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Life Sciences

Functional Response Models and Consumer Temperature

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Abstract

this is the abstract.

1 Introduction

The functional response describes how predators respond to changes in prey density Holling (1959*a*)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 Holling (1959*a*). Holling modelled the functional response and suggested three different forms which worked for different types of organisms Holling (1959*a*). These are Type I, where the rate of increase in prey consumption with prey density is constant before the plateau, type II where the rate of increase in prey consumption with prey density is decreasing and type III, where the rate of increase in prey consumption with prey density increases then decreases Holling (1959*a*). 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 and h is the handling time Dawes & Souza (2013)Holling (1959*b*). The type III model can be described by a generalised version of equation 2, equation 3 where q changes the shape of the curveDawes & Souza (2013). When $q = 0$, the model is type II and when $q > 0$,the model is type III Dawes & 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 $c = \frac{Y}{T}$.

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

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

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

Models can be phenomenological or mechanistic. The Holling models described above are mechanistic however the type III model is more phenomenological due to the non-biological parameter q.

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 off accessing files and files contents compared to other languages as well as its ability to run python and R 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 ggplot2's plotting is very flexible.

2.2 Initial Data Sorting

The data used was from the Biotraits database Dell et al. (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. The

2.3 Model Fitting

The data were fitted to five different models, a quadratic model, a cubic model and the three Holling models Holling (1959*b*) using R 3.6.2 R Core Team (2019). The Holling models were the type I model (equation 1, a linear model), 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, h and q were estimated, 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. 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 set at 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. The confidence intervals for values of q were calculated and (using 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 on the consumer temperatures and parameter values which where 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 search rate and handling time for each of the Holling models. A chi-square (χ^2) test carried out on resource temperature and best model. 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.

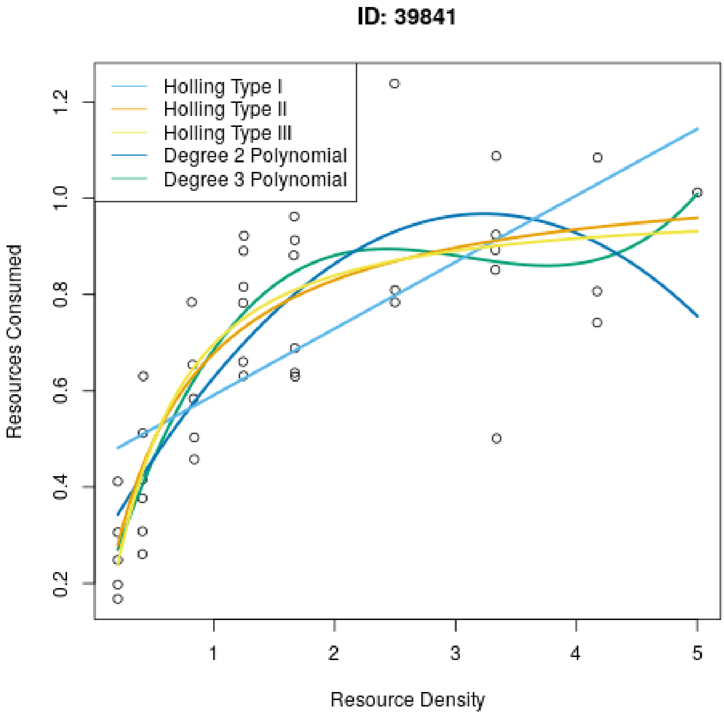


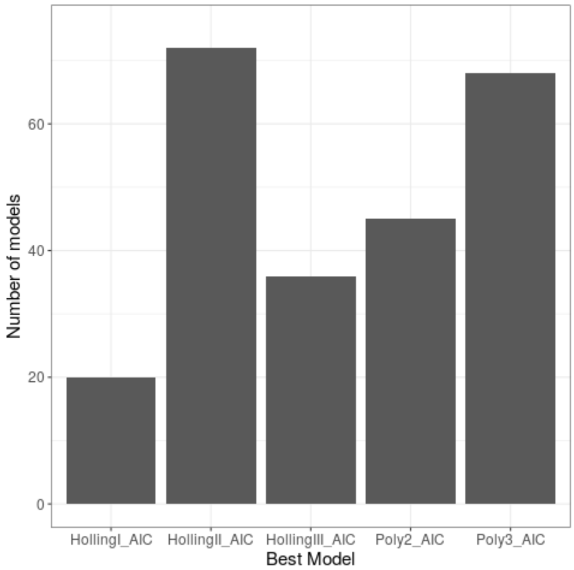
Figure 1: This is a graph for the experiment with ID 39841

3.2 Best Model

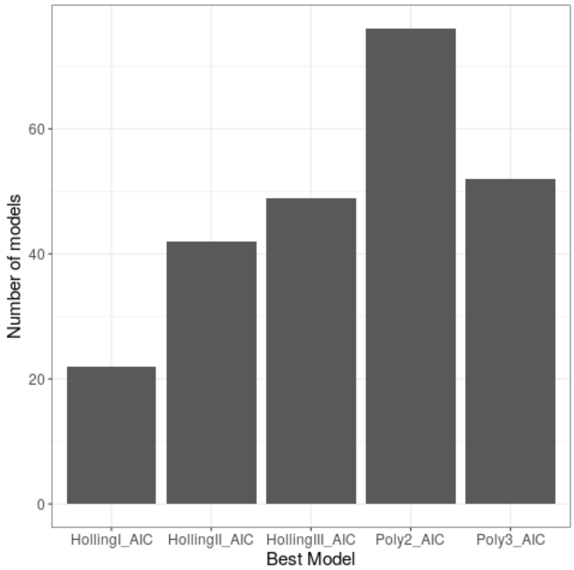
The Holling's type II model was most frequently the best model (29.5%) and the polynomial of degree 2 was most frequently the second best model (31.5%) (Figure 2). The mechanistic models were marginally more often the best model (53.1%)than the mechanistic models (Figure 3) The distribution of the best model was not best described by a uniform distribution ($p<0.01$) but the distribution of the best model type was ($p<0.05$) (Table1),

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	39.68	0.00
Best Model Type	0.93	0.33



(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. $n = 241$

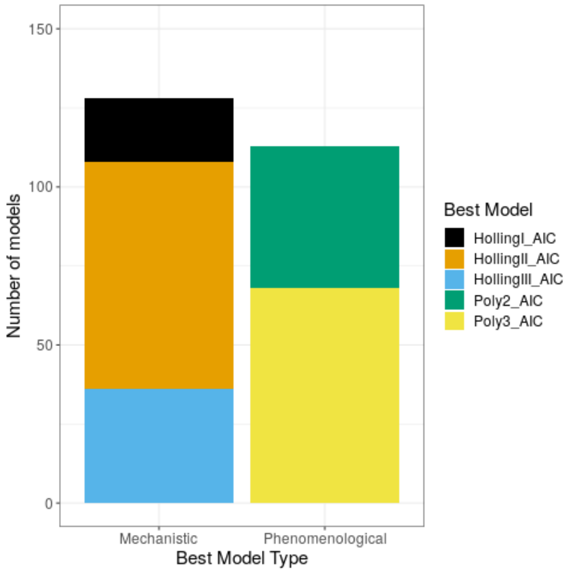
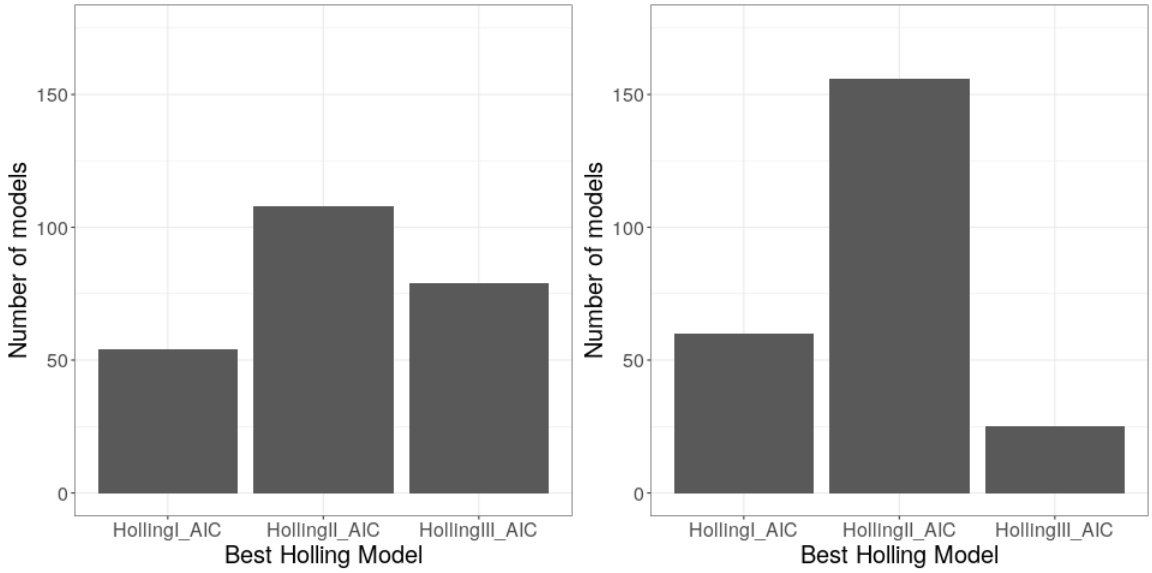


Figure 3: Number of models where the best type was phenomenological or mechanistic. Colour is the model. $n = 241$

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 affected 57 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 (Figure4)



(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

3.4 Temperature and Best Model

The consumer temperature did not effect which model fit the data the best($\chi^2 = 14.55$,$p = 0.27$,Figure 5).

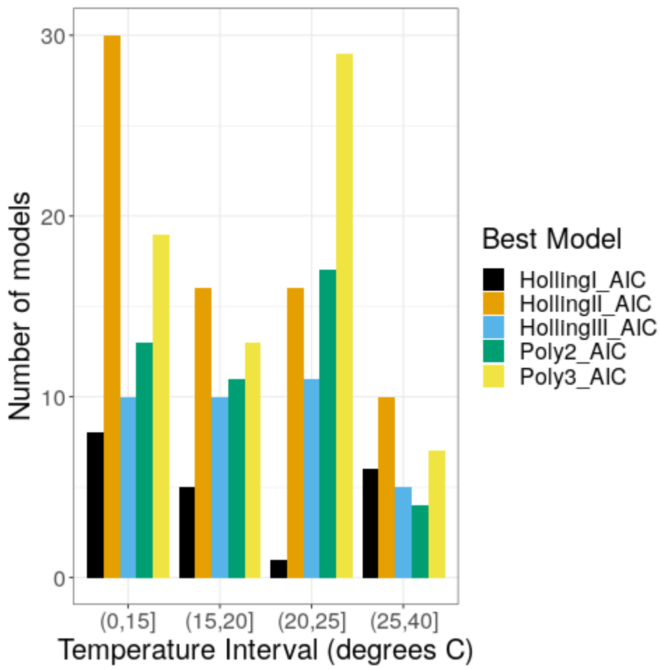


Figure 5: Number of times that each model was the best model at each consumer temperature interval. Colour is the best model. $n = 241$

3.5 Temperature and Parameter Values

The consumer temperatures are associated with the search rate and handling time (Figure 6,Table 2)

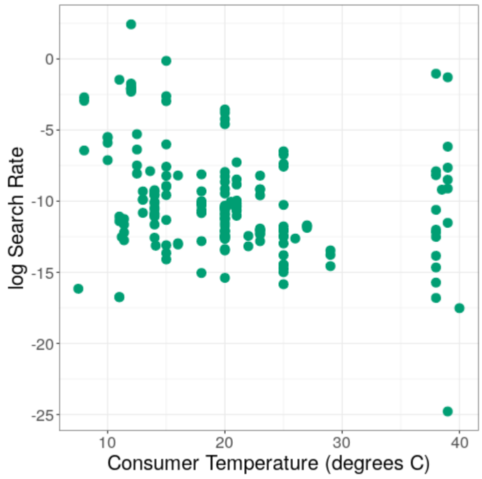
Table 2: Table of results for Kendall rank order correlation tests for consumer temperature and parameter values.

	z	tau	p-value	n
Search rate type I	-4.96	-0.25	0.00	189.00
Search rate type II	-3.15	-0.19	0.00	138.00
Handling time type II	3.80	0.23	0.00	138.00
Handling time type III	2.27	0.14	0.02	131.00

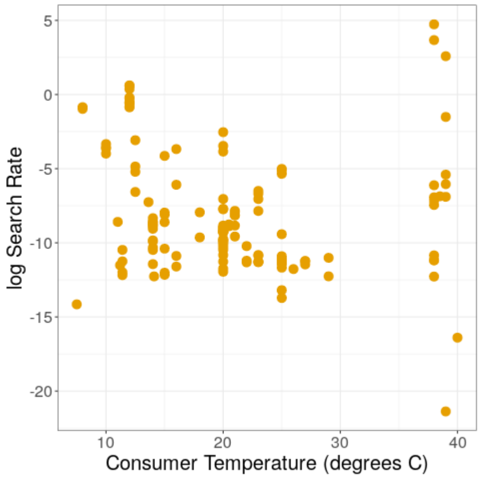
The search rate is smaller and less varied at intermediate temperatures, however at very low and very high temperatures, the temperature is very varied and can be very high. There is a weak negative correlation. The handling time shows a weak positive correlation with consumer temperature.

4 Discussion

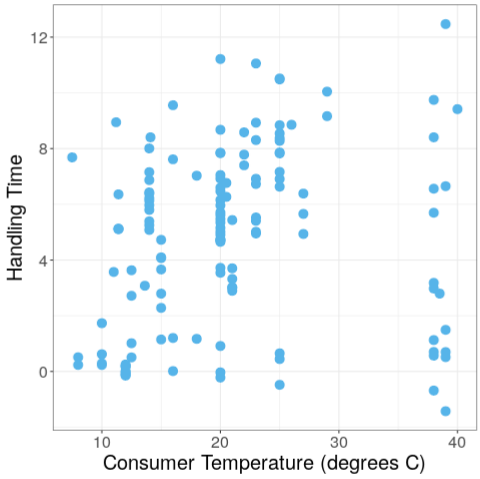
5 Conclusion



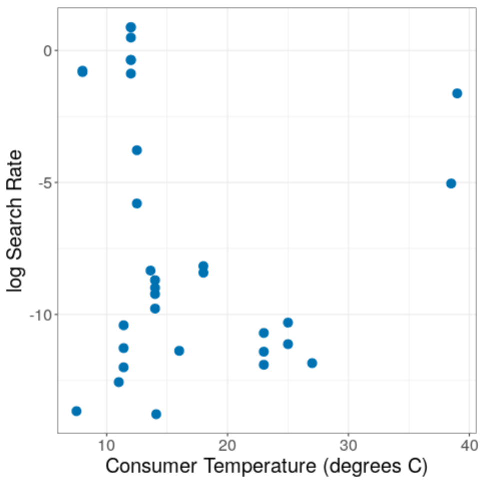
(a) Consumer temperature and log search rate for type I Holling model



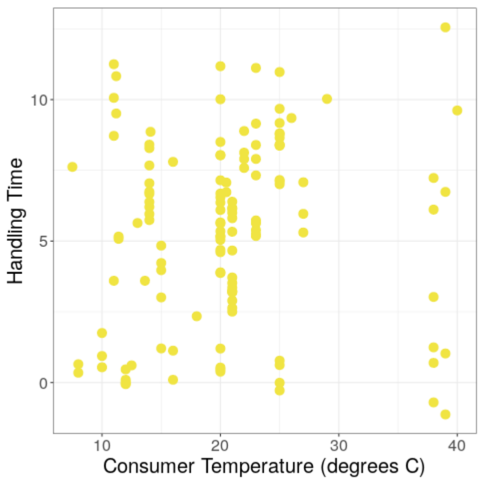
(b) Consumer temperature with log search rate for type II Holling model



(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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