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Temperature-dependent development and stage-specific mortality of immature *Oulema duftschmidi* (Redtenbacher) life stages, in comparison to *O. melanopus* (L.) and *O. gallaeciana* (Heyden) (Coleoptera Chrysomelidae)

Abstract - In a restricted temperature range, the development and stage-specific mortality of *Oulema duftschmidi* (Redtenbacher) eggs, larvae and pupae, are compared to the responses of corresponding *O. melanopus* (L.) and *O. gallaeciana* (Heyden) life stages. The developmental rates are similar on the egg stage, while *O. duftschmidi* larvae and pupae developed slower than the corresponding life stages of the two other species. The developmental threshold of all life stages was highest for *O. duftschmidi*. For the three life stages of each species, a linear model was found satisfactory to describe the developmental rate - temperature relationship. In general, the stage-specific mortality is highest in *O. duftschmidi* life stages. On the larval and pupal stages, *O. duftschmidi* responds with increasing, and the other two species with decreasing mortality rates to a temperature increase from 20 to 25°C.

Riassunto - *Sviluppo e mortalità a temperature diverse degli stadi preimmaginali di* Oulema duftschmidi *(Redtenbacher), a confronto con* O. melanopus *(L.) e* O. gallaeciana *(Heyden) (Coleoptera Chrysomelidae).*

Lo sviluppo e la mortalità a temperature diverse di uova, larve e pupe di *Oulema duftschmidi* (Redtenbacher) sono stati confrontati con quelli corrispondenti di *O. melanopus* (L.) e *O.gallaeciana* (Heyden). I valori del tasso di sviluppo sono simili per lo stadio di uovo, mentre le larve e le pupe di *O. duftschmidi* hanno un accrescimento più lento rispetto alle altre due specie. La soglia di sviluppo di tutti gli stadi di *O. duftschmidi* risulta più alta. Per uova, larve e pupe di ciascuna specie è stato trovato un modello lineare che descrive in modo soddisfacente la relazione tasso di sviluppo – temperatura. In generale la mortalità specifica dei diversi stadi è maggiore per *O. duftschmidi*. All'aumentare della temperatura da 20 a 25°C la mortalità delle larve e delle pupe di *O. duftschmidi* aumenta mentre nelle altre due specie diminuisce.

Key words: *Oulema duftschmidi*, temperature-dependent development, stage-specific mortality

INTRODUCTION

As opposed to North America (Borror *et al.*, 1976) the genus *Oulema* Gozis is represented in Europe by several species. In Italy for example, eight species have been found (Biondi *et al.*, 1994). Three among them are xeric [*O. hoffmannseggi* (Lacordaire), *O. rufocyanea* (Suffrian) and *O. tristis* (Herbst)], *O. magistrettiorum* (Ruffo) is an endemic Appennine species, while *O. erichsoni* (Suffrian) has a limited distribution only. Apparently, these five species are of no economic importance and not considered in this study. In Europe, the name Cereal Leaf Beetle is often used for both *O. melanopus* (L.) and *O. gallaeciana* (Heyden). Note that the name *O. lichenis* is often erraneously used for *O. gallaeciana* (Monrós, 1959).

While examining the collection of the Museum of Paris, Berti found that *O. duftschmidi* was listed under *O. melanopus* from which it can only be separated by an expert who can rely on few morphological differences expressed in characteristics of the genitalia. Berti (1989) published a map of Europe, North Africa and West Asia on which the distribution of *O. melanopus* and *O. duftschmidi* is depicted. Accordingly, they share almost the same area, *O. melanopus* going further north, while *O. duftschmidi* extending more to south, east and west. There are three Cereal Leaf Beetle species (*O. melanopus*, *O. gallaeciana* and *O. duftschmidi*) with similar but not identical distributions in Europe in general and in Italy in particular (Biondi *et al.*, 1994).

The distributions of these three species can only be explained on the basis of their ecological requirements and of environmental factors to which they are exposed. The temperature influence on developmental time and on intrinsic mortality of immature life stages is given priority when analysing the dynamics of poikilothermic populations (Gilbert *et al.*, 1976; Curry & Feldman, 1987; Gutierrez, 1996). In a favourable temperature range, poikilotherms typically respond with low intrinsic mortalities and linearly increasing developmental rates to increasing temperatures. At high and low temperatures, however, the mortality rate typically increases and developmental rates deviate from the linear response observed in the favourable range. As a consequence, a linear developmental rate-temperature relationship formulated for favourable temperatures needs revision when extended to temperature extremes.

This indicates that there are advantages for initiating the study on temperature-dependent immature development of the three *Oulema* species in a favourable temperature range. The inital focus on favourable conditions can also be justified on technical ground. In fact, the results obtained may permit efficient planning of additional experiments if required by statistical considerations (Campbell *et al.*, 1974) and facilitate the planning of experiments at high and low temperature extremes. This is particularly important in the case under study, since the necessary equipment is available for limited periods only and the insects are readily available only in spring.

The purpose of this paper is to represent development and mortality of immature *O. duftschmidi* life stages (eggs, larvae, pupae) as a function of constant temperatures in a restricted favourable temperature range. The stage-specific development and the mortality of *O. duftschmidi* is compared with the same parameters reported for *O. melanopus* and *O. gallaeciana* by Ali *et al.* (1977; 1979) who used the same experimental procedures in a similar temperature range.

MATERIALS AND METHODS

Development and intrinsic survival of immature O. duftschmidi *life stages*

REARING. Adults of *O. duftschmidi* were collected during the years 1994-1995-1996 in Lombardy's Po valley (Northern Italy) in wheat and barley fields as well as on uncultivated Gramineae boarding the crops. Sampling started at the end of February and lasted till the end of March. The adults were kept at 24±1 °C and fed wheat seedling leaves. Each newly formed couple was put in a Petri dish.

In 4 different experiments eggs were reared to the adult stage at constant temperatures (T_i °C, i = 1, 2, 3, 4) of T_1 = 19±1 °C, T_2 = 22±1 °C, T_3 = 24±1 °C, T_4 = 26±1 °C. The first two experiments were performed during the year 1994 at temperatures T_1 and T_2, the third in the year 1995 at temperature T_3 and the fourth in 1996 at T_4. At the beginning of each experiment newly laid eggs were transferred one by one into different Petri dishes, labelled n = 1, 2, …, N_i (i = 1, 2, 3, 4). Thus, N_i represents the initial number of eggs available in the *i-th* experiment (N_1 = 237, N_2 = 239, N_3 = 396, N_4 = 397).

Each Petri dish contained moist paper and, after egg hatching, a leaf of wheat seedling was given as food for larvae. The observations were made on 3 life stages, i.e. on eggs (j=1), larvae (j=2) and pupae (j=3). The Petri dishes were controlled daily in order to record the life stage and the age a_{inj} at which the *n-th* individual of the *i-th* experiment leaves the *j-th* life stage, and N_{ij} is the number of individuals that, in the *i-th* experiment, survived the *j-th* stage.

DEVELOPMENTAL RATES. Let $a_{in0} = 0$ indicate the age at birth (i.e. the age of the newly laid eggs) of all the individuals. Then

$$\Delta_{inj} = a_{in(j-1)} - a_{inj} \qquad [1]$$

is the duration, in days, of the j-th stage at temperature T_i of the *n-th* individual. Hence

$$r_{nj} = \frac{1}{\Delta_{inj}} \qquad [2]$$

is, by definition, the developmental rate of the same individual. The average developmental rate of *O. duftschmidi* individuals of the *j-th* stage at temperature T_i is obtained from

$$r_{ij} = \frac{1}{N_{ij}} \sum_{n=1}^{N_{ij}} r_{inj} \qquad [3]$$

The theory of poikilothermic development (De Réaumur, 1735; Gilbert *et al.*, 1976; Sharpe & DeMichele, 1977; Gutierrez, 1996) states that the developmental rate is a function of temperature

$$r_{ij} = r_j[T_i] \qquad [4]$$

Empirical evidence suggests that equation [5] is linearly related to temperatures in the favourable temperature range (Gilbert *et al.*, 1976)

$$r_j = A_j\left(T - T_{0j}\right) \qquad [5]$$

where A_j and T_{0j} are stage-specific parameters, whose numerical values can be estimated through a linear regression. T_{0j} is called the thermal threshold of the j-th stage, because the model predicts that no development occurs at this temperature. Likewise, it is assumed that r_j=0 at $T<T_{oj}$

STAGE-SPECIFIC MORTALITY. Provided that $N_{i0} > N_I$ we obtain the number of individuals which have died under temperature T_i in the j-th stage, i.e. the intrinsic stage-specific mortality by

$$d_{ij} = N_{i(k-1)} - N_{ik} \qquad [6]$$

This equation permits the calculation of the percentual stage-specific mortality generally used in this work. There is empirical evidence put forward, among others, by Curry and Feldman (1987), who state that the intrinsic stage-specific mortality is a function of temperature.

Development and intrinsic survival of immature O. melanopus *and* O. gallaeciana *life stages.*

Ali *et al.* (1977; 1979) carried out a research work on temperature dependent developmental rate and stage-specific mortality of *O. melanopus* and *O. gallaeciana.* Cohorts were reared under three constant temperatures (T_1' = 15±1 °C, T_2' = 20±1 °C, T_3' = 25±1 °C) which differ from T_1, T_2, T_3 used for *O. duftschmidi.* However, a visual examination of the data shows that they also fall into a favourable temperature range. For comparison purposes, we extract the relevant information to parametrize equation [5] and use the stage-specific mortality for comparison purposes.

RESULTS

Table 1 shows the response of stage-specific developmental rates to the different experimental temperatures. The standard deviations divided by the mean developmental rates yield coefficients of variation between 0.06 and 0.22, which broadly fall in the

Table 1 - Regression line equations, thermal thresholds and regression coefficients for Oulema duftschmidi, *calculated from observations on individuals.*

STAGE	REGRESSION LINE EQUATION	THERMAL THRESHOLD (°C)	REGRESSION COEFFICIENT
Egg	$R(T) = 0.016T + 0.1948$	$T_0 = 12.2$	$r = 0.81$
Larva	$R(T) = 0.0094T + 0.127$	$T_0 = 13.5$	$r = 0.89$
Pupa	$R(T) = 0.008T + 0.1168$	$T_0 = 14.6$	$r = 0.94$

Table 2 - Stage-specific mortalities of Oulema duftschmidi *at different experimental temperatures.*

STAGE	EGG	LARVA	PUPA
TEMPERATURE			
$T_1 = 19$ [°C]	50.9	73.0	57.7
$T_2 = 22$ [°C]	59.9	73.5	77.1
$T_3 = 24$ [°C]	35.6	93.0	86.7
$T_4 = 26$ [°C]	39.3	93.0	100

Table 3 - Stage-specific parameters (A , T_0) of the linearized developmental rate functions for Oulema duftschmidi compared to that of Oulema melanopus *and* Oulema gallaeciana *(Ali* et al., *1977).*

STAGE	EGG		LARVA		PUPA	
	A	T_0	A	T_0	A	T_0
O. duftschmidi	0.0160	12.2	0.0094	13.5	0.0080	14.6
O. melanopus	0.0114	10.0	0.0080	8.8	0.0047	8.8
O. gallaeciana	0.0128	10.4	0.0082	8.6	0.0090	11.0

Table 4 - *Stage-specific mortality for* Oulema duftschmidi *(O. duft) compared to that of* Oulema melanopus *(O. melan) and* Oulema gallaeciana *(O. gallae) (Ali* et al., *1977) at two different temperatures.*

STAGE	EGG			LARVA			PUPA		
TEMP.	O. duft.	O. melan.	O. gallae.	O. duft.	O. melan.	O. gallae.	O. duft.	O. melan.	O. gallae.
20 °C	51	21	16	73	25	22	58	29	19
25 °C	36-39	16	15	93	11	12	87 - 100	22	9

range observed for other arthropods (Curry & Feldman, 1987; Shaffer, 1983). Table 2 shows a very high stage specific mortality for pupae, that restricts the temperature range for observations on pupae and allows observations on few individuals only.

Fig. 1 shows by visual examination that, for the three species under study, the developmental rates of the different life stages are linearly related to temperatures in the temperature range under study. According to Table 3 the developmental threshold of eggs is lowest in the case of *O. duftschmidi* and highest in the case of *O. melanopus.*

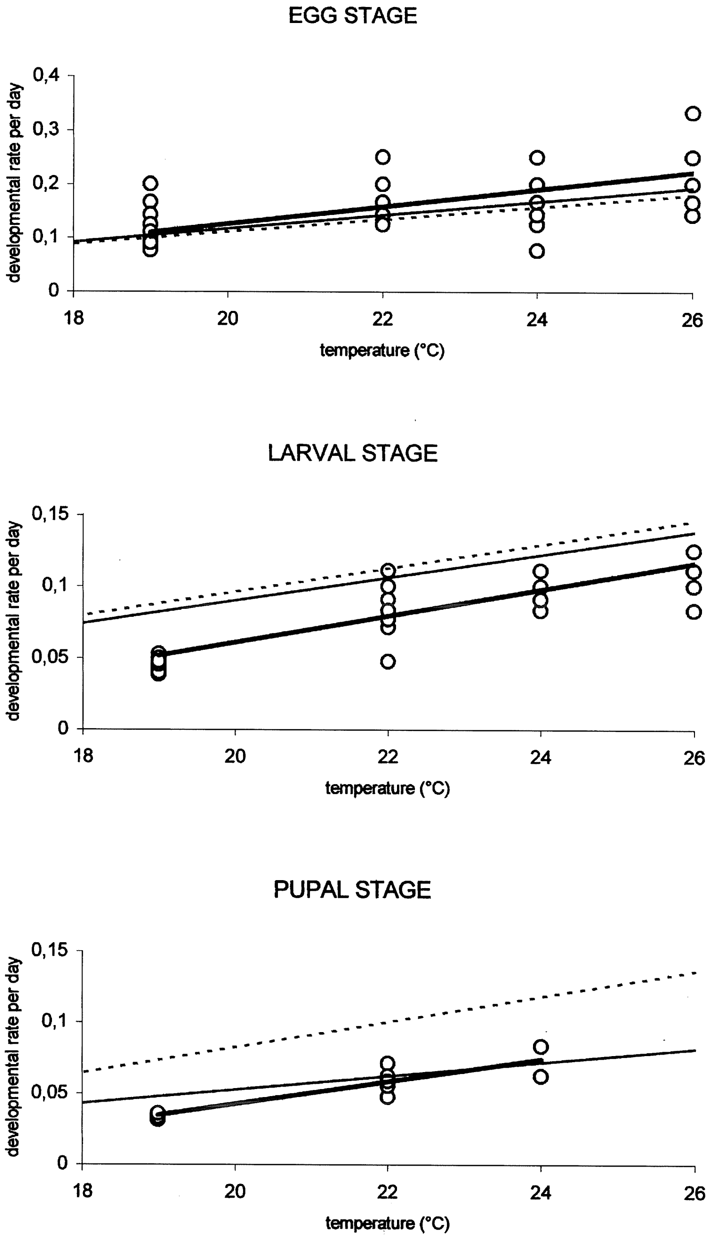

Fig. 1 - Stage-specific developmental rates of *Oulema duftschmidi* (empty circles), compared with *Oulema melanopus* (thin lines) and *Oulema gallaeciana* (dotted lines) as reported by Ali *et al.* (1977). The parameters of the linear models are given in Table 1.

In the case *of O. gallaeciana* the lowest threshold has been found for larvae. Fig. 1 and Table 3 show that *O. duftschmidi* life stages have higher thresholds than the corresponding life stages of the other species and that, with exception of the egg stage, *O. duftschmidi* develops slower than the other species in the temperature range under study. The adequacy of the linear model for describing both life stage specific developmental rates and mortalities indicates that the selected temperature range is favourable for all three species

Tab. 4 shows, for the eggs of all the species under study, a decrease in mortality with a temperature increase from 20 to 25°C. This comparison is made possible through the approximation of the experimental temperatures for *O. duftschmidi* by 20 and 25°C, respectively. The aforementioned variability in temperature regimes of ±1 °C permit, for the purpose of this work, such an approximation. In general, the mortality is higher for *O. duftschmidi* than for two other species. Larvae and pupae of *O. duftschmidi* respond with increasing mortality to a temperature increase from 20 to 25°C , whereas the corresponding life stages of the other two species suffer from decreasing mortality.

DISCUSSION

O. duftschmidi was reared under conditions of high humidity and low radiation. Presumably, Ali *et al.* (1977; 1979) also used conditions, which allow to approximate insect body by ambient temperature. Many studies rely on this approximation, although Baumgärtner and Severini (1987) and Severini *et al.* (1990; 1996) among others, have demonstrated, by means of measurements and by model predictions, that insect body temperatures often considerably deviate from air temperatures and that the predictive capabilities of population models are improved when taking into account this differences. In fact, Gutierrez *et al.* (1974) found that body temperatures of *O. melanopus* were higher than ambient air temperatures under field conditions. Therefore, we strongly recommend the use of insect body rather than ambient air temperatures when studying the population dynamics of the three species.

The observations on *O. duftschmidi* and on the other two species have been made on similar number of insects in a similar temperature range. However, Guppy & Harcourt (1978) made observations on a small number of *O. melanopus* at a wider range of temperatures, which renders difficulty in comparing their results with the ones obtained and used in this study. The different experimental procedures are a major but not the only impediment for comparing different studies. We also refrain from comparisons with the results of other investigations because of possible uncertainties in the taxonomic status of the insects under study. As indicated above, Berti (1989) clarified the identification of the species and their distribution only recently. We assume a correct identification in the case of Ali *et al.* (1977; 1979) only because they compared two species with responses different from the ones found for *O. duftschmidi* in this work. The accurate identification of the species is not only a prerequisite for analysing the spatial distribution but also for undertaking possible biological control operations. Parasitoids for example, may display species-specific responses, which may have great significance in biological control programs (e.g. DeBach, 1964).

The response of the mortality to temperature is very different between the three species under study. In general, the levels of stage-specific intrinsic mortalities appear to be very high in comparison with other arthropods (see for example, Curry & Feldman, 1987). The increase in mortality of *O. duftschmidi* larvae and pupae to a temperature increase from 20 to 25°C, i.e. in a favourable range, is not only different from the other two species but also from other insects (see for example, Curry & Feldman, 1987). This response may not directly be related to food quality or quantity, since it is manifested on both larval and pupal stages, and a carry-over effect from larvae to pupae is unlikely to have occurred.

The results of the studies on development and mortality enable us to make some preliminary remarks on the distribution. *O. gallaeciana* and *O. melanopus* have relatively low thresholds and stage specific mortalities. This may enable them to inhabit a wide range of ecological conditions. *O. duftschmidi* on the other hand has a relatively high threshold and responds faster to temperatures than the other two species. However, it appears to suffer from relatively high mortality when exposed to high temperature. This indicates that *O. duftschmidi* may be found in a restricted area with warm climates. However, additional experiments, including on adults, at a wider temperature range than used so far, are necessary to further detail the geographical distribution.

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