Developmental polymorphism and the Brooks-Dyar law

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Introduction

Many protocols for research in insect biology and ecology require accurate determination of larval instar. The Brooks-Dyar Law (1886, 1890) states that the measurement of sclerotized structures follows a predictable regular geometric progression that can be used to determine accurately both larval instar of single larvae and the number of instars before pupation in a population. The Brooks-Dyar Law has been used extensively in studies of a number of holometabolous and hemimetabolous orders.

Although the Brooks-Dyar's Law describes the variation in size among insect larvae as a function of development, the mathematical formula of the law has only been defined empirically, without any insights on the biological meaning of parameters (but see Hutchinson *et al.* [1997]). Moreover, the current definition assumes that insects go through a fixed number of instars before pupation, which is not always the case for many insect orders (Esperk *et al.* 2007).

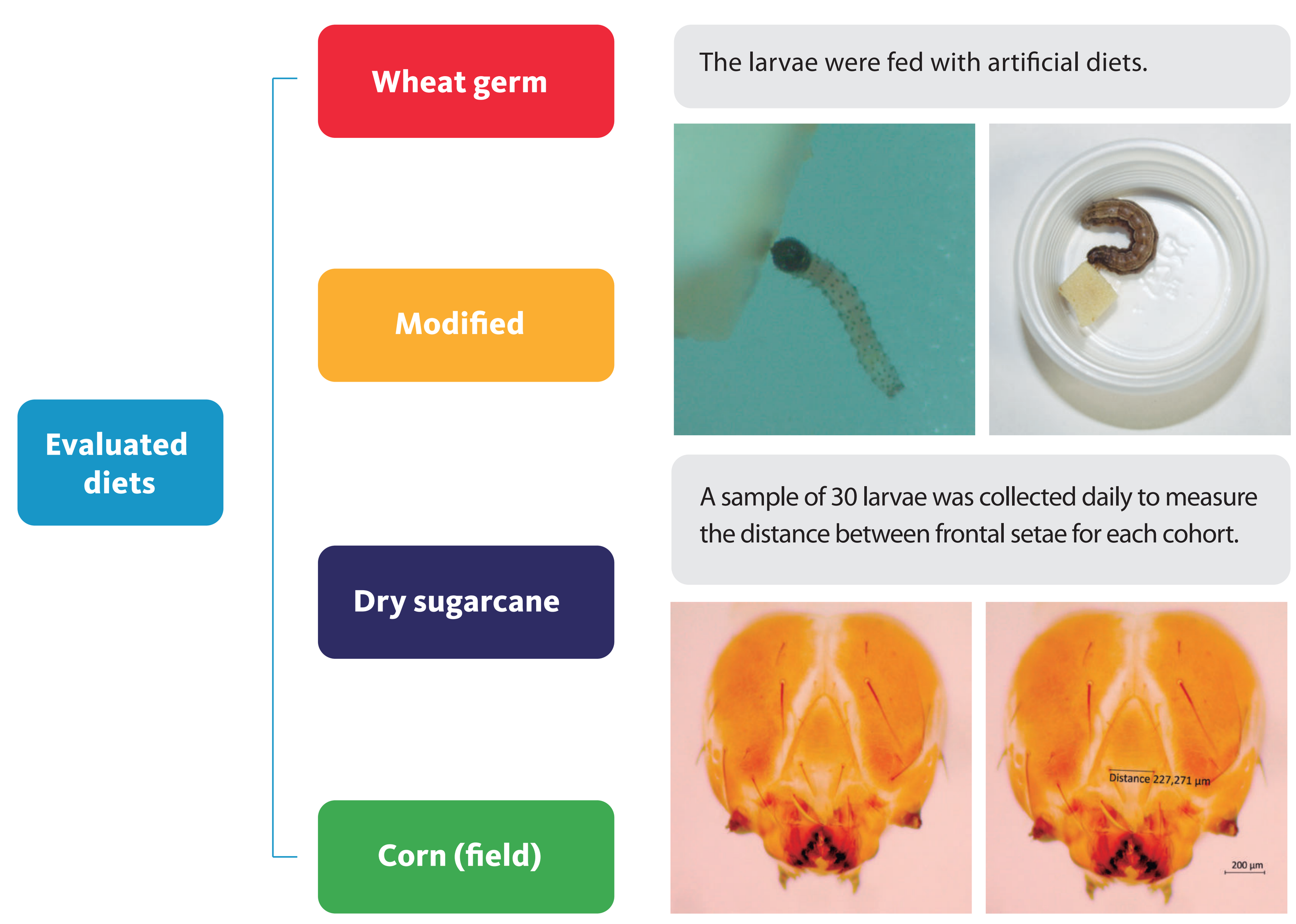
Developmental polymorphism describes how environmental factors, such as food quality, can alter the development of certain species and vary the number of larval instars. Since developmental polymorphism seems to be common in insects (Etilé and Despland 2008), the Brooks-Dyar Law needs to be adjusted to account for epigenetic factors, such as food quality, which may affect the number of instars before pupation. Furthermore, a mechanistic mathematical definition of the Brook-Dyar's law would be useful to more accurately describe the relative properties of a given epigenetic factor.

We used the fall armyworm (*Spodoptera frugiperda*) as a model to test if the Brooks-Dyar Law holds true for larvae reared on different natural and artificial diets. We studied whether the distance between frontal setae can be used as a reliable measurement for the application of the Brooks-Dyar Law. Finally, we propose a mathematical formula for the Brooks-Dyar's law, which includes a constant and two parameters, all defined in light of food quality as a driving epigenetic factor.

Objectives

- To determine if the Brooks-Dyar Law holds true for larvae reared on different natural and artificial diets
- To propose a mathematical definition for the Brooks-Dyar Law.

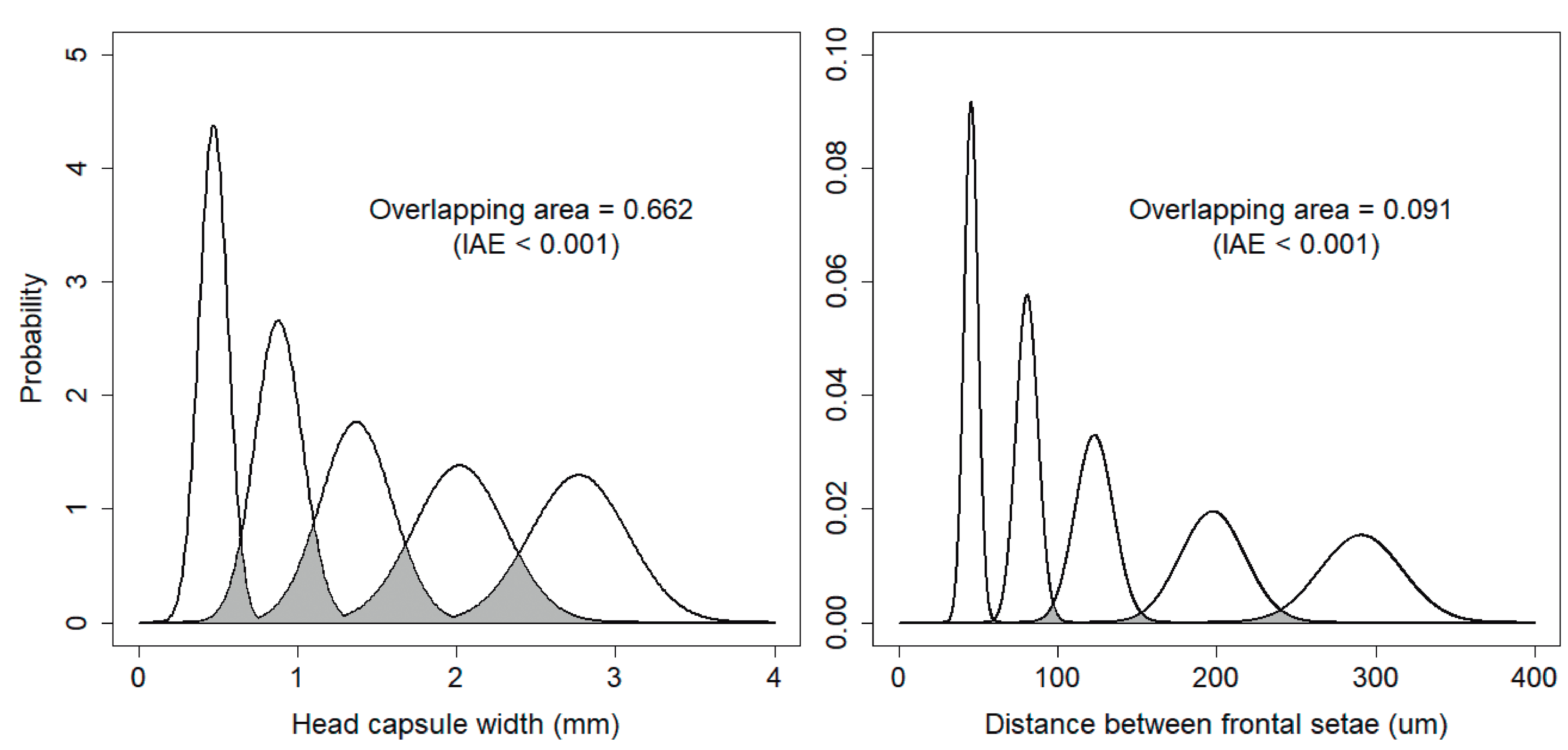
Materials and methods



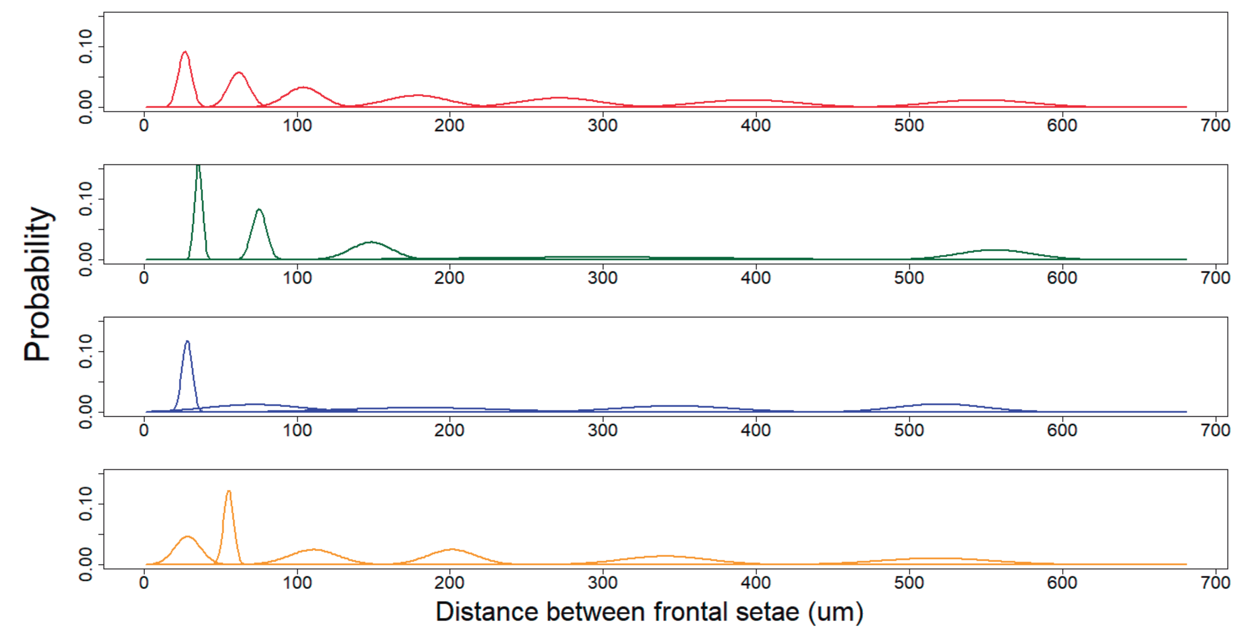
An expectation–maximization (EM) algorithm was used to estimate means and variances for each normal variate within the normal mixture of distances between frontal setae for each cohort.

Results and discussion

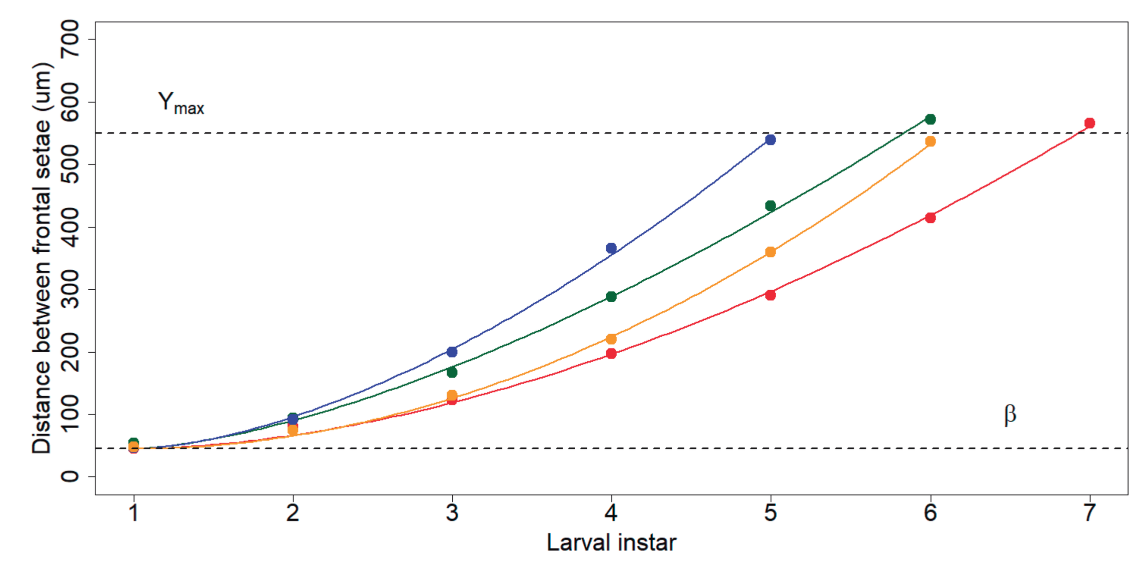
We found that estimation of larval size based on the distance between frontal setae might be more accurate than that based on the entire head capsule width. The probability distribution functions that describe the random variates of larval sizes showed less overlapping area when the distance between frontal setae was used as an indicator, compared with the width of the whole head capsule.



The frequency distribution of the data were similar for the first two instars for the diets evaluated. However, data were more dispersed in all diets as larvae grew. We found a misalignment on the average larval sizes where ecdysis occurred, and a difference in the number of total instars. In contrast, we found no significant differences in the average size at which larvae pupated.



We found that FAW larval size followed a geometric progression, as predicted by Brooks-Dyar's law. However, size progressions differed among diets. Such variation was strongly affected by the ability of FAW to go through a variable number of instars before reaching a genetically defined size of pupation (~ 550um).



The current mathematical definition of the Brooks-Dyar's law lacks biological meaning and is unable to predict the number of instars for species exhibiting developmental polymorphism. The proposed model is:

Brooks-Dyar's law equation:

$$Y = a * exp(bi), \quad \text{(Eq. 1)}$$

Proposed equation:

$$Y = \beta + a\,(i-1)^b, \text{ for } i \in \mathbb{Z}^+,\ \beta < Y < Ymax, \quad \text{(Eq. 2)}$$

where *Y* is the larval size, *Ymax* is the maximum larval size before pupation, *β* represents a constant that explicitly incorporates the size of neonate larvae, and *a* and *b* are parameters estimated from data. If one wants to estimate the instar of a given larva, Eq. 2 can be solved for *i*, provided *b*, *β*, *a* and *Y* are known:

$$i = \left(\frac{Y-\beta}{a}\right)^{1/b} + 1, \quad \text{(Eq. 3)}$$

where *i* should be approximated to nearest integer.

Parameter biological meaning

a and *b* may have different interpretations depending on the number of factors being considered as drivers of larval size progression. As our data only considers the influence of different diets on larval growth, we present the biological meaning of *a* and *b* solely in light of food quality.

a = Base nutritional food value

base nutritional value of diet, independent of consumption rate

b = Food nutritional efficiency

Consumption-dependent added nutritional value of diet

Although all neonate larvae have roughly the same size (β ~ 45um) and reached approx. the same size at the end of the larval stage (Y_{max} ~ 550um), differences in base nutritional value (*a*) and efficiency (*b*) led to different shapes in the growth progression. Some diets with a high base nutritional distributed relatively evenly the growth among instars. Other diets, highly efficient, led to an increase in growth rate when consumption rates increased with larval size.

Conclusions

We found that the distance between frontal setae is a better indicator of larval size compared to the width of the head capsule.

This work presents the first formal mathematical definition of the Brooks-Dyar's law definition. Our formula includes parameters and constants with sound biological meaning and can be easily fit to data using common iterative methods, such as MLE.

Our model is useful in determining the instar of single larvae and the total number of instar for a population with and without developmental polymorphism.

References

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