

Modelling influence of quantitative factors on arthropod demographic parameters

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1 Introduction

Fertility life table (FLT) parameters are important quantitative indicators of interactions between arthropod population and the environment. By summarizing information on both fertility and survivorship, they can capture chronic sub lethal effects not detected by acute survival assays (MARINHO-PRADO, 2011; NASCIMENTO et al., 1998; NARDO et al (2001) LIU et al, 2005; LUMBIERRES et al, 2004). In life table studies, oviposition and survival data are collected over time (usually daily) and summarized into fertility life tables (FLT) for posterior estimation of the following parameters: net reproductive rate (R_0), intrinsic rate of increase (R_m), doubling time (DT), mean generation time (MGT) and finite rate of increase (λ), for each of treatments evaluated. As FLT parameters summarize data from experimental units into a single estimate for each group (treatment), the information on within treatment variance is not readily available, thus requiring the use of computationally intensive methods for its estimation. Among them, jackknife method, as proposed by MEYER (1986), is the most widely used for variance estimation in FLT analysis. Jackknife-based software available for life table analysis (HULTING et al, 1990 ; MAIA et al, 2000) was developed for analysing qualitative treatments, but such approach is frequently misused for contrasting quantitative factors (GANJISAFFAR et al., 2011; PAKYARI et al., 2011; RAZMJOU et al., 2011). Some authors use regression analysis after estimating FLT parameters for each factor level but do not account for the uncertainty of parameter estimates (CONTI et al, 2010). Here we present methods for adequately quantifying the influence of quantitative factors (e.g. temperature, pesticide level) on FLT parameters by combining the jackknife method with a regression analysis framework.

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Material and Methods

In this work, we consider analyses of life table data coming from completely randomized designs for which n experimental units (females) are randomly allocated to G groups (treatments). Females are mated and followed up until death. Survivorship and oviposition data are recorded at regular time interval (days, weeks). We propose the use of regression models to characterize the influence of quantitative factors on FLT parameters, according to the following steps:

- a) Jackknife-based methods described in MAIA et al (2000) are used for obtaining pseudo-values for each parameter;
- b) Linear (polynomial) or nonlinear regression models are fit to the jackknife-derived pseudo-values thus allowing description of continuous patterns of quantitative factor's effect;
- c) Residual analysis and influence diagnostics are performed for checking outliers and model adequacy.

As illustration, we present a case study on the effect of temperature (20, 23, 25, 27 and 30 °C) on the demographic parameters of a predaceous ladybird *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae). *Hippodamia variegata* is an important aphidophagous ladybird with Palaearctic origin and cosmopolitan distribution (KRAFSUR *et al.*, 1996; FRANZMANN, 2002; OMKAR and PERVEZ, 2004). It could potentially be used as a biocontrol agent of variety of aphids (NEDVED, 1999), hence information on its ecology and life table could be of great potential value. However, little is known about its ecology and demographic attributes. Temperature has a major impact on the demographic attributes of arthropods, especially ladybirds (PERVEZ and OMKAR, 2004). Hence, for the optimal augmentative rearing of the ladybird, it is necessary to optimize the temperature. Thus, the study presented here designed to determine the influence of temperature on demographic attributes of *H. variegata*.

We proposed the following polynomial model for describing the non-symmetrical patterns of temperature influence on FLT parameters :

$$Y_{ij} = \beta_0 + \beta_1 T + \beta_2 T^2 + \beta_3 T^3 + e_{ij}$$

In which Y_{ij} is the j -th FLT parameter pseudo-value for temperature level i ; the model parameters $\beta_0 ; \beta_1 ; \beta_2$ and β_3 correspond to the intercept, linear, quadratic and cubic effects

respectively and e_{ij} is the random error associated to each Y_{ij} pseudo-value, $e_{ij} \sim N(0, \sigma^2)$. The pseudo-values were obtained via jackknife method applied to the life table data as described in MAIA et al (2000). Analysis were performed using the R program *lifetable.R* developed by the authors.

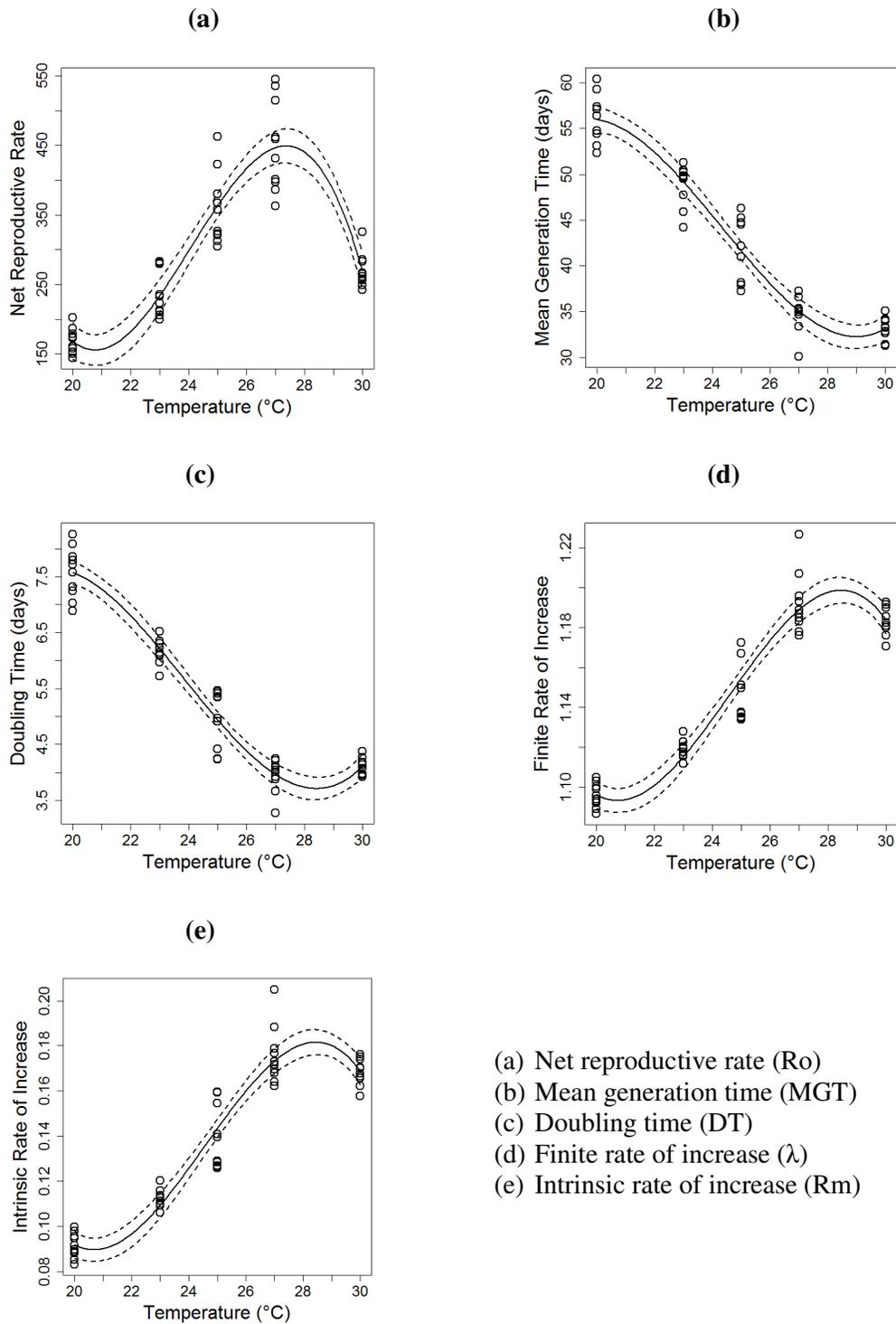
2 Results and discussion

Estimates of polynomial model coefficients used to represent the influence of temperature on *H. variegata* FLT parameters are presented in Table 1. Intrinsic and finite rates of increase along with net reproductive rate of *H. variegata* increased with temperature upto 27°C and later on decreased (Figure 1). Such pattern corresponds to negative estimates for β_1 , positive ones for β_2 and negative ones for β_3 . The reverse was observed in the case of generation and doubling times – reversal patterns are also observed for coefficient signs (Figure 1, Table 3).

Table 1. Estimates of polynomial model coefficients used to represent the influence of temperature on *Hippodamia variegata* fertility life table parameters.

FLT Parameter	Effect	Estimate	Standard Error	t-statistic	p-value*
Net reproductive rate (Ro)	β_0	27332.73	3626.12	7.538	<0.01
	β_1	-3503.00	444.71	-7.877	<0.01
	β_2	148.33	17.98	8.251	<0.01
	β_3	-2.05	0.2396	-8.575	<0.01
Intrinsic rate of increase (Rm)	β_0	5.59	0.8390	6.589	<0.01
	β_1	-0.6941	0.1029	-6.746	<0.01
	β_2	0.0290	0.0042	6.968	<0.01
	β_3	-0.00039	0.00006	-7.096	<0.01
Finite rate of increase (λ)	β_0	7.48	0.9790	7.638	<0.01
	β_1	-0.8136	0.1201	-6.776	<0.01
	β_2	0.0339	0.0048	6.99	<0.01
	β_3	-0.00046	0.00006	-7.11	<0.01
Generation time (GT)	β_0	-719.39	208.28	-3.454	<0.01
	β_1	101.73	25.54	3.982	<0.01
	β_2	-4.33	1.0325	-4.198	<0.01
	β_3	0.059	0.0138	4.311	<0.01
Doubling time (DT)	β_0	-119.10	30.40	-3.916	<0.01
	β_1	16.98	3.73	4.555	<0.01
	β_2	-0.7430	0.1507	-4.906	<0.01
	β_3	0.0103	0.0020	5.145	<0.01

*Nominal significance value.



(a) Net reproductive rate (R_0)
 (b) Mean generation time (MGT)
 (c) Doubling time (DT)
 (d) Finite rate of increase (λ)
 (e) Intrinsic rate of increase (R_m)

Figure 2. Fitted linear regression models used to describe the influence of temperature on life table parameters (R_0 , MGT, DT, λ and R_m) of the predaceous ladybird, *Hippodamia variegata*. Dashed lines represent 95% confidence bands for predicted values.

We are using polynomial models as an approximation to more adequate non linear models for describing temperature effect. They are valid only for the range of observed data; out of that interval patterns can be not consistent with expect behaviour for temperature influence on demographic parameters. We are currently developing R codes for non linear regression fitting by combining jackknife method with non linear procedures available in the *nlme* package.

Despite being used worldwide for life table analysis, the jackknife method itself presents limitations in cases for which survival patterns or fertility distributions are highly asymmetrical. Whenever influence analysis shows critical outliers the use of alternative methods such as parametric or nonparametric bootstrap is needed. These methods applied to life table analysis are still no readily available for users thus requiring research efforts for both methodological and software development.

3 Conclusions

The proposed method allows an adequate assessment of patterns of quantitative factor's influence on fertility life table parameters. It is adequate for data sets without critical asymmetrical behaviour for key variable such as survival and fertility. The availability of R codes for life regression analysis for demographic parameters will be helpful for sound and appropriate analysis of life table assays.

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