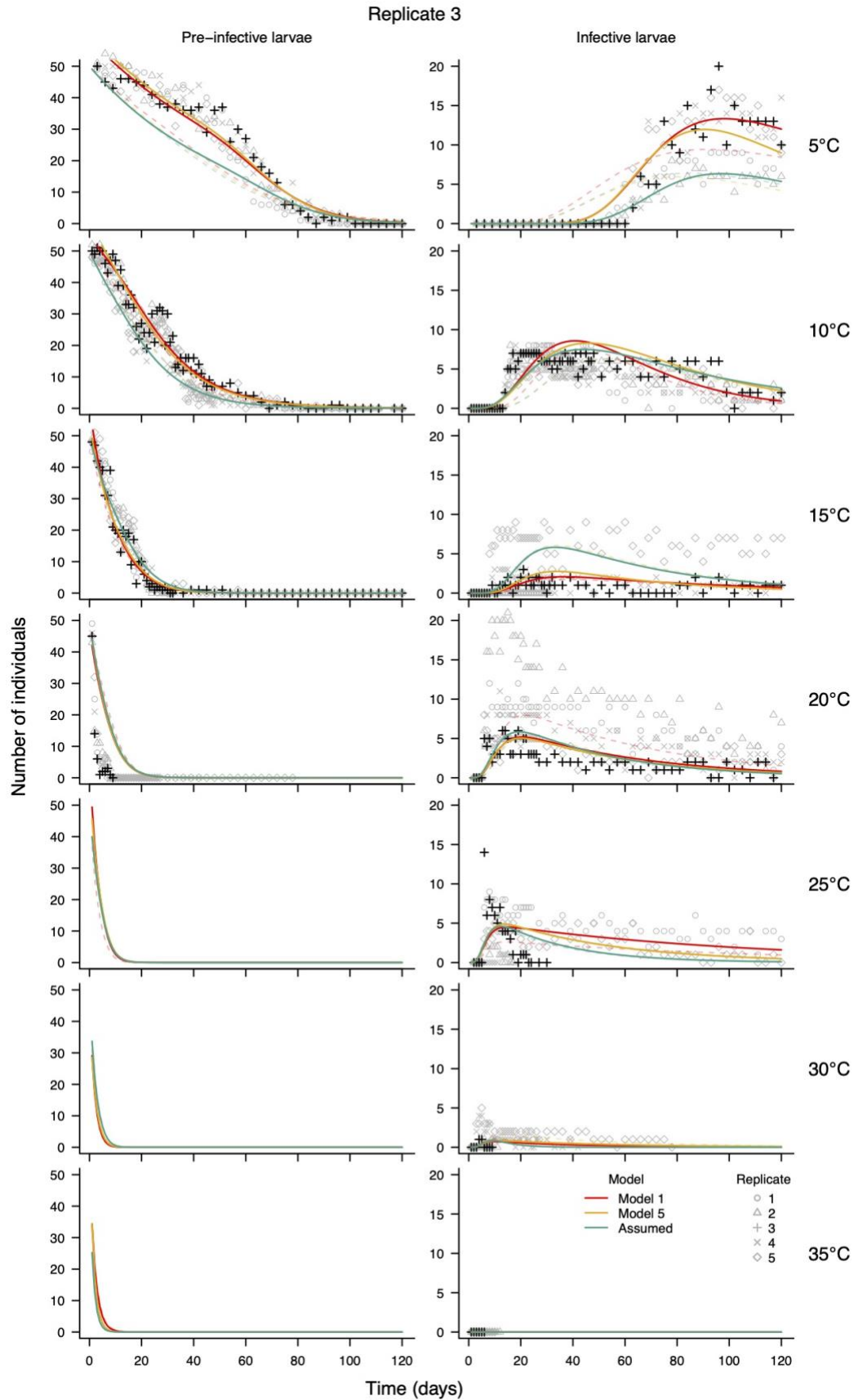
Figure A4. **Instantaneous** rates of (A) pre-infective mortality (μ_0) (B) development from pre-infective to infective (ρ_0), (C) infective mortality (μ_1), and (D) the proportion of eggs that survive to the infective stage ($\exp(-\mu_0 \rho_0)$) throughout the year at $x = 660$ km (approximate calving grounds). For each panel, rates are shown for current temperatures (black) and under RCP 2.6 (blue) and RCP 8.5 (red) climate change scenarios. These rates were calculated using the relationships from Fig. 5 and temperature curve from Fig. 4C.

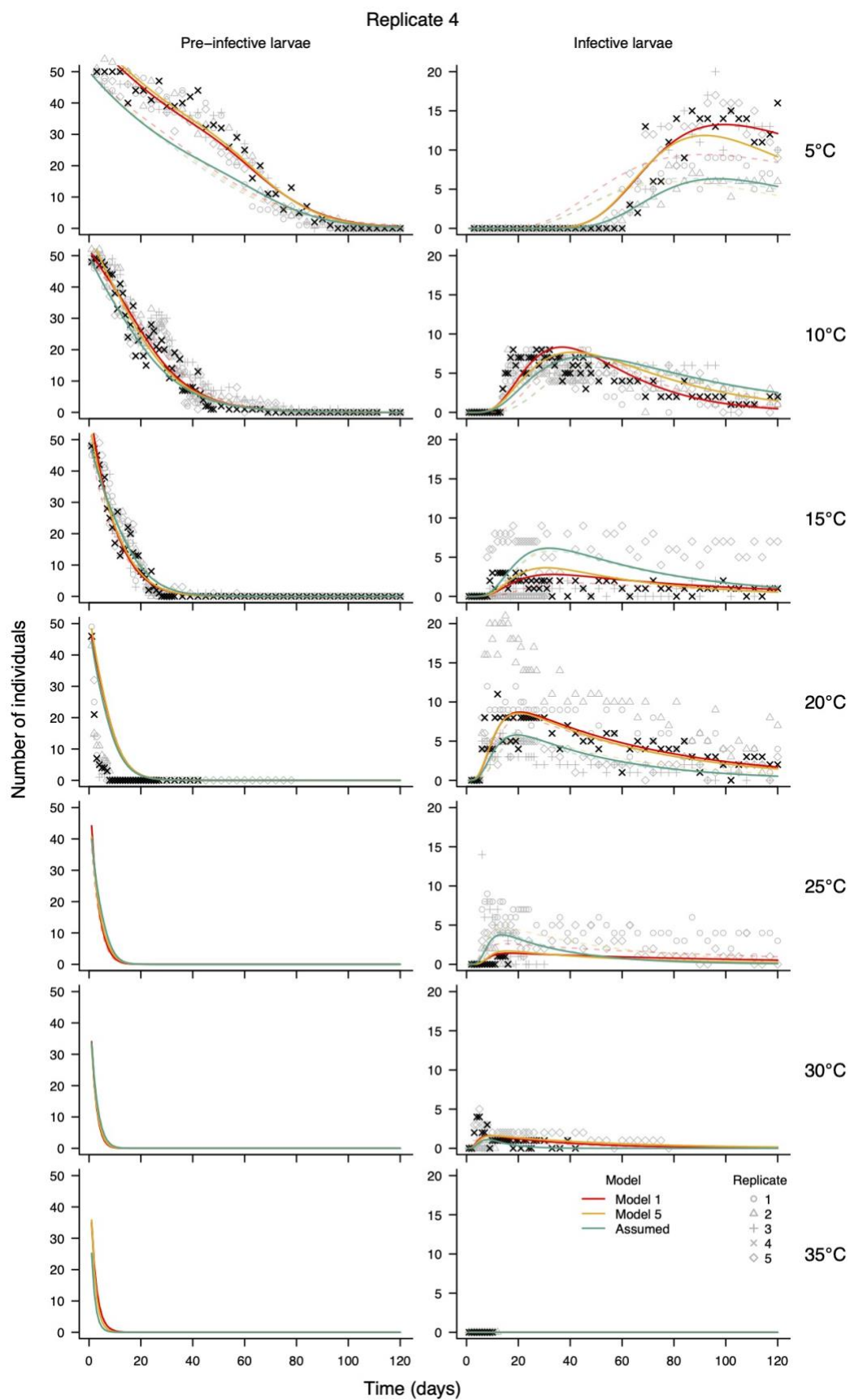


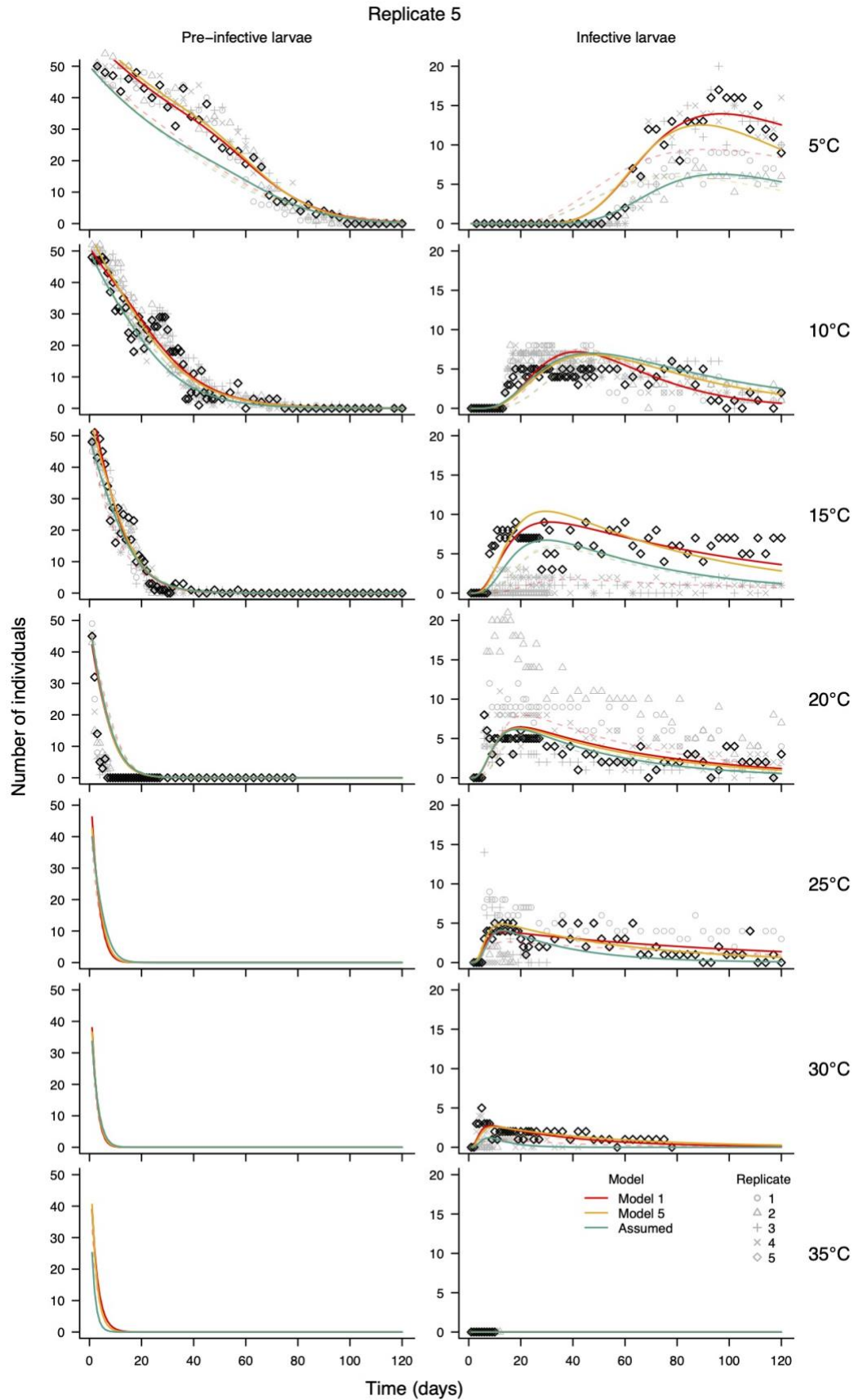
289 Figures A5. Plot of experimental data showing the number of pre-infective (left) and infective (right) larvae alive
290 from time 0 to 120 days at seven temperature treatments (rows) and 5 replicates within each temperature
291 treatment (symbols). The lines show three different model predictions: the independent fits to each temperature
292 treatment (model 1; red), the best-fitting MTE model (model 5; orange) and the assumed SSU model used in the
293 host-parasite population modelling (Assumed; turquoise). The following plots show the same data, but highlight
294 each replicate in turn (black points) and show the replicate-specific predictions using replicate-specific parameters
295 from the hierarchical model. The average model, corresponding to that shown above, is also shown in a lighter
296 dashed line.











References

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