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Functional Response Models and Consumer Temperature

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Contents

Abstract

this is the abstract.

1 Introduction

1.1 Functional Responses and existing models

The functional response describes how predators respond to changes in prey density C. Holling 1959; Solomon 1949. As prey numbers increase, the consumption rate of predators initially increases then levels out, however the specific shape of the period of increase can vary C. Holling 1959. Holling modelled the functional response and suggested three different forms which he proposed worked for different types of organisms C. Holling 1959. These are Type I, where the rate of increase in prey consumption with prey density is constant before a plateau, type I, where the rate of increase in prey consumption with prey density is decreasing (i.e the curve is hyperbolic Jeschke, Kopp, and Tollrian 2002) and type III, where the rate of increase in prey consumption with prey density increases then decreases C. Holling 1959. The type I model can be described by equation 1, the type II model can be described by equation 3 where x_R is the resource density, c is the number of prey consumed per predator per unit time, a is the discovery or search rate of the consumer (individual mortality of the resource at low densitiesEnglund et al. 2011) and h is the handling time Dawes and Souza 2013; C. S. Holling 1959. The type III model can be described by a generalised version of equation 2, equation 3 where q changes the shape of the curve Dawes and Souza 2013. This is due to reduced predator efficiency when predator densities are low, so at lower densities prey mortality is decreased Taylor and Collie 2003; Hassell 1978. When $q = 0$, the model is type II and when $q > 0$,the model is type III Dawes and Souza 2013. These equations are often written with Y, the number of prey consumed per predator, instead of c and T, the time, on the right side of the equation, however these equations are equivalent as $c = \frac{Y}{T}$.

$$c = ax_R \tag{1}$$

$$c = \frac{ax_R}{1 + hax_R} \tag{2}$$

$$c = \frac{ax_R^{q+1}}{1 + hax_R^{q+1}} \tag{3}$$

It is important to note that both the search rate and handling times are functions of different aspects of attacking and eating prey Hassel, Lawton, and Beddington 1976 The handling time is made up of the time predators spend pursuing, subduing, eating and digesting their prey. The search rate (or attack rate) combines the distance at which a predator will attack prey, the speed of both the prey and the predator and the success rate of attacks C. S. Holling 1966. In general, the Holling type II model is very successful, especially considering its simplicity however there are examples where data is better described by a more complex model, such as a type III Holling model Hassel, Lawton, and Beddington 1976 . Many other models exist to describe the functional response, often based on variations of the Holling equation accounting for different behavioural aspects Jeschke, Kopp, and Tollrian 2002. Jeschke, Kopp, and Tollrian 2002 attempted to separate handling and digestion time from h. The model curve is mostly similar to the Holling type II functional response curve, but is more flexible and when both handling time and digestion time are high, the curve is quite different. In addition, if values of a or h change with prey density, then the Holling II model may not fit well (as a and h are constant in this model). In these examples, the type III Holling model can be a good model Hassel, Lawton, and Beddington 1976.

1.2 Temperature and Functional Responses

Many biological traits are dependent on temperature. Dell, Pawar, and Savage 2014; Dell, Pawar, and Savage 2011. The way in which traits vary with temperature can depend on many factors including life stageCator et al. 2019, habitat Dell, Pawar, and Savage 2011 and thermy Dell, Pawar, and Savage 2014. In addition often there is asymmetry between predator and prey response to temperatureDell, Pawar, and Savage 2014. This means that understanding how the functional response of predators changes with temperature can be very complicated. Information about both predator and prey responses to temperature is necessary to fully predict how functional responses might change with temperature. The functional response of predators has important applications in nature and agriculture (for example in biological control of agricultural pests Gilioli, Baumgärtner, and Vacante 2005). The response of the functional response to changes in temperature is important in predicting the effect of climate change Öhlund et al. 2014. Temperature is important in determining body velocity so it is likely to be the main way in which temperature affects predator-prey interactions Dell, Pawar, and Savage 2014.

Search rate is predicted to increase with temperature according to the metabolic theory of ecology Brown et al. 2004. The Arrhenius equation predicts a linear increase in log-linear space Englund et al. 2011). Increases in search rate when temperature is changed have been found in multiple predator-prey systems both linearly Gilioli, Baumgärtner, and Vacante 2005; Zamani et al. 2006 and exponentially Lefébure, Larsson, and Byström 2014. Many studies have found that this increases reaches a plateau McCoull, Swain, and Barnes 1998; Thompson 1978 or reaches a maximum and decreasesEnglund et al. 2011; Zamani et al. 2006; Sentis, Hemptinne, and Brodeur 2012.

The metabolic theory of ecology Brown et al. 2004 also predicts that handling time reduces exponentially when temperature is increased. Experimentally changing the temperature in predator prey systems does reduce the handling timeThompson 1978; McCoull, Swain, and Barnes 1998; Jalali, Tirry, and De Clercq 2010; Zamani et al. 2006, sometimes exponentially Sentis, Hemptinne, and Brodeur 2012.

The response between type of functional response and temperature is less clear. Some studies have found no effect of temperature on type of functional response Sentis, Hemptinne, and Brodeur 2012 but there are examples of the functional response changing with temperature Taylor and Collie 2003.

1.3 Models

Models can be phenomenological or mechanistic. In mechanistic models, all parameters have biological meaning and in phenomenological models they do not; instead a function is used that fits the data or processes Otto and Day 2007; Geritz and Kisdi 2012.Phenomenological models may fit better to data and can be very useful in the absence of mechanistic models. They can be easier to understand, however do not have as much biological meaning as mechanistic models Otto and Day 2007. Geritz and Kisdi 2012 claim that this could stop them being valid for use in biological systems. Mechanistic models can improve our understanding of biology and are useful for making predictions more accurately because when the meanings of parameters of known, biological constraints can be included. They can include as much information about the system as is available Otto and Day 2007; Kendall et al. 1999. Mechanistic models are simplifications of systems and may have strong assumptions but they can still be very useful tools in understanding a biological system. How well a simplified model fits to data can give important insight into what aspects of a system are important in determining the dynamics Geritz and Kisdi 2012. The Holling models described above are mostly mechanistic. The type III model is more phenomenological than they type I and type II models due to the non-biological parameter q. Even the Holling type II model may be partially phenomenological because the values of a and h are a functions of multiple biological components Hassel, Lawton, and Beddington 1976.

1.4 This work

In this paper, five models were fitted to experimental functional response data: Holling's type I, Holling's type II, Holling's type III, a polynomial model of degree two (to capture increasing and levelling out of the functional response) and a polynomial model of degree three (to capture a change in the rate of increase of the functional response. Then the best model for each experiment was determined. The Holling II model was predicted to be the best model. It was expected that the Holling type III model would be able to fit better to the data but may have a higher AIC value due the the extra parameter. The best model was found at different temperature ranges to explore whether studies in particular consumer temperature ranges led to different models fitting better. In addition the search rate and handling times from the Holling's models were compared to the consumer temperature to explore whether functional response parameters for systems with different consumer temperatures would show similar responses to the studies looking at different temperatures within the same system. It was expected that search rate would increase with temperature, then reach a maximum and decrease. It was expected that handling time would decrease with temperature.

2 Methods

2.1 Computing Tools

Bash was used to compile the pdf of the tex file, to calculate and format the word count of the project (using teXcount) and to run the project files. This was used due to the ease of accessing files and files contents in bash. In addition, bash can run python, R and other bash scripts. Python was used to initially sort the data, add new columns to the dataset and remove datasets with an insufficient number of points and export this updated dataframe as a csv. These tasks are well suited to Python's abilities. R was used to model to data, plot graphs and analyse the data. This is due to R's dataframe structures which make it very easy to store and manipulate variables. In addition plotting in ggplot2 is very flexible. "xtable" in R was used to store results for some parts of data analysis because it allows tabular results from R to be integrated in tex files. "minpack.lm" in R was used to fit Holling models using Levenberg-Marquardt nonlinear least squares Elzhov et al. 2016.

2.2 Initial Data Sorting

The data used was from the Biotraits database Dell, Pawar, and Savage 2013, which contains information collated from different studies about how biological traits respond to environmental drivers. The parameters of interest here were the number of prey the predator consumed per unit time and the resource density. Data sorting was carried out in python version 2.7. New columns were added and experiments with less than six experiments were removed. This new dataset was exported to a csv for model fitting.

2.3 Model Fitting

The data were fitted to five different models: a quadratic model, a cubic model and the three Holling models C. S. Holling 1959 using R 3.6.2 R Core Team 2019. The Holling models were the type I model (equation 1, a linear model where the intercept was the origin), type II model (equation 2) and generalised type III model (equation 3). Models were fitted sequentially for each experiment and plotted. This allowed the fit to be visually inspected as the model fitting process was improved.

2.3.1 Linear models

The Holling type I, quadratic and cubic models models were fitted using lm (base R). For the quadratic and cubic models, poly was used to compute orthogonal polynomials to avoid correlation of variables.

2.3.2 Non-linear Models

The Holling type II and type III models were fitted using NLSlm (from the package minpack.lm Elzhov et al. 2016). The coefficients a, h, and q were given a lower bound of zero and the maximum number of iterations was set to 1000. For both type II and type III models, starting values were calculated using starting value functions where a and h were estimated. The initial value for h was the maximum value of c. The initial value for a was the initial steep part of the curve which was calculated by repeatedly fitting linear models the dataset then deleting the maximum value of x_R and storing the largest gradient of these models. For the type III model, this initial value of q was picked from a random uniform distribution between -2 and 2. Finding the starting values was followed by sampling positive values around these initial values and repeatedly running the models and storing the coefficients and AIC values of these models. The coefficients of the model with the lowest AIC were used as the initial values for the main model fitting step. Once the starting values had been determined, the models were rerun with these initial values and plotted (with the other models).

2.4 Data Analysis

Data analysis was carried out in R 3.6.2R Core Team 2019.The models were compared using AIC and the most appropriate model was determined for each dataset. AIC was used because other techniques to compare models are not appropriate for non linear models. Between AIC and BIC, AIC was used because it penalises extra parameters more at lower sample sizes than BIC Johnson and Omland 2004. As this data set contains a number of models with small sample sizes, this could prevent an overfitted model being selected as the best model.

The confidence intervals for values of q were calculated (from the mean $\pm$ two times the standard error). When the confidence interval for q overlapped zero, the best AIC was recalculated for the remaining Holling models (because when the confidence interval for q is zero, the type III model is the same as the type III model). A chi-square (χ^2) goodness of fit test was carried out on the best model and the best model type (phenomenological or mechanistic) to determine if the number of models in each category was significantly different.

The p-value of each parameter was stored and if the model was not significant, the parameter was removed from analysis of that parameter. Shapiro-Wilk tests were used to test the log consumer temperatures and log parameter values and found that they were not normally distributed. In addition, there were ties in the data so Spearman's rank correlation could not be calculated. Kendall rank order correlation tests were carried out on consumer temperatures and log search rate and consumer temperatures and log handling time for each of the Holling models. Log of the parameters was used because both search rate and the handling time values were mostly very low with a few very large values. The search rate for type III models could not be tested due to a low number of models were search rate was significant.

Chi-square (χ^2) tests were carried out to determine the association between consumer temperature and best model type and consumer temperature and best Holling model (recalculated). The temperature values were discretised by creating an expectation table with intervals of five degrees and combining these intervals until the expected values were all greater than five.

3 Results

3.1 Number of Fits

Many of the models fit well to the data, for example (Figure1). Most models successfully fit the data. Of the 241 datasets, only 19 Holling type II models and 20 Holling type II models did not converge.

3.2 Best Model

The Holling's type II model was most frequently the best model (0.29%) and the polynomial of degree 2 was most frequently the second best model (0.23%) (Figure 2). The mechanistic models were marginally more often the best model (%)than the mechanistic models (Figure 3) The distribution of the best model was not best described by a uniform distribution ($p < 0.05$,Table1). The distribution of the best model type was best described by a uniform distribution (p>0.05,Table1).

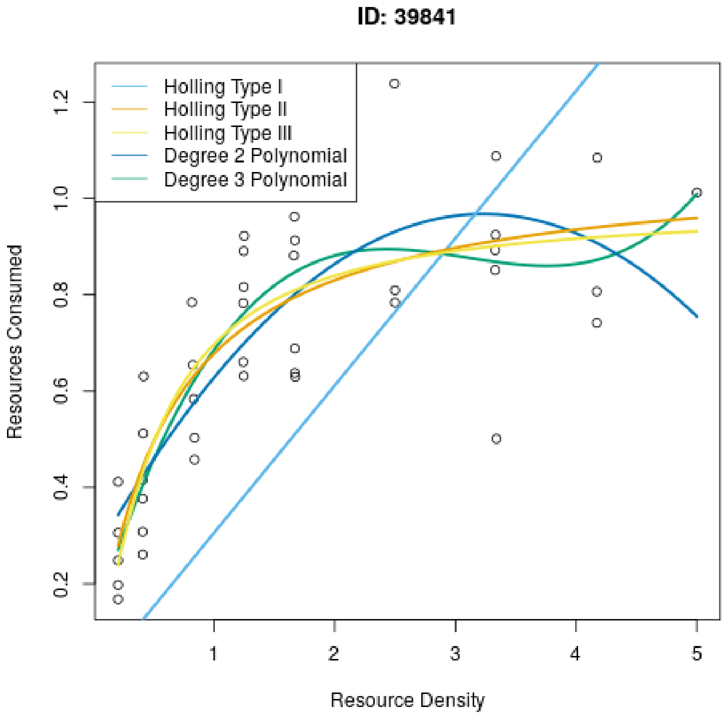
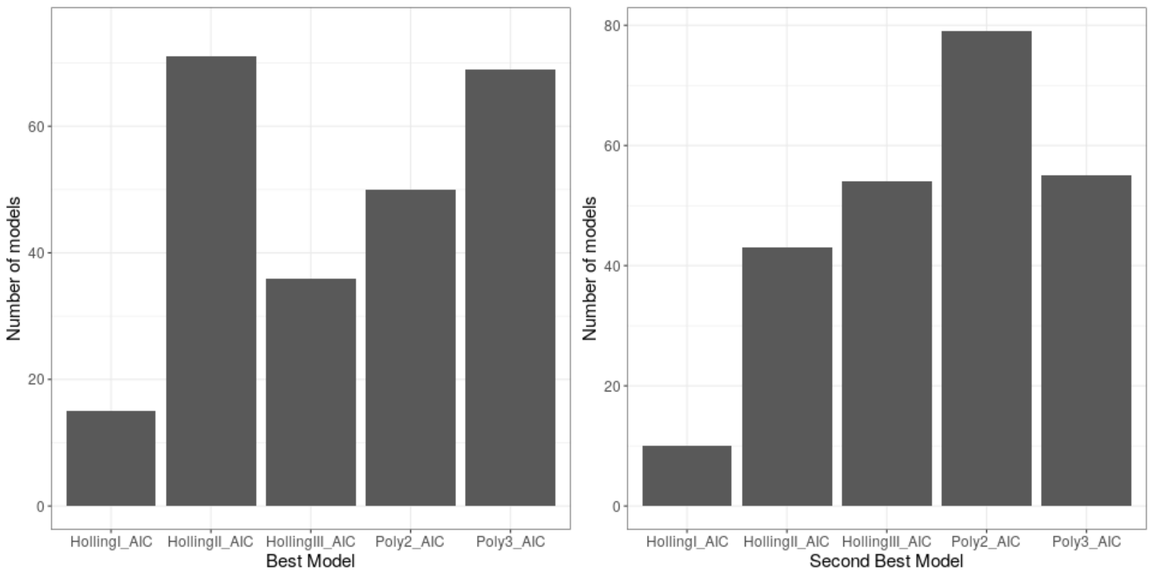


Figure 1: This is a graph for the experiment with ID 39841



(a) Number of times that each model was the best model (b) Number of times that each model was the second best model

Figure 2: Best and second best model from the lowest and second lowest AIC values. Models are Holling type I, Holling type II, Holling type II, polynomial of degree 2, polynomial of degree 3. $n = 241$

Table 1: Results of chi-squared tests for whether the best model and the best model type (i.e phenomenological or mechanistic) are uniformally distributed

	Chi-squared	p-value
Best Model	45.78	0.00
Best Model Type	0.04	0.85

3.3 Best Holling Model

Of the three Holling models, the type II model was the best (Figure4). The best Holling model was recalculated, removing the type III Holling model when the confidence interval for q spanned 0. This occured for 62 models. The majority of these were best described by the Holling type II model of the other Holling models, but some were better described by the type I model (Figure 4)

3.4 Temperature and Best Model

The type of the best Holling model did not vary much with the temperature (Figure 5 and the temperature interval was not associated with the best Holling model.($\chi^2 = 4.36$,$p = 0.36$,$df = 4$). At most temperatures (< 20 degrees), more mechanistic models fit the best better . Below 10 degrees this difference was extreme. However at the interval $20-25$ degrees, more phenomenological models fit the best (Figure 5). The temperature interval was associated with the best model type ($\chi^2 = 10.63$,$p = 0.03$,$df = 4$). This difference seemed to be due to the polynomial of degree three being particularly successful in the interval $20 - 25$ degrees.

3.5 Temperature and Parameter Values

The handling time was and the search rate was The consumer temperatures are weakly negatively correlated with the search rate for type I and type II Holling models (Figure 6,Table 2).The search rate is smaller and less varied at intermediate temperatures, however at very low and very high temperatures, the temperature is very varied and can be very high. The consumer temperatures are weakly positively correlated with handling time for type II and type III Holling models(Figure 6,Table 2).

Table 2: Table of results for Kendall rank order correlation tests for consumer temperature and parameter values.

	z	tau	p-value	n
Search rate type I	-4.58	-0.21	0.00	229.00

Search rate type II	-2.94	-0.18	0.00	137.00
Handling time type II	3.60	0.21	0.00	137.00
Handling time type III	2.26	0.14	0.02	131.00

4 Discussion

Three Holling models were successfully fit to

4.1 Type

4.2 Mechanistic and Phenomological

4.3 Recalculating Holling Model

4.4 Temperature

4.4.1 Functional Response

4.4.2 Handling Time and Search Rate

4.5 Importance

5 Conclusion

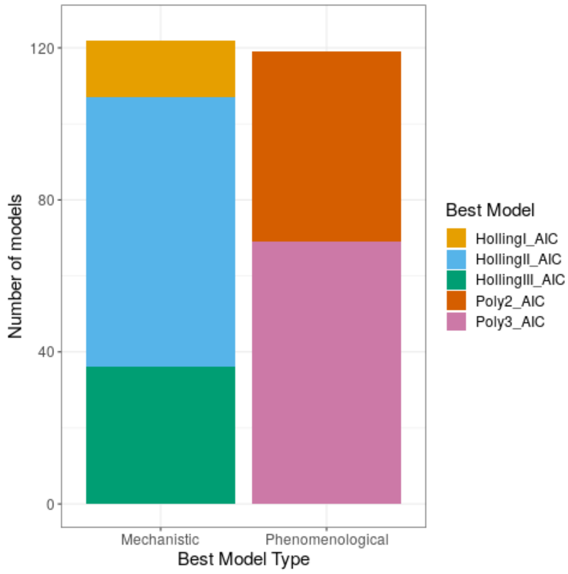
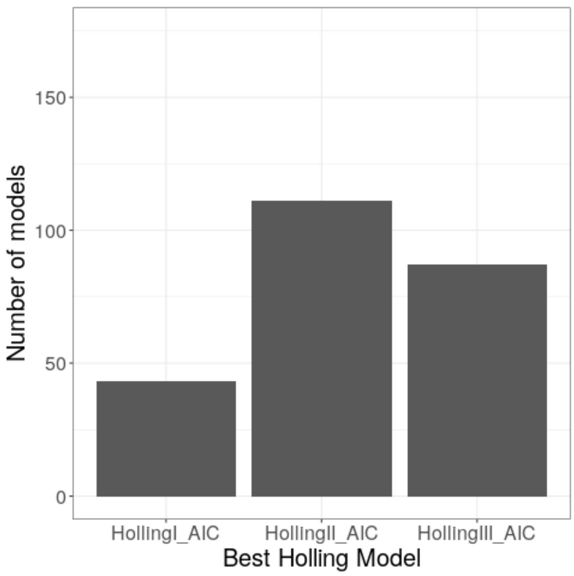
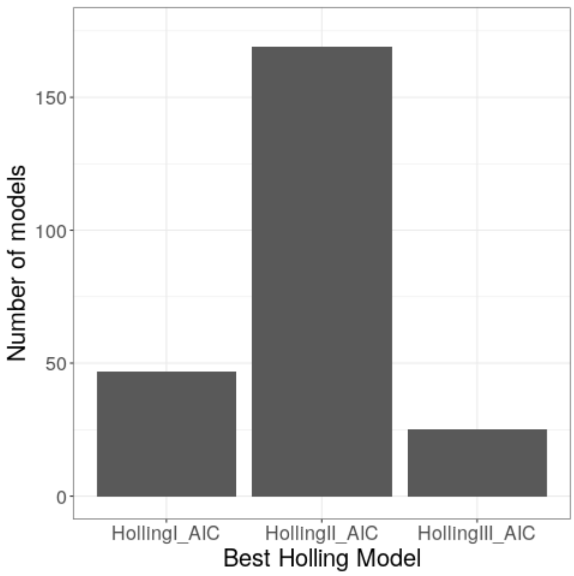


Figure 3: Number of models where the best type was phenomenological or mechanistic. Colour is the model. $n = 241$

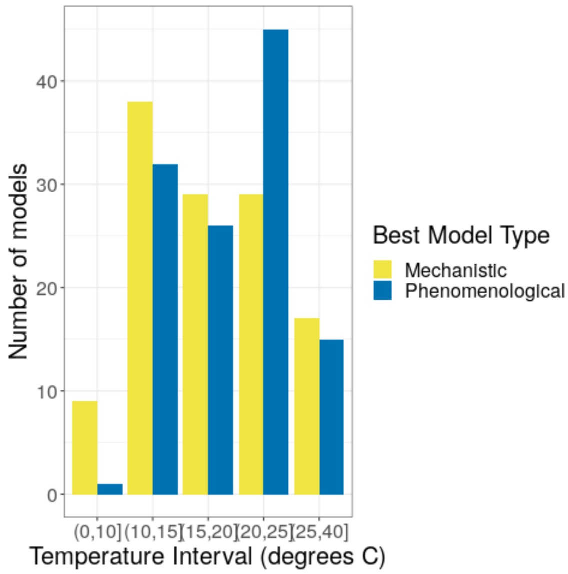


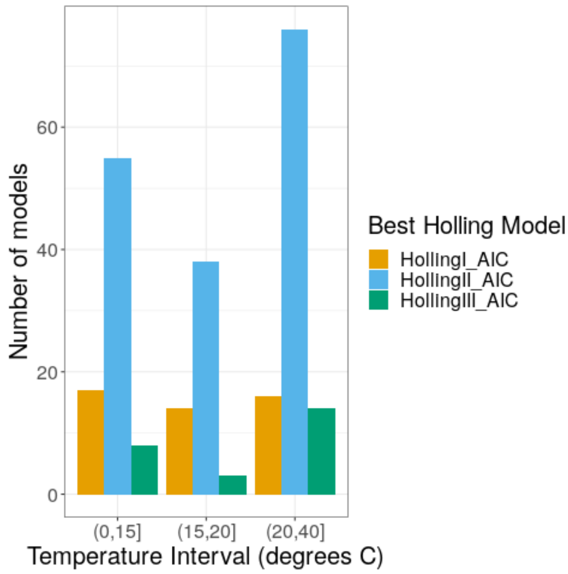
(a) Number of times that each model was the best Holling model



(b) Number of times that each model was the best Holling model, when the best Holling model was recalculated if the confidence intervals of q spanned 0

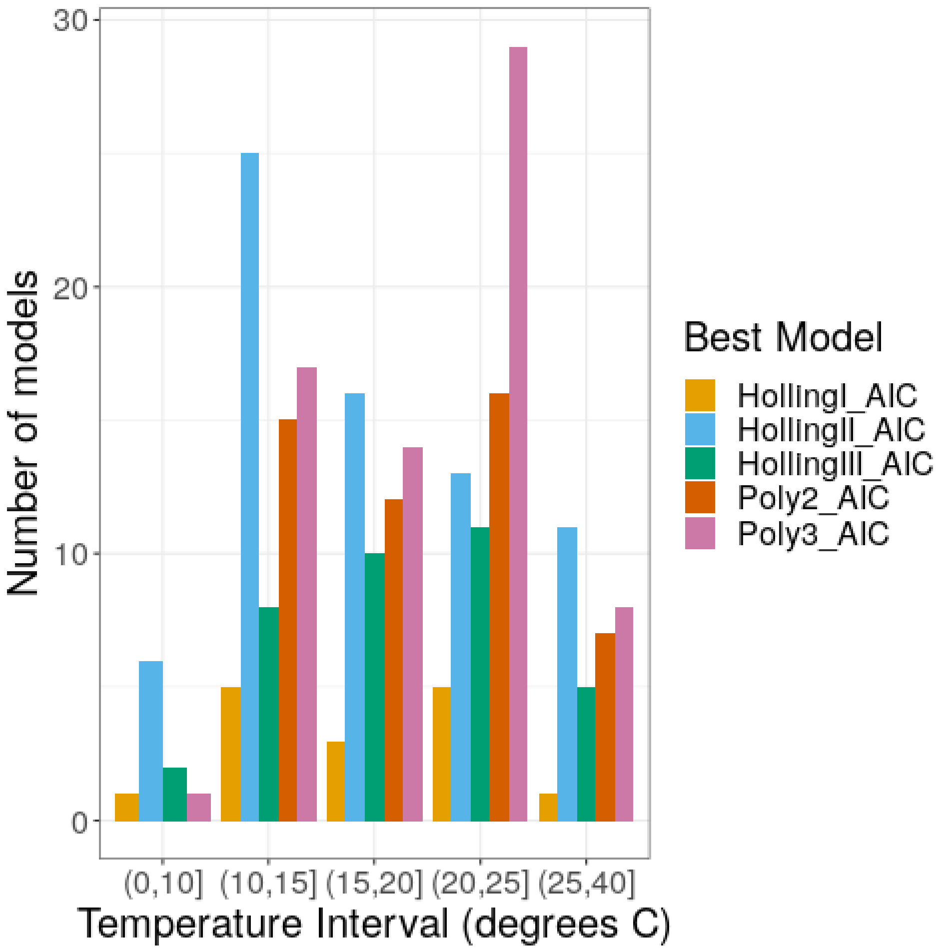
Figure 4: Best model from the lowest AIC values (of the Holling model). Models are Holling type I, Holling type II and Holling type II. $n = 241$





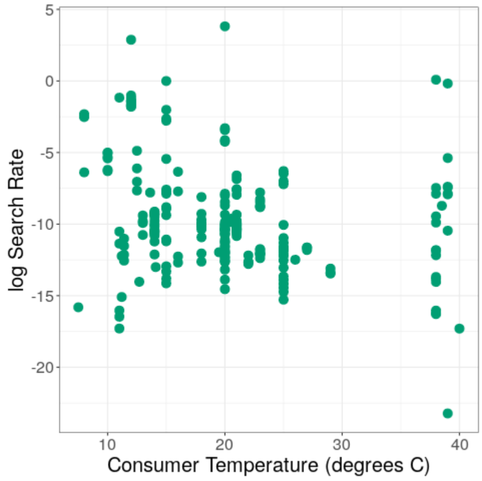
(a) Number of times a mechanistic or a phenomenological model was the best model at each consumer temperature interval.

(b) Number of times the recalculated Holling model was the best model at each consumer temperature interval.

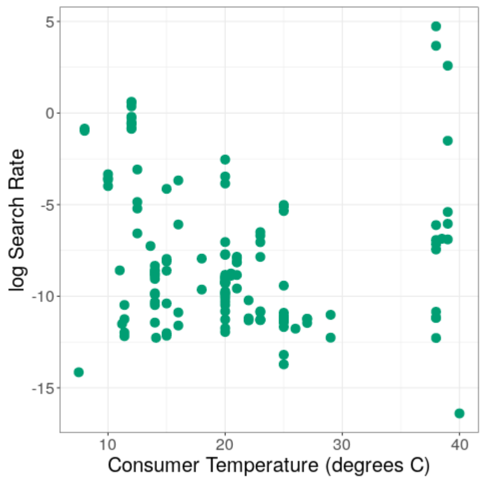


(c) Number of times each model was the best model at each consumer temperature interval.

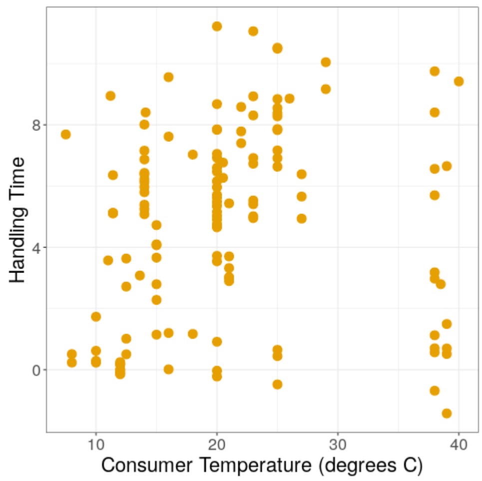
Figure 5: Best model is determined from the lowest AIC values. Colour is the best model type. $n = 241$



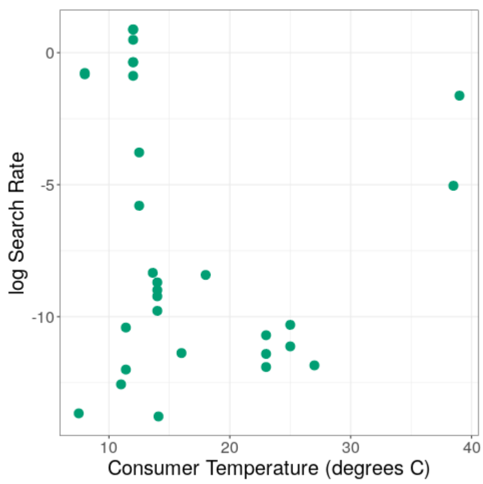
(a) Consumer temperature and log search rate for type I Holling model



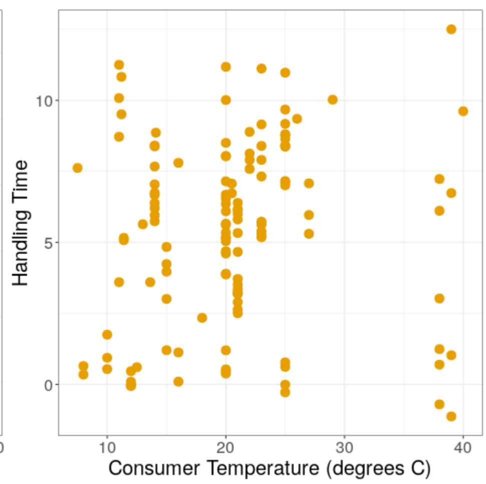
(b) Consumer temperature with log search rate for type II Holling model



(c) Consumer temperature with log handling time for type II Holling model



(d) Resource temperature with log search rate for type III Holling model



(e) Consumer temperature with log handling time for type III Holling model

Figure 6: Logged parameter values and Consumer temperature for Type I, Type II and Type II Holling Models.

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