The Impact of Supplementary Food on a Prey-Predator Interaction
van Rijn, P.C.J.

Citation for published version (APA):
van Rijn, P. C. J. (2002). The Impact of Supplementary Food on a Prey-Predator Interaction Amsterdam: in eigen beheer

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
2.1

Comparative life history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber

Paul C.J. van Rijn¹, Chris Mollema² & Greet M. Steenhuis-Broers²

¹University of Amsterdam, Institute of Biodiversity and Ecosystem Dynamics, Kruislaan 320, 1098 SM Amsterdam, The Netherlands; ²DLO-Centre for Plant Breeding and Reproduction Research (CPRO-DLO), P.O. Box 16, 6700 AA Wageningen, The Netherlands

**Abstract** Shortly after its invasion in Europe, Western Flower Thrips, *Frankliniella occidentalis* (Pergande), became a more severe pest in greenhouse crops than the Onion Thrips, *Thrips tabaci* Lindeman. To test whether this differential pest status is due to a larger capacity of population increase, a comparative life history study was carried out on cucumber (*Cucumis sativus* cv. Corona). Experiments at 25 °C showed that the egg-to-egg period of *F. occidentalis* is shorter, but its peak ovipositional rate is lower and its offspring sex ratio is more male biased. These differences result in a slightly lower intrinsic rate of population increase (rm) for *F. occidentalis* than for *T. tabaci* (0.166 vs. 0.176 day⁻¹). It is shown experimentally that between 15 and 28 °C developmental rate of *F. occidentalis* is linearly related to temperature, with a theoretical threshold temperature similar to the value reported for *T. tabaci* (10.9 vs. 11.5 °C). It is argued that the rm-value of *F. occidentalis* will not be higher than that of *T. tabaci* for any temperature within this range. Alternative explanations for the difference in pest status between the two thrips species are discussed.

The Onion Thrips, *Thrips tabaci* Lind., and the Western Flower Thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera) are major pests of greenhouse crops in Europe. Whereas *T. tabaci* is native to Europe and has been considered to be a pest for a long time (see e.g. Morison, 1957), *F. occidentalis* invaded Europe c. 10 years ago via plant material from North America (Zur Strassen, 1986), became a more important pest and has remained so.

Thrips damage is either caused directly by parenchyma feeding and consequent reduction of photosynthetic capacity (Hunter and Ullman, 1989; Rosenheim *et al.*, 1990; Royer *et al.*, 1986) or indirectly by transmission of plant viruses, such as the Tomato Spotted Wilt Virus (*Broadbent et al.*, 1987; Vierbergen, 1990; German *et al.*, 1992). Among the factors that contributed to the pest status of both thrips species are (1) high capacities for population growth (Watts, 1934; Trichilo and Leigh, 1988), (2) broad host
The impact of supplementary food on a prey – predator interaction

plant ranges (Sakimura, 1932; Yudin et al., 1986; EPPO, 1988) and (3) rapid build-up of resistance against pesticides (Royer et al., 1986; Brødsgaard, 1991a; Immerajan et al., 1992).

Methods to control thrips pests are being developed in essentially three directions: 1. Biological control with natural enemies, such as predatory mites (De Klerk and Ramakers, 1986; Ramakers et al., 1989), anthocorid bugs (Van den Meiracker and Ramakers, 1991), hymenopterous parasites (Loomans et al., 1993), and fungal pathogens (Samson et al., 1979; Helyer, 1993); 2. Breeding for resistance of host plants, such as cucumber and chrysanthemum (Mollem et al., 1993; De Jager et al., 1993); 3. Chemical control (Binns et al., 1982; Van Geel, 1991; Helyer and Brobyn, 1992).

Insight into the effectiveness of these control measures can be improved by measuring life history components. In particular, the capacity of population increase (Birch, 1948) may serve as a simple summary-statistic to evaluate plant resistance (Trichilo and Leigh, 1985) or to determine strategies of chemical control. In addition, it may serve as a yardstick for selecting suitable natural enemies (Janssen and Sabelis, 1992). Detailed information on thrips life history may also be helpful in understanding biological control by predators; for example, the time spent in stages vulnerable to natural enemies can be decisive for predator impact (e.g. Murdoch et al., 1987).

The aim of this study was to test whether the differential pest status of F. occidentalis and T. tabaci is due to differences in population growth capacities. To this end a comparative life history study was made and the intrinsic rates of population increase ($r_m$) were estimated (cf. Birch, 1948).

Several life history studies have been published on T. tabaci (Sakimura, 1932; Watts, 1934; Harris et al., 1936; Ghab and El-Sayed, 1948; Lall and Singh, 1968; Gewaad and El-Shazli, 1969; Edelson and Magaro, 1988) as well as on F. occidentalis (Bryan and Smith, 1956; Lublinkhof and Foster, 1977; Trichilo and Leigh, 1988; Lowry et al., 1992). None of these studies provide a comparison of the two species on the same host plant and under the same environmental conditions. Moreover, most studies lack age-specific data, needed for an accurate estimation of $r_m$ (with the exception of Trichilo and Leigh, 1988, and Lowry et al., 1992), and were done on host plants other than greenhouse crops, such as bean, cotton, onion and peanut.

Cucumber (Cucumis sativus L.) was selected as host plant for our comparative life history study, because it represents one of the crops where the differential pest status is manifest in practice. Detailed studies of all life history components have been made at 25 °C (i.e. developmental rate and survival of the different life stages, age-related ovipositional and survival rates of adult females, and offspring sex ratio). For other temperatures only developmental time and survival of young stages were measured (F. occidentalis) or obtained from the literature (T. tabaci; Edelson and Magaro, 1988). These parameters suffice to reconstruct the full life history under the assumption that ratios between different developmental and ovipositional rates are constant. The temperature-independence of these ratios is supported by empirical evidence (see e.g. Rivnay, 1935; Kawai, 1985).
Chapter 2.1 – Comparative life history studies of thrips

Materials and Methods

Rearing methods and experimental conditions

Frankliniella occidentalis was collected from cucumber plants in a greenhouse at the Center for Plant Breeding and Reproduction Research (CPRO-DLO) in Wageningen. Thrips tabaci was collected from cucumber plants in a greenhouse at the University of Amsterdam. The plants had been infested for more than two months before the experiments started. Thrips were collected with a small aspirator.

Experimental arenas consisted of leaf disks (12 mm diameter) placed upside down in multiwells (Greiner no.662160, containing 24 wells), filled with water. The leaf disks were punched from nearly full-grown cucumber leaves (C. sativus cv. Corona). Each multiwell was closed with a plastic lid. In this way relative humidity approximated 100%. Thrips were transferred to the leaf disks with a small brush, after anaesthetizing them for a few seconds with carbon dioxide, from which they revived within a minute.

Unless stated otherwise, the experiments were carried out in a climatized room (25 ± 1 °C) under long day conditions (L16 : D8). Observations were done with a stereo microscope, provided with a cold light source.

Development and juvenile survival

Cohorts of eggs were obtained by allowing c. 200 adult female thrips to oviposit on cucumber leaf disks for 5 hours. Progress in development and juvenile survival was assessed every 12 hours. Newly emerged larvae were isolated on fresh leaf disks, and transferred every two or three days, until the thrips matured.

Six developmental stages were distinguished. Since the eggs hatch inside the leaf, the start of the first larval stage was defined by emergence of a larva on the leaf surface. The transition from first to second larval stage was inferred from the occurrence of a moulting skin on the leaf disk, since there are no clear morphological differences between the two stages. Second larval instars were put on larger leaf disks (24 mm) on submerged cotton wool. In this way the thrips were forced to pupate on the leaf disks without many losses. The prepupae can be recognized by their short wing sheaths and erected antennae. The pupae have long wing sheaths, which almost reach the end of the abdomen, whereas the antennae are bent backwards along the head. Both (pseudo-)pupal stages do not eat and move only after disturbance. Adults can be recognized by their wings.

Oviposition and adult survival

To obtain females of known age, second-instar larvae were reared to adults on cucumber leaf disks. Forty-eight newly emerged females were isolated on fresh leaf disks, and provided with a male to ensure mating. The females were transferred to fresh leaf disks every eight hours, for an accurate estimation of the pre-oviposition period. From the third morning onwards transfers were made every 24 hours, until the number of females in the experiment became too low (n < 7). Leaf disks were examined for numbers of larvae and non-hatched eggs, four days (F. occidentalis) or five days (T. tabaci) after removing females.

Sex ratio

Thrips tabaci, reported to be thelytokous in Europe (Morison, 1957; O'Neill, 1960), was checked for its capacity to produce females without insemination. F. occidentalis is
known to be arrhenotokous (Bryan and Smith, 1956), therefore the secondary sex ratio was determined, by rearing the offspring of inseminated females to adults. The sex ratio was estimated in two groups of offspring: firstly offspring produced during 11 days by females from the oviposition experiment, and secondly offspring produced during one day by females randomly collected from the rearing cage. For both pupae and adults, females were distinguished from males by their larger and wider abdomen, and their abdominal end which is more pointed.

Population parameters

Life tables were constructed from the life history data. The intrinsic rate of increase ($r_m$) was calculated from the Lotka equation (Lotka, 1925). Net reproduction ratio ($R_0$) and cohort generation time ($T_c$, defined as the mean age of mothers at birth of their daughters) were estimated (Birch, 1948; May, 1975).

Effects of temperature

The effect of temperature was studied only with respect to duration and survival of the egg and first larval stage of *F. occidentalis*. To obtain synchronized eggs, adult females (c. 100 for each temperature) were incubated at 25 °C on cucumber leaf disks for five hours. The leaf disks (48 for each temperature) were placed in different climate incubators at c. 12, 15, 20, 25, 28, 29.5, 30.5, 32.5 and 35 °C, respectively. The actual temperature, just above the leaf disks, was measured with a bimetal thermometer. Newly emerged larvae were isolated on fresh leaf disks, and observed until they moulted to the second stage. Time between oviposition and second moult was observed with a precision between 5 and 10%, i.e. twice a week at 12 °C, once a day at 15 °C and every 8 hours at higher temperatures.

Two types of mathematical models have been used to describe the temperature-rate relationship: the double-exponential models derived by Logan et al. (1976), and the biophysical models derived by Sharpe and DeMichele (1977; see also Wagner et al., 1984). A first estimation of the model parameters was obtained graphically. The final parameter values were obtained by a Marquardt (1963) fitting procedure, minimizing the sum of squares of the proportional differences between model predictions and data points.

Results and Conclusions

Juvenile Survival

Eggs of thrips become visible within the cucumber leaf tissue near the end of development. Egg mortality during this visible phase is less than 1%. The mortality observed between egg hatching and adulthood is 19% for *T. tabaci* and 7% for *F. occidentalis*. Mortality occurs mainly during the larval period. Most mortality of the relatively small *T. tabaci* is probably due to manipulation of the very young larvae.

Development

Males of *F. occidentalis* have a somewhat longer juvenile period than females (Table 1; *t*-test: $p < 0.05$). The juvenile period of (female) *T. tabaci* is clearly longer than that of female *F. occidentalis* (12.9 vs. 12.4 days; *t*-test: $p < 0.01$), mainly due to a longer egg
period (Table 1). The total egg-to-egg period reflects this difference as well, since the mean pre-oviposition period is very similar for the two species (c. 2 days; Table 1).

Oviposition

The oviposition curve (ovipositional rate plotted against age) approximates a triangular shape (Fig. 1A). It has its peak shortly after the beginning of the oviposition period, and shows a steady decline afterwards. Oviposition curves of similar shape have been reported by Trichilo and Leigh (1988). The peak ovipositional rate of *T. tabaci* is higher than that of *F. occidentalis*: over the first two days of oviposition the means (± SE) are 5.5 ± 0.30 and 4.1 ± 0.27 (hatched) eggs per day respectively (t-test: *p* < 0.01).

Adult mortality

Adult mortality is higher for *T. tabaci* than for *F. occidentalis* (Fig. 1B). The cumulative Weibull function (Table 2; Pinder *et al*., 1978) gives accurate descriptions of the survival curves of both species, using day 4 after adult emergence as the starting point (Fig. 1B). Using this function for interpolation, the median life-span of the adult females is 11.9 days for *T. tabaci* and 20.5 days for *F. occidentalis*. The underlying instantaneous rate of mortality appears to follow very different patterns for the two species. For *F. occidentalis* mortality rate increases quadratically with age (since γ-1 = 2); for *T. tabaci* mortality rate is almost constant (since γ-1 ≈ 0).

Table 1 Duration of the developmental stages of *T. tabaci* and *F. occidentalis* at 25 °C on cucumber leaf disks.

<table>
<thead>
<tr>
<th>Life stage</th>
<th><em>T. tabaci</em> X</th>
<th><em>F. occidentalis</em> X</th>
<th><em>F. occidentalis</em> X</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>100</td>
<td>3.96 ± 0.32</td>
<td>40</td>
</tr>
<tr>
<td>Larva 1</td>
<td>78</td>
<td>2.13 ± 0.45</td>
<td>39</td>
</tr>
<tr>
<td>Larva 2</td>
<td>62</td>
<td>3.17 ± 0.45</td>
<td>32</td>
</tr>
<tr>
<td>Prepupa</td>
<td>60</td>
<td>1.09 ± 0.23</td>
<td>32</td>
</tr>
<tr>
<td>Pupa</td>
<td>58</td>
<td>2.43 ± 0.23</td>
<td>32</td>
</tr>
<tr>
<td>Egg to Adult</td>
<td>58</td>
<td>12.90 ± 0.89</td>
<td>32</td>
</tr>
<tr>
<td>Pre-oviposition</td>
<td>40</td>
<td>1.90 ± 0.26</td>
<td>40</td>
</tr>
<tr>
<td>Egg to Egg</td>
<td></td>
<td>14.80</td>
<td>14.20</td>
</tr>
</tbody>
</table>

Table 2 Models for life history traits as functions of age (*x*) or temperature (*T*).

<table>
<thead>
<tr>
<th>Name or source</th>
<th>Trait</th>
<th>Model,</th>
<th>where</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cumulative Weibull function</td>
<td>survival</td>
<td><em>l(x) = e^x_T^\gamma</em>,</td>
<td>(X = \frac{x-x_0}{b})</td>
</tr>
<tr>
<td>Gamma distribution function</td>
<td>net reproduction rate</td>
<td>(V(x) = \frac{x-x_0}{\theta} x^{x-1} e^x),</td>
<td>(X = \frac{x-x_0}{b})</td>
</tr>
<tr>
<td>Logan <em>et al</em>. (1976), eq. (10)</td>
<td>developmental rate</td>
<td>(d(T) = \alpha \left[ (1 + ke^{-\beta T})^{1/\lambda} - e^{-\beta T} \right],)</td>
<td>(\tau = \frac{x_0-T}{\delta T})</td>
</tr>
<tr>
<td>this paper</td>
<td>mortality rate</td>
<td>(k(T) = \mu + e^{\tau},)</td>
<td>(\tau = \frac{x_0-T}{\delta T})</td>
</tr>
</tbody>
</table>
The impact of supplementary food on a prey–predator interaction

Figure 1 Age-related life history parameters of *F. occidentalis* (*) and *T. tabaci* (•) at 25 °C on cucumber. (A) Ovipositional rate (*n*). (B) Survival of adult females (*l*). Solid lines represent best fit by cumulative Weibull function (Table 3; *x*₀ = 4 days (fixed), β = 18.9 days and γ = 2.73 for *F. occidentalis* (residual mean square, MSₙres = 11.6·10⁻⁴), *x*₀ = 4 days (fixed), β = 11.6 days and γ = 0.949 for *T. tabaci* (MSₙres = 4.8·10⁻⁴). (C) Net reproduction rate (*lₘ*). Solid lines represent best fit by Gamma distribution function (Table 3; *x*₀ = 1.53 days, *R₀* = 22.1, *b* = 6.09 days and *c* = 1.21 for *F. occidentalis* (MS₁res = 0.74 day⁻²), *x*₀ = 1.70 days, *R₀* = 26.0, *b* = 4.14 days and *c* = 1.20 for *T. tabaci* (MS₁res = 4.12 day⁻²). Adult age is represented by *x*. Addition of the juvenile period to *x* gives total age.
Chapter 2.1 – Comparative life history studies of thrips

Table 3 Secondary sex ratio (proportion of mature daughters) of fertilized females of *F. occidentalis*.

<table>
<thead>
<tr>
<th>Trial number</th>
<th>Age females (days)</th>
<th>N (offspring)</th>
<th>Offspring sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1–11</td>
<td>98</td>
<td>0.65</td>
</tr>
<tr>
<td>2</td>
<td>random</td>
<td>157</td>
<td>0.67</td>
</tr>
</tbody>
</table>

Table 4 Intrinsic population parameters of *T. tabaci* and *F. occidentalis* at 25 °C on cucumber. Juvenile survival is assumed to equal 90% for both species.

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>T. tabaci</em></th>
<th><em>F. occidentalis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_0$ (net reproduction) (female$^{-1}$)</td>
<td>27.5</td>
<td>22.1</td>
</tr>
<tr>
<td>$T_c$ (mean generation time) (days)</td>
<td>20.4</td>
<td>20.1</td>
</tr>
<tr>
<td>$s_T$ (SD of reproductive period) (days)</td>
<td>4.9</td>
<td>5.3</td>
</tr>
<tr>
<td>$r_m$ (intrinsic growth rate) (day$^{-1}$)</td>
<td>0.176</td>
<td>0.166</td>
</tr>
<tr>
<td>$c_a$ (stable age distribution) (% adults)</td>
<td>13.5</td>
<td>14.5</td>
</tr>
</tbody>
</table>

**Sex ratio**

Unmated females of *T. tabaci* produce only female offspring, thus adding evidence to the finding that European populations of this species are thelytokous (Morison, 1957; O'Neill, 1960; Kendall and Capinera, 1990; Vierbergen, 1990). Unmated females of *F. occidentalis* appear to produce only male offspring, whereas fertilized females produce both males and females (arrhenotoky), in agreement with Bryan and Smith (1956). The offspring of fertilized females is clearly female biased. On average, they produce twice as many daughters as sons (Table 3), which is similar to the values reported by Trichilo and Leigh (1988) and Higgins and Myers (1992). The latter authors and Terry and Kelly (1993) discuss possible reasons for the female bias. The thelytokous nature of *T. tabaci* implies a twofold advantage over *F. occidentalis*. First, population growth is promoted by all-female offspring. Second, at low densities population growth is not limited by availability of males.

**Population parameters**

Net reproduction curves at 25 °C are obtained by multiplying survival, ovipositional rate and sex ratio (Fig. 1C). Sex ratio is assumed to be constant with age. The Gamma density function (Table 2; Mood *et al.*, 1974) gives adequate descriptions of these curves, especially for *F. occidentalis* (Fig. 1C). This model is used to extrapolate the data of *F. occidentalis* beyond day 19, and for sensitivity analysis (Appendix 1 and 2).

Together with the duration of the juvenile period, these net-reproduction data form the basis for estimating the population parameters, listed in Table 4. The net reproduction ratio ($R_0$) appears to be higher for *T. tabaci* than for *F. occidentalis*. This is the result of a higher peak oviposition rate and, being thelytokous, a sex ratio equal to one.

Compared to *F. occidentalis*, net reproduction of *T. tabaci* is more concentrated in the beginning of the ovipositional period (the mean reproductive period is 6.3 and 5.6 days respectively). This offsets the difference in the egg-to-egg period, resulting in a similar mean generation time ($T_c$) of 20 days for both species.

The differences in life history features result in only a small difference in the intrinsic growth rate ($r_m$), which is c. 0.17 day$^{-1}$ for both species (Table 4). This is similar to a doubling time of 4 days.
The impact of supplementary food on a prey–predator interaction

**Table 5** Development time of eggs and first-instar larvae of *F. occidentalis* on cucumber leaf disks at 9 different temperatures.

<table>
<thead>
<tr>
<th>Mean temperature (°C)</th>
<th>Egg</th>
<th>mean duration (days)</th>
<th>Egg + Larva</th>
<th>mean duration (days)</th>
<th>Ratio({\text{egg/egg+L1}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.2</td>
<td>53</td>
<td>19.9</td>
<td>29</td>
<td>36.4</td>
<td>0.55</td>
</tr>
<tr>
<td>15.4</td>
<td>78</td>
<td>10.6</td>
<td>48</td>
<td>17.1</td>
<td>0.62</td>
</tr>
<tr>
<td>20.4</td>
<td>58</td>
<td>4.7</td>
<td>55</td>
<td>8.1</td>
<td>0.58</td>
</tr>
<tr>
<td>25.3</td>
<td>170</td>
<td>2.9</td>
<td>149</td>
<td>5.1</td>
<td>0.57</td>
</tr>
<tr>
<td>27.5</td>
<td>66</td>
<td>2.5</td>
<td>64</td>
<td>4.7</td>
<td>0.53</td>
</tr>
<tr>
<td>29.8</td>
<td>64</td>
<td>2.4</td>
<td>42</td>
<td>4.5</td>
<td>0.53</td>
</tr>
<tr>
<td>30.5</td>
<td>64</td>
<td>2.4</td>
<td>52</td>
<td>4.4</td>
<td>0.57</td>
</tr>
<tr>
<td>32.5</td>
<td>60</td>
<td>2.5</td>
<td>26</td>
<td>4.7</td>
<td>0.53</td>
</tr>
<tr>
<td>35.0</td>
<td>c. 120</td>
<td>high</td>
<td>–</td>
<td>(high)</td>
<td>–</td>
</tr>
</tbody>
</table>

**Table 6** Comparison of four models describing temperature-rate relationships, fitted to mean developmental rates of *F. occidentalis* (Table 5).

<table>
<thead>
<tr>
<th>Model</th>
<th>No. of parameters</th>
<th>Residual sum of squares</th>
<th>Optimum temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logan et al. (1976), eq. 6</td>
<td>4</td>
<td>0.097</td>
<td>30.3</td>
</tr>
<tr>
<td>Logan et al. (1976), eq. 10</td>
<td>5</td>
<td>0.004</td>
<td>30.6</td>
</tr>
<tr>
<td>Biophysical, high temp. inhibition</td>
<td>4</td>
<td>0.213</td>
<td>29.2</td>
</tr>
<tr>
<td>Biophysical, high and low temp. inhibition</td>
<td>6</td>
<td>0.003</td>
<td>31.1</td>
</tr>
</tbody>
</table>

**Effects of temperature**

Effects of temperature on development of the first two life stages of *F. occidentalis* are presented in Table 5. At 12 °C development of egg and first larval stage together takes 20 days. At 30 °C this period is reduced to 2.4 days. At 35 °C no eggs hatch within five days.

Developmental rate is plotted against temperature in Fig. 2A. For the description of this temperature-rate relationship four models have been fitted (Table 6). Of the two double exponential models proposed by Logan et al. (1976), the 5-parameter model offers a much better description of the experimental results than the 4-parameter model. A good description is also obtained by the (6-parameter) biophysical model (Sharpe and DeMichele, 1977) with low-temperature as well as high-temperature inhibition; this in contrast with the (4-parameter) model with high-temperature inhibition only. According to the models with good descriptive properties, the optimum temperature is near 31 °C.

Survival of the first larval stage is clearly lower at both ends of the temperature range (Fig. 2B). At the lower end, the high mortality can be attributed to the long developmental time. Over the range from 12 to 28 °C, the relative rate of mortality shows no correlation with temperature (Fig. 2B, \(p = 0.63\)). Above 28 °C, mortality rate increases rapidly with temperature. For the whole range, the temperature-related rate of mortality is adequately described by an exponential function. Here, the exponent is proportional to the difference between the actual temperature and the upper threshold temperature for survival (\(T_M\)) (Table 2; Fig. 2B). When fitted to the survival data, this model predicts maximum survival at 23 °C and no survival at 34 °C.
Figure 2 The effect of temperature on life history traits of *F. occidentalis*. (A) Rate of development from egg to second larval stage. Solid line represents best fit by Logan's 5-parameter model \(d(T)\); Table 3; \(a = 0.243 \text{ day}^{-1}, \ k = 185, \ \rho = 0.261 \text{ °C}^{-1}, \ \delta_T = 1.13 \text{ °C}, \ T_M = 35.29 \text{ °C}\). Straight line represents the linear regression for values between 15 and 28 °C (slope = 0.0131 day\(^{-1}\) °C\(^{-1}\) and \(T_c = 19.85 \text{ °C}\)). (B) Survival (●) and relative rate of mortality (■) during first larval stage. Drawn lines represent best fit by exponential model for temperature-dependent mortality \(k(T)\); Table 3; \(\mu = 0.0318 \text{ day}^{-1}, \ \delta_T = 1.80 \text{ °C}, \ T_M = 34.33 \text{ °C}\). Survival equals \(\exp(-k(T)D(T))\) where \(D(T)\) is the predicted duration of the first larval stage. (C) Predicted intrinsic rate of population increase. Curved line for whole range of temperatures (see text for explanation). Straight line for temperatures between 15 and 28 °C (based on linear temperature-rate relationship and constant mortality rate).
The impact of supplementary food on a prey – predator interaction

The temperature-dependent survival of *F. occidentalis* has been studied by Shipp and Gillespie (1993). When their data with respect to the larvae are described by the exponential function, the basic mortality (i.e. the temperature-independent part termed μ in Table 2) appears to be three times higher than shown in Fig. 2B, and the upper threshold temperature (*T*_μ) much lower (24 instead of 34 °C). The absence of food during the experimental period is a likely explanation for the high mortality rates reported by Shipp and Gillespie.

**Temperature-*r_m* relationship**

To calculate the overall effect of temperature on the intrinsic rate of population increase (*r_m*), two assumptions were made: 1. The instantaneous mortality rate is equal for both larval stages and negligible for the other juvenile stages, as was the case at 25 °C; 2. The ratios between different (developmental and ovipositional) rates do not alter with temperature (‘rate isomorphy’).

The data on the ratio between the developmental period of egg and first instar (Table 5) support the second assumption. Life history studies on this and other thrips species show this rate isomorphy as well (Rivnay, 1935; H.V. Andrewartha, 1935; vs. H.G. Andrewartha, 1936; Kawai, 1985; Robb, 1989; Teulon and Penman, 1991; Lowry *et al.*, 1992). (Exceptions are the studies by Herr (1934) and Tanigoshi *et al.* (1980); their data suggest a lower developmental threshold for pupae (Herr) and second instars (Tanigoshi *et al.*), compared to all other stages.

The temperature-*r_m* curve thus obtained (Fig. 2C), has a similar shape to the one for the developmental rate, but with a maximum at a lower temperature (28 in stead of 31 °C), as a consequence of temperature-dependent mortality.

*Thrips tabaci* has only been studied at temperatures between 17 and 28 °C (Edelson and Magaro, 1988). Within this range, it shows a linear temperature-rate relationship, with a theoretical threshold temperature (the intercept with the temperature axis) of c. 11.5 °C. For temperatures between 12 and 28 °C the temperature-rate relationship of *F. occidentalis* can also be described by linear regression (Fig. 2A, *R*² = 0.998). The theoretical threshold temperature appears to be 10.4 (± 0.4) °C. When using the data points between 15 and 28 °C only, the theoretical threshold temperature becomes 10.9 (± 0.6) °C (Fig. 2A, *R*² = 0.998), which is not very different from the value reported for *T. tabaci*. Within this range, the relative rate of mortality is apparently independent of temperature (Fig. 2B). Starting from the two assumptions mentioned above, it can be shown that *r_m* now has a linear relationship with temperature as well (Appendix 3). Provided zero mortality, the threshold temperature of this relationship equals the threshold temperature with respect to developmental rates. Incorporating mortality in the calculation of *r_m* leads to an increase of the threshold temperature by 0.8 °C (see Fig. 2C). Such a small shift can only cause small differences between the threshold temperatures of the two species. Consequently, the conclusion that the *r_m*-value of *F. occidentalis* is not higher than that of *T. tabaci*, is likely to hold for all temperatures between 17 and 28 °C.
Discussion

Previous estimates of the \( r_m \) of \( F. \) occidentalis at 25 °C are presented by Trichilo and Leigh (1988) and Brodsgaard (1991b). They give lower values than reported here: 0.1577 day\(^{-1}\) on a susceptible cotton variety, and 0.14 day\(^{-1}\) on bean leaves, respectively. The main reason for these lower values is a larger developmental time. Robb (1989) offers an estimate very similar to the value reported here (0.171 day\(^{-1}\)) using chrysanthemum as host plant. In this case, the larger developmental time is compensated by a much higher fecundity. Lowry et al. (1992) report a very low \( r_m \)-value on peanut (0.02 day\(^{-1}\)), mainly due to a very high juvenile mortality rate.

Although there are many reports on life history traits of both \( T. \) tabaci and \( F. \) occidentalis, no other \( r_m \) estimates have been presented. Such estimations would result in \( r_m \) values lower than 0.17 day\(^{-1}\), as developmental rates and mean ovipositional rates reported in the literature are all lower than found in this study (Sakamura, 1932; Harris et al., 1936; Ghabn and El-Sayed, 1948; Gawaad and El-Shazli, 1969; Lall and Singh, 1968; Edelson and Magaro, 1988; Bryan and Smith, 1956; Lublinkhof and Foster, 1977). Possibly, cucumber is a better host plant than those used in the earlier studies (\( E. \) sagitata, bean, cotton and onion). For \( T. \) palmi Karny, a species with a comparable host plant range and pest potential, the highest \( r_m \)-values are found on cucumber as well (0.134 day\(^{-1}\); Kawai, 1986).

\( r_m \) sensitivity to life history changes

The more severe pest status of \( F. \) occidentalis relative to \( T. \) tabaci is apparently not related to a higher intrinsic rate of population increase; the \( r_m \)'s are approximately the same, or even somewhat lower for \( F. \) occidentalis. How sensitive is this conclusion to variation in the life history parameters?

In Appendix 2 the sensitivity of \( r_m \) to its main life history components is analyzed, for the case where net reproduction is Gamma-distributed over age. The proportional sensitivity of \( r_m \) to proportional changes in age (\( r_m \)-elasticity with respect to age) is equal to minus one; so, multiplying age with a factor somewhat bigger than one decreases \( r_m \) by the same factor. The elasticity of \( r_m \) with respect to the egg-to-egg period alone (\( x_0 \)) is somewhat smaller than (minus) one (-0.83 and -0.79 for \( F. \) occidentalis and \( T. \) tabaci respectively; Fig. 3A). The elasticity of \( r_m \) with respect to the net reproduction ratio (which includes oviposition rate, juvenile survival and sex ratio) is only c. 0.34 for both species (Fig. 3A). Consequently, \( r_m \) is at least two times more sensitive to relative changes in egg-to-egg period than to relative changes in net reproduction. Age will be more important than net reproduction as long as \( R_0 \) is above c. 2.8 (Appendix 2).

Numerical sensitivity analysis based on the original data (Fig. 1C) shows that to decrease \( r_m \) by 1%, the ovipositional rate has to decrease by 2.9 or 3.0% for \( F. \) occidentalis and \( T. \) tabaci respectively. This means an elasticity with respect to ovipositional rate of 0.33 or 0.34, which is similar to its value mentioned above. Consequently, the actual differences between net reproduction curves and their descriptions by the Gamma distribution function do not alter the conclusions on \( r_m \)-sensitivity.

In conclusion, for estimating \( r_m \) with a precision of 5%, about the same precision is required for measuring the egg-to-egg period (\( i.e. \) c. 1/2 day at 25 °C), while for the net reproduction ratio a precision of 15% suffices. In this study a precision of 1/2 day was achieved at 25 °C, whereas the standard error of the oviposition rate was ca. 11 and 14% of the mean for \( F. \) occidentalis and \( T. \) tabaci respectively. Consequently, measurement errors are unlikely to cause deviations in the \( r_m \)-value of more than 5% (c. 0.008 day\(^{-1}\)) and will
The impact of supplementary food on a prey–predator interaction

not affect the conclusion that the $r_m$-value is not higher for *F. occidentalis* than for *T. tabaci*.

The $r_m$-values reported in the literature are calculated with data obtained at intervals of one day (Trichilo and Leigh, 1988; Robb, 1989; Brodsgaard, 1991b; Lowry et al., 1992) or even longer (Kawai, 1985; 1986), with obvious consequences for the accuracy.

Calculations of $r_m$ based on the Lotka-equation can be used to evaluate the population consequences of host plant resistance and pesticide application measured at the individual level (see e.g. Trichilo and Leigh, 1985; Romanow et al., 1991). The sensitivity analysis shows that, relative to other life history components, reduction of developmental rate (e.g. by host-plant resistance) is the most effective way of reducing the capacity of population increase. However, Soria and Mollema (pers.comm.) found that developmental rate on cucumber leaf disks is much less affected by plant genotype than some components of net reproduction (such as juvenile survival and ovipositional rate). In this case, the relatively large variation in net reproduction compensates for the relatively low sensitivity of $r_m$ for this life history parameter.

**Alternative hypotheses for differences in pest status**

We conclude that the more severe pest status of *F. occidentalis* relative to that of *T. tabaci* cannot be attributed to a higher capacity of population increase. This conclusion applies to the cucumber cultivar 'Corona' which is the most commonly used cultivar in Dutch horticulture, and one of the cultivars most susceptible to *F. occidentalis* (Mollema et al., 1993). It remains to be seen whether our conclusion also applies to other host plant cultivars and species.

Alternative hypotheses for the difference in pest status in greenhouse crops are:

**Alternative food hypothesis**

Pollen may serve as an important additional food source. Modern F1 cucumber cultivars are sterile, and therefore do not provide pollen. However, several other greenhouse crops supply pollen during at least part of the growing season. Trichilo and Leigh (1988) showed that by adding pollen to a diet of (susceptible) cotton leaves, the $r_m$ of *F. occidentalis* increased from 0.16 to 0.22 day$^{-1}$. Although *T. tabaci* is able to feed on pollen as well (Murai, 1990). *F. occidentalis*, being a flower thrips, might be more efficient in using this high-quality food source (Kirk, 1984; 1985).

**Pesticide effectiveness hypothesis**

There are only few pesticides available for control of *F. occidentalis*, at least partly because it has developed resistance to a wide range of pesticides (Brodsgaard, 1991a; Immerajn et al., 1992). Although *T. tabaci* is likely to have developed resistance as well (Royer et al., 1986), a higher number of pesticides are listed to be effective for its control (Van Geel, 1991).

**Prey defence hypothesis**

The defensive ability against natural enemies might be larger for *F. occidentalis* than for *T. tabaci*. For the relatively small predatory mites, capture success decreases rapidly with increasing size of thrips larvae (Bakker and Sabelis, 1989; Van der Hoeven and Van Rijn, 1990). Consequently, small thrips species, like *T. tabaci*, are expected to be more vulnerable to these predators.

**Pupal survival hypothesis**

The prepupal and pupal stages of neither of the species suffer from mortality under laboratory conditions (this paper; Shipp and Gillespie, 1993). However, most greenhouse vegetables are nowadays cultivated on artificial substrates such as rockwool. Here, the
availability of suitable sites for pupation is likely to be critical. Possibly, interspecific differences in pupation site requirements exist.

**Overwintering hypothesis**
Like most native plant-inhabiting arthropods (Danks, 1987), it is likely that *T. tabaci* has a diapausing phase, but the possibility of greenhouse races without diapause cannot be ruled out. Evidently, *F. occidentalis* does not show a real diapause under greenhouse conditions (Van Houten and Van Stratum, 1993), probably because it originates from mild climatic regions in western USA. In greenhouses, where crops are grown in winter as well, the absence of diapause will clearly be an advantage as it prolongs the period of population growth.

**Quiescence hypothesis**
A state of low energy demands which, unlike diapause, is directly induced by adverse conditions (quiescence), will enable the thrips to persist in periods when no crop is present. Possibly, interspecific differences in quiescence ability exist.

**Dispersal hypothesis**
High migration rates between greenhouses may contribute to the pest status of the species as well. Although thrips mainly depend on air currents for their dispersal, species may differ in their migration rate, due to differences in take-off responses, flight ability and settling responses (Lewis, 1973). The importance of flight for mate finding in *F. occidentalis* (Terry and Gardner, 1990) might increase the number of thrips present in the aerial plankton, thereby enlarging the chance of being transported to other greenhouses.

**Interspecific interference hypothesis**
In addition to feeding on plant tissue and pollen, *F. occidentalis* may also feed on other herbivores, such as spider mite eggs (Trichilo and Leigh, 1986; Wilson *et al*., 1991); this includes the larvae of their own species (pers. obs.) and possibly larvae of other thrips species, such as *T. tabaci*. This may lead to asymmetric interference between *F. occidentalis* and *T. tabaci* when competing on the same host plant.

Testing these hypotheses may elucidate why *F. occidentalis* is such a severe pest in greenhouse crops such as cucumber, whereas its intrinsic rate of increase is apparently not different from that of the minor pest species *T. tabaci*.

An important issue for future research is the extent to which the two thrips species are differentially adapted to greenhouse conditions. For instance, the population of *F. occidentalis* that invaded Europe was probably small and characterised by a lower amount of genetic variation than the populations of *T. tabaci*, which invaded greenhouses from nearby fields. Moreover, the selection regime may have been different for the two thrips species; on the one hand, *T. tabaci* has been subject to selection under greenhouse conditions for a longer time than *F. occidentalis*; on the other hand, *F. occidentalis* occurs exclusively in greenhouses, and may therefore be subject to more intense selection than *T. tabaci*, which occurs both in the field and in greenhouses (Theunissen and Legutowska, 1991). However, it cannot be excluded that specific greenhouse populations have evolved, making selection on the *T. tabaci* populations as intense as on the *F. occidentalis* populations.

**Acknowledgements** We thank J. Bruin, A. Janssen and especially M.W. Sabelis for their critical comments on the manuscript. A.M. de Roos is thanked for his useful comments on the
appendixes. The first author was supported by grant LB177.1250 from the Dutch Technology Foundation (STW).

References


Chapter 2.1 – Comparative life history studies of thrips


The impact of supplementary food on a prey – predator interaction


Chapter 2.1 – Comparative life history studies of thrips


**Note added in proof**

After acceptance of our paper the publication of Gaum *et al.* (1994) was brought to our attention. They found lower developmental and ovipositional rates (on another variety of cucumber), but surprisingly report higher values of *r* and shorter cohort generation times (*T*). This must be due to a misinterpretation of the age variable *x* in the related formulas, which was taken to be the age since maturation rather than the age since birth.

Appendix 1

Value of r when net reproduction is Gamma-distributed over age

Under a stable age distribution, the relation between life history variables and population growth rate \( r \) is given by the classic Lotka-equation (Lotka, 1925):

\[
\int_0^\infty e^{-rx}l(x)m(x)dx = 1, \tag{1}
\]

where \( l(x) \) is the probability of surviving to age \( x \), and \( m(x) \) is the daughter production rate at age \( x \). From this equation \( r \) can be solved numerically. Writing the net reproduction function

\[
\int_0^\infty e^{-rx}l(x)m(x)dx = 1, \tag{2}
\]

where \( R_0 \) is the net reproduction ratio and \( f(x) \) a density function (thus, with an integral equal to one), the Lotka-equation can be written as

\[
R_0 \int_0^\infty e^{-rx}f(x)dx = 1. \tag{3}
\]

The remaining integral can be regarded as the expected value of \( e^{-r\tilde{x}} \), when \( \tilde{x} \) is distributed according to \( f(x) \):

\[
E[e^{-r\tilde{x}}] = \int_0^\infty e^{-rx}f(x)dx. \tag{4}
\]

This is the so-called moment generating function of \( x \) (Mood et al., 1974), which has explicit solutions for particular density functions.

Fig. 1C showed that for the thrips species studied the net reproduction curve can be described by the product of \( R_0 \) and a shifted Gamma density function

\[
f(x) = \frac{1}{b\Gamma(c)}y^{c-1}e^{-y}, \quad \text{where} \quad y = \frac{x-x_0}{b} \tag{5}
\]

and where \( x_0 \) is the age of first reproduction, \( c \) the shape parameter, and \( b \) the time scaling parameter. \( \Gamma(c) \) denotes the gamma function, which is equal to \((c-1)!\) provided that \( c \) is an integer.

The moment generating function of \( y \) (Mood et al., 1974) is

\[
E[e^{t\tilde{y}}] = (1-t)^{-c} \quad \text{for all} \quad t < 1. \tag{6}
\]

Since \( \tilde{x} = x_0 + by \),

\[
E[e^{-r\tilde{y}}] = E[e^{-rx_0}]E[e^{-rb\tilde{y}}] = e^{-rx_0}(1+rb)^{-c} \quad \text{for all} \quad rb > -1. \tag{7}
\]

Substitution of this result for the integral in equation (3) yields

\[
R_0e^{-rx_0}(1+rb)^{-c} = 1 \quad \text{for all} \quad rb > -1 \tag{8}
\]

or

\[
\ln R_0 = r x_0 + c \ln(1+rb) \quad \text{for all} \quad rb > -1. \tag{9}
\]

When \( x_0 = 0 \), \( r \) can explicitly be solved:

106
Chapter 2.1 - Comparative life history studies of thrips

\[ rb = R_0^{1/e} - 1. \]  

(10)

When equation (8) is used to calculate the \( r \)-values of \( F. \ occidentalis \) and \( T. \ tabaci \) (see Fig. 1C for the parameter values) they deviate -0.05% and 2.8% from the values obtained directly by the Lotka-equation, due to differences between the measured data and their description by the Gamma distribution function.

Appendix 2

Sensitivity of \( r \) when net reproduction is Gamma-distributed over age

Cole (1954) and especially Lewontin (1965) have stimulated much work on how changes in different life history components will affect the value of \( r \) (Meats, 1971; Green and Painter, 1975; Snell, 1978; Caswell and Hastings, 1980; Sibly and Calow, 1986). The main conclusion was that for higher values of \( r \) or \( R_0 \) changes in developmental time are more effective than changes in net reproduction ratio. However, the exact conditions have not yet been identified. Based on Appendix 1, for the case where net reproduction follows a Gamma distribution with respect to age, explicit solutions are obtained for the sensitivity of \( r \).

To make the analysis independent of arbitrarily chosen dimensions, a relative measure for the sensitivity is used, which is called 'elasticity' (De Kroon et al., 1986; Caswell, 1989), by analogy to the concept in economics. The elasticity of \( r \) with respect to parameter \( p \) is defined as the proportional change in \( r \) resulting from a proportional change in \( p \):

\[ e_p = \frac{\partial r}{\partial p} \frac{r}{p}. \]  

(11)

By implicit differentiation of equation (8) expressions can be obtained for the elasticity of \( r \) with respect to net reproduction (\( R_0 \)), pre-reproductive (or egg-to-egg) period (\( x_0 \)), and rescaling of age (\( x \)):

\[ e_{R_0}^{-1} = \frac{\partial R_0}{\partial r} \frac{r}{R_0} = r \left( x_0 + \frac{bc}{1 + rb} \right) = c rb a \left( 1 + \frac{1}{a(1 + rb)} \right). \]  

(12)

\[ e_{x_0}^{-1} = \frac{\partial x_0}{\partial r} \frac{r}{R_0} = \left( 1 + \frac{1}{a(1 + rb)} \right). \]  

(13)

\[ e_{x}^{-1} = \frac{\partial X}{\partial r} \frac{r}{X} = -1. \]  

(14)

where \( X \) is a scaling parameter of \( x \), and \( a \) represents the ratio between the pre-reproductive period and mean reproductive period:

\[ a = \frac{x_0}{bc}. \]  

(15)

The elasticities \( e_{R_0} \) and \( e_{x_0} \) cannot be expressed in life history parameters only, since \( r \) can only be solved numerically (equation 8), except for certain parameter values. In
The impact of supplementary food on a prey - predator interaction

Fig. 3 numerical estimations for the elasticities are presented as functions of the two main parameters \( a \) and \( R_0 \).

The elasticity of \( r \) with respect to age \( (e_x) \) equals -1, independent of the actual life history parameters. When \( R_0 \) approaches one (and consequently \( r \) approaches zero) the elasticity of \( r \) with respect to the pre-reproductive period \( (e_{\text{pre-reprod}}) \) becomes

\[
\lim_{r \to 0} e_x = -\frac{a}{a+1}.
\]

For increasing \( a \) asymptotically approaches -1. Fig. 3A shows that this conclusion also holds for \( R_0 > 1 \).

For \( x_0 = 0 \) (and thus \( a = 0 \)) \( r \) has the explicit solution (10) and the formula for \( e_{\text{pre-reprod}} \) reduces to:

\[
e_{\text{pre-reprod}} = c\left[1 - R_0^{-c} \right].
\] (16)

For increasing \( x_0 \) and \( a \) the elasticity \( e_{\text{pre-reprod}} \) rapidly approaches \( 1/\ln R_0 \) (Fig. 3A). This means that, as long as \( a \) is not too small \( (a > 1) \), \( e_{\text{pre-reprod}} \) is a hyperbolic function of \( \ln R_0 \) with both axes as the asymptotes (Fig. 3B). Thus, \( e_{\text{pre-reprod}} \) is equal to \( |e_x| = 1 \) when \( \ln R_0 \) is close to unity \( (i.e. \) the 'critical' value of \( R_0 \) is between 2.7 and 3). When \( R_0 \) is below the critical value, \( r \) is more sensitive to changes in net reproduction than to changes in age, and above this value it is the other way around. For a somewhat higher value of \( R_0 \), there is another critical value of \( R_0 \) for which the elasticity \( e_{\text{pre-reprod}} \) is again \( 1 \) when \( a \) and \( c \) values of the thrips are applied.

Appendix 3

Linear temperature-\( r \) relationship

The rate of population increase, \( r \), is linearly related to (temperature-dependent) developmental rate and instantaneous mortality rate under the following assumptions: 1. the instantaneous mortality rate is not affected by age or temperature, and 2. the ratios between different \( (\text{developmental and ovipositional}) \) rates are not affected by temperature \( ('rate-isomorphy') \). Under the first assumption, time-dependent survival to age \( x \) can be expressed as:

\[
l(x) = e^{-\mu x}.
\] (18)

where \( \mu \) is the constant instantaneous mortality rate.

The net reproduction function can now be written as

\[
l(x)m(x) = e^{-\mu} M(x),
\] (19)

where \( M(x) \) contains all other components of net reproduction.

Substitution of this expression into the Lotka equation (1) yields

\[
\int_0^r e^{(r-x)\mu} M(x)dx = 1.
\] (20)

Under the second assumption, changing temperature is equivalent to multiplying all rates by the same factor, say \( v(T) \) (read: 'relative developmental rate'). When \( M(x) \) represents
the maturation function at a reference temperature (where \( v(T) = 1 \)), this function becomes \( vM(vx) \) at other temperatures. Consequently, equation (21) can be written as

\[
\int_0^\infty e^{-(x/R)x} M(vx)vdx = 1.
\]  

(21)

Introducing a new age variable \( y = vx \) (read: ‘physiological age’) yields

\[
\int_0^\infty e^{-x/R} y M(y)dy = 1.
\]  

(22)

Figure 3 Elasticity of \( r \) with respect to age, \( x \), (\( e_x \)), juvenile period, \( x_0 \), (\( e_{x_0} \)), and net reproduction ratio, \( R_0 \), (\( e_{R_0} \)). See Appendix 2 for definition of elasticity, \( p = c(1-R_a^{-1/c}) \).

(A) As a function of \( a \), the ratio of pre-reproductive period and mean reproductive period (while \( R_0 = 22 \) and \( c = 1.2 \)). (B) As a function of \( R_0 \), the net reproduction ratio (while \( a = 1.9 \) and \( c = 1.2 \)). For \( F. occidentalis \) and \( T. tabaci \), \( a \) equals 1.9 and 2.9 respectively, whereas \( c = 1.2 \) for both.
The impact of supplementary food on a prey – predator interaction

Since all other components of this equation are constant,

\[
\frac{r + \mu}{v} \equiv C \tag{23}
\]

must be constant as well, showing a linear relationship between \( r \), \( v \) and \( \mu \).

Consequently, when developmental rate \( v \) is linearly related to temperature \( T \),

\[ v = k(T - T_c), \]

\( r \) must be this as well:

\[
r = Ck\left( T - \left( T_c + \frac{\mu}{Ck} \right) \right). \tag{24}
\]

Here, \( T_c \), the theoretical threshold temperature of \( r \), increases linearly with the instantaneous mortality rate.

Relaxing the assumption that juvenile mortality rate is constant with age does not affect the conclusions, as long as \( \mu \) is regarded as the mean mortality rate over the juvenile period. Relaxing the assumption that adult mortality rate equals juvenile mortality rate does violate the conclusions on linearity between \( r \) and mortality rate, but not on linearity between \( r \) and \( v \) or temperature.