



## Could the intrinsic rate of increase represent the fitness in terrestrial ectotherms?

Peijian Shi <sup>a,\*</sup>, Hardev S. Sandhu <sup>b,1</sup>, Feng Ge <sup>a</sup>

<sup>a</sup> State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 10010, China

<sup>b</sup> Everglades Research and Education Center, Institute of Food and Agricultural Sciences, University of Florida, Belle Glade, USA

### ARTICLE INFO

#### Article history:

Received 12 December 2012

Accepted 24 January 2013

Available online 31 January 2013

#### Keywords:

Intrinsic optimum temperature

Propensity

Temperature

Body size

Population size

### ABSTRACT

The intrinsic rate of increase ( $r_m$ ) has been considered as an important indicator of fitness in terrestrial ectotherms since long. It is actually an equivalent to the instantaneous growth rate of the exponential equation for describing the density-independent population growth. In terrestrial ectotherms,  $r_m$  has been demonstrated to be temperature-dependent. The temperature at which  $r_m$  was maximal, was considered to be the “optimal” temperature for fitness in Amarasekare and Savage (2012), but this definition needs further analysis. Only  $r_m$  cannot provide thorough representation of fitness. Because body size can affect the competitive abilities in many terrestrial ectotherms, both population size and body size should be considered in measuring the fitness of ectotherms. The rule of “bigger is better” requires relatively low temperature to increase in body size, whereas relatively high temperature is required for a rapid increase in population size. Thus, there is presumably a trade-off in temperature for adjusting individual body size and population size to achieve maximum fitness. We hypothesized that this temperature could be reflected by the intrinsic optimum temperature for developmental rate in the Sharpe–Schoolfield–Ikemoto model, and it led to a temperature estimate around 20 °C. However, the traditional viewpoint based on the temperature corresponding to the maximal intrinsic rate of increase provides a temperature estimate around 30 °C. This study suggests that a low temperature around 20 °C might authentically represent the optimal ambient temperature for fitness in terrestrial ectotherms. It implies that thermal biologists who are interested in the effect of temperature on the fitness in terrestrial ectotherms should pay more attention to their performance at low temperature rather than high temperature.

© 2013 Elsevier Ltd. All rights reserved.

## 1. Introduction

The concept of “fitness” is a notion of central importance to evolutionary theory (Mills and Beatty, 1979). However, the definition of fitness has remained obscure. In terrestrial ectotherms (ectotherms for simplicity below), the intrinsic rate of increase ( $r_m$ ) was considered to be an appropriate measure of fitness (Huey and Berrigan, 2001). Based on this concept, Amarasekare and Savage (2012) provided a mathematical framework to explain the temperature dependence of fitness. The premise of this mathematical frame is that the intrinsic rate of increase at any temperature can represent the fitness of ectotherms at this temperature. According to this assumption, they stated that the temperature at which the intrinsic rate reached its maximum was an “optimal” temperature for fitness.

Fitness was considered to be closely linked with natural selection (Sober, 2001). The temperature at which fitness of a species is maximal should also be the optimum temperature for their active performance. This temperature stands for the most suitable physiological temperature developed during the long-term natural selection in that species. However, Shi et al. (2012) reported that the damage caused by the diamondback moth (*Plutella xylostella*) did not peak in summer when the daily average temperature approximated to the temperature at which its  $r_m$  was maximal. In the current study, we further analyzed whether  $r_m$  could represent the fitness in ectotherms as an appropriate measure.

## 2. Cognitive constraints on the fitness in ectotherms

The definition of fitness is usually related to the expected number of offspring. The value of  $r_m$  calculated from the life table methods reflects the instantaneous rate of population increase.

\* Corresponding author. Tel.: +86 10 6480 7130; fax: +86 10 6480 7099.

E-mail addresses: [peijianshi@gmail.com](mailto:peijianshi@gmail.com), [shi\\_peijian@163.com](mailto:shi_peijian@163.com) (P. Shi).

<sup>1</sup> These two authors contributed equally to this work.

In fact, it is an equivalent of the Malthusian constant (Sun, 2001)

$$\frac{dN}{dt} = r_m N \quad (1)$$

where  $N$  denotes the population size at time  $t$ . Since the intrinsic rate of increase could reflect the expected population size, it was then considered reasonable to measure fitness. However, Eq. (1) is only a density-independent equation and the effect of the environmental capacity ( $K$ ) is neglected. When the environmental capacity is fixed, the population cannot increase without density-dependence. Therefore, Eq. (1) should be replaced with the logistic model. However, almost all the reported intrinsic rates of increase were based on Eq. (1). Moreover, body size in ectotherms has also been largely neglected in calculating the intrinsic rate of increase by the life table methods. In fact, body size has been reported to have a significant effect on the fitness in ectotherms (Kingsolver and Huey, 2008). Amarasekare and Savage (2012) stated, “body size is fixed within a species and should have negligible effects on temperature dependence within species”. However, it is an absolutely incorrect conclusion based on other studies. Temperature has been demonstrated to have a significant effect on body size in ectotherms (van der Have and de Jong, 1996; Karan et al., 1998; Gibert and de Jong, 2001). In the mid-temperature range, we can use the following equation to describe the effect of absolute temperature ( $T$ ) on body size ( $m$ )

$$m = m_\phi \exp \left[ \frac{H_{A,g} - H_{A,d}}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] \quad (2)$$

where  $T_\phi$  represents the temperature at which the probability of the enzyme (controlling the developmental rate or growth rate) being in the active state can reach its maximum;  $m_\phi$  represents the body size at  $T_\phi$ ;  $R$  is the universal gas constant ( $= 1.987 \text{ cal deg}^{-1} \text{ mol}^{-1}$ );  $H_{A,g}$  represents the enthalpy of activation of the reaction that is catalyzed by the enzyme controlling the growth rate, whereas  $H_{A,d}$  represents the enthalpy of activation that is catalyzed by the enzyme controlling the developmental rate. Eq. (2) is derived from the SSI model (Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Ikemoto, 2005) assuming that in the mid-temperature range there is little difference between the probability of the active enzymes in controlling the developmental rate and the growth rate (see Appendix A). Eq. (2) can be further simplified into

$$\ln(m) = a + b \left( \frac{1}{T} \right) \quad (3)$$

where  $m$  is the body size at absolute temperature  $T$ ; and  $a$  and  $b$  are constants. In order to exhibit the validity of Eq. (2) in the mid-temperature range, we used this equation to fit the data of temperature-dependent body weight in *Drosophila buzzatii* male (de Jong, 2010) (see Fig. 1).

Body size plays an important role in the intraspecific competition. For example, in *Allomyrina dichotoma*, males having long horns can have higher probabilities to win fights than those having short horns (Karino et al., 2005). However, the long horns do not affect other performances such as flight (McCullough et al., 2012). If temperature also had a significant effect on the horn length of this species, we would expect a trade-off between population size and individual body size for a better measure of fitness. The statement “bigger is better” (Kingsolver and Huey, 2008) indicates that the fitness increases with increase in body size, which is favored by relatively low temperature for most insects. However, for most insects and mites, the intrinsic rates of increase are maximal around 30 °C (Shi et al., 2012), which means relatively high temperature is better for population increase. Therefore, we can assume a trade-off in temperature to meet two aspects of requirements for increasing individual body size (low temperature above 15 °C) and for increasing population size

(high temperature below 30 °C). The temperature that makes the trade-off possible can be regarded as the “optimal” temperature for the fitness in ectotherms.

### 3. Evolutionary propensity for temperature

Mills and Beatty (1979) suggested a propensity in interpretation of fitness. However, few investigators have considered that the fitness had a propensity for temperature which means fitness components are expressed naturally at a specific temperature. It needs a very long evolutionary time to develop this temperature. After this temperature is developed, fitness remains stable for a long time at this temperature. Now the question is: how do we measure this temperature? The concept of “intrinsic optimum temperature” may be useful to answer this question (Ikemoto, 2005). In fact, it is  $T_\phi$  in Eq. (2). To understand it better, we need

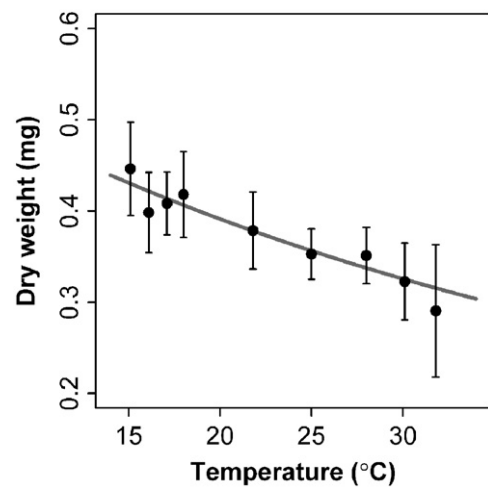


Fig. 1. Effect of temperature on the body weight of *Drosophila buzzatii* male. The raw data were provided by Dr. Gerdien de Jong. These data were re-analyzed by using Eq. (2) in the text, which consequently produced the present figure. This figure can be regarded as a simplification of Fig. 3B published in de Jong (2010). The coefficient of determination ( $R^2$ ) equals 0.45 based on 1218 data points in body weight. The sample sizes at nine temperatures (from low to high temperature) are 145, 147, 148, 147, 150, 150, 148, 143, and 40. Here, the points represent the average values of dry weight at different temperatures, and the corresponding standard errors are represented by error bars.

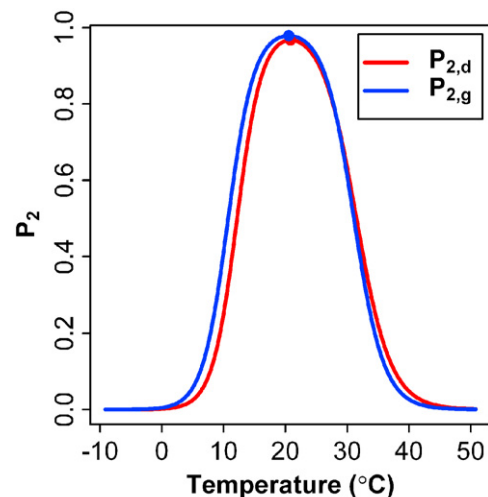


Fig. 2. Probability of the enzyme controlling developmental rate of *Drosophila buzzatii* male in the active state ( $P_{2,d}$ ), and that controlling growth rate ( $P_{2,g}$ ).

**Table 1**  
Parameter estimates of the SSI model for developmental rate and growth rate.

	$T_\phi$ (K)	$\rho_\phi$	$\Delta H_A$	$\Delta H_L$	$\Delta H_H$	$T_L$ (K)	$T_H$ (K)	$\chi^2$	$R^2$
Development (d)	293.98	0.060519	19428.78	-80537.4	66538.19	285.33	304.65	0.181825	0.99
Growth (g)	293.69	0.022055	17438.9	-76568.6	76206.73	283.89	304.24	0.406385	0.92

to look into its original definition. The relationship between developmental rate in ectotherms and temperature was found to be non-linear (Uvarov, 1931; Campbell et al., 1974). Sharpe and DeMichele (1977) proposed a thermodynamic non-linear model to describe the relationship between developmental rate (or growth rate) and temperature. Schoolfield et al. (1981) potentially improved this model by assuming that the probability of the enzyme being in the active state can be maximal at 25 °C. However, Ikemoto (2005) demonstrated that most insects and mites have different temperatures to meet the maximization of this probability rather than 25 °C. These temperatures were referred to as the intrinsic optimum temperatures. Based on the above finding, Ikemoto (2005) further improved the model proposed by Schoolfield et al. (1981) to the following

$$r = P_2 \rho_\phi \frac{T}{T_\phi} \exp \left[ \frac{H_A}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] \quad (4)$$

where  $r$  is the developmental rate (or growth rate) at absolute temperature  $T$ ;  $\rho_\phi$  is the developmental rate (or growth rate) at  $T_\phi$  assuming no enzyme inactivation; and  $P_2$  is the probability of the enzyme being in the active state, also an approximate bell-shaped function of absolute temperature ( $T$ ).

$$P_2 = \frac{1}{1 + \exp[(\Delta H_L/R)((1/T_L) - (1/T))] + \exp[(\Delta H_H/R)((1/T_H) - (1/T))]} \quad (5)$$

where  $\Delta H_L$  is the change in enthalpy associated with low temperature inactivation of the enzyme ( $\text{cal mol}^{-1}$ );  $\Delta H_H$  is the change in enthalpy associated with high temperature inactivation of the enzyme ( $\text{cal mol}^{-1}$ );  $T_L$  is the temperature (K) at which the enzyme is 1/2 active and 1/2 low temperature inactive; and  $T_H$  is the temperature (K) at which the enzyme is 1/2 active and 1/2 high temperature inactive. Eq. (4) was used to fit the developmental rate and growth rate data of *D. buzzatii* male. At temperature  $T_\phi$ ,  $P_2$  reaches its maximum (see Fig. 2). Table 1 exhibited the fitted parameters and goodness-of-fit by using the SSI model based on the data of *D. buzzatii* male. The intrinsic optimum temperature for developmental rate was assumed to be the same as that for growth rate in van der Have and de Jong (1996). There is seemingly a slight difference between two fitted parameters (i.e.,  $T_{\phi,d}$  and  $T_{\phi,g}$ ) as shown in Table 1. However, the difference was not statistically significant when analyzed by using the bootstrap percentile method (Efron and Tibshirani, 1994; Sandhu et al., 2011; Ikemoto et al., 2013). The 95% confidence interval of the differences between the bootstrap replications of  $T_{\phi,d}$  and the bootstrap replications of  $T_{\phi,g}$  is [-0.0361, 0.6413], including zero. Bonato et al. (2011) suggested that the developmental rates for closely related species within a taxon might be constant at temperature  $T_\phi$ . According to previous studies (see Shi et al., 2012, and references therein), for most insects and mites,  $T_\phi$  is around 20 °C with a range of 15–25 °C. This estimate is significantly different from the temperatures around 30 °C for most insects and mites at which the intrinsic rates of increase were maximal. Daily air temperature seems not to be a selective factor to influence the fitness because daily air temperature is variable during the day. Therefore, ectotherms can come out when daily air temperatures are suitable, and can hide when daily air temperatures are unsuitable. In this case, we assume that

the intrinsic optimum temperature might represent a propensity of fitness, and other temperatures are only non-selective factors. Therefore, we have grounds for believing that the intrinsic optimum temperature represents the “optimal” temperature for fitness in ectotherms.

## Acknowledgments

We thank Dr. Gerdien de Jong for providing the data of *Drosophila buzzatii* male. We are also deeply thankful to Drs. Christopher Gordon, Bai-Lian Li, and Takaya Ikemoto for their valuable comments on the early version of this manuscript. Two anonymous reviewers provided valuable comments on this study.

## Appendix A. Temperature-dependent body size in the mid-temperature range

van der Have and de Jong (1996) proposed a model to describe the effect of temperature on body size in ectotherms

$$m = \frac{m/D}{1/D} = \frac{r_g}{r_d} \quad (A1)$$

where  $m$  is the body size;  $D$  is the developmental time;  $r_g$  is the growth rate, and  $r_d$  is the developmental rate, which are functions of absolute temperature ( $T$ ). The equations to describe the growth rate (A2) and the developmental rate (A3) by using the SSI model (Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Ikemoto, 2005) are

$$r_g = P_{2,g} \rho_{\phi,g} \frac{T}{T_\phi} \exp \left[ \frac{H_{A,g}}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] \quad (A2)$$

and

$$r_d = P_{2,d} \rho_{\phi,d} \frac{T}{T_\phi} \exp \left[ \frac{H_{A,d}}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] \quad (A3)$$

The subscript “g” represents growth, and the subscript “d” represents development.  $\rho_{\phi,g}$  is the growth rate at  $T_\phi$ , and  $\rho_{\phi,d}$  is the development rate at  $T_\phi$ .  $P_2$  is the probability of the enzyme being in the active state, which is an approximate bell-shaped function of absolute temperature. Other parameters are constant. In the mid-temperature range, assuming  $P_{2,g} \approx P_{2,d}$ , Eq. (A1) can be rewritten as

$$m = \frac{\rho_{\phi,g}}{\rho_{\phi,d}} \exp \left[ \frac{H_{A,g} - H_{A,d}}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] = m_\phi \exp \left[ \frac{H_{A,g} - H_{A,d}}{R} \left( \frac{1}{T_\phi} - \frac{1}{T} \right) \right] \quad (A4)$$

## References

- Amarasekare, P., Savage, V., 2012. A framework for elucidating the temperature dependence of fitness. *Am. Nat.* 179, 178–191.
- Bonato, O., Ikemoto, T., Shi, P., Ge, F., Sun, Y., Cao, H., 2011. Common-intersection hypothesis of development rate lines of ectotherms within a taxon revisited. *J. Therm. Biol.* 36, 422–429.
- Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., Mackauer, M., 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11, 431–438.

- de Jong, G., 2010. A biophysical interpretation of temperature-dependent body size in *Drosophila aldrichi* and *D. buzzatii*. *J. Therm. Biol.* 35, 85–99.
- Efron, B., Tibshirani, R.J., 1994. An Introduction to the Bootstrap. Chapman & Hall/CRC, New York.
- Gibert, P., de Jong, G., 2001. Temperature dependence of development rate and adult size in *Drosophila* species: biophysical parameters. *J. Evol. Biol.* 14, 267–276.
- Huey, R.B., Berrigan, D., 2001. Temperature, demography, and ectotherm fitness. *Am. Nat.* 158, 204–210.
- Ikemoto, T., 2005. Intrinsic optimum temperature for development of insects and mites. *Environ. Entomol.* 34, 1377–1387.
- Ikemoto, T., Kurahashi, I., Shi, P., 2013. Confidence interval of intrinsic optimum temperature estimated using thermodynamic SSI model. *Insect Sci.*, <http://dx.doi.org/10.1111/j.1744-7917.2012.01525.x> In press.
- Karan, D., Morin, J.P., Moreteau, B., David, J.R., 1998. Body size and developmental temperature in *Drosophila melanogaster*: analysis of body weight reaction norm. *J. Therm. Biol.* 23, 301–309.
- Karino, K., Niyama, H., Chiba, M., 2005. Horn length is the determining factor in the outcomes of escalated fights among male Japanese horned beetles, *Allomyrina dichotoma* L. (Coleoptera: Scarabaeidae). *J. Insect Behav.* 18, 805–815.
- Kingsolver, J.G., Huey, R.B., 2008. Size, temperature, and fitness: three rules. *Evol. Ecol. Res.* 10, 251–268.
- McCullough, E.L., Weingarden, P.R., Emlen, D.J., 2012. Costs of elaborate weapons in a rhinoceros beetle: how difficult is it to fly with a big horn? *Behav. Ecol.*, <http://dx.doi.org/10.1093/beheco/ars069> In press.
- Mills, S.K., Beatty, J.H., 1979. The propensity interpretation of fitness. *Philos. Sci.* 46, 263–286.
- Sandhu, H.S., Shi, P., Kuang, X., Xue, F., Ge, F., 2011. Applications of the bootstrap to insect physiology. *Fla. Entomol.* 94, 1036–1041.
- Schoolfield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor. Biol.* 88, 719–731.
- Sharpe, P.J.H., DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64, 649–670.
- Shi, P., Li, B.-L., Ge, F., 2012. Intrinsic optimum temperature of the diamondback moth and its ecological meaning. *Environ. Entomol.* 41, 714–722.
- Sober, E., 2001. The two faces of fitness. In: Singh, R.S., Krimbas, C.B., Paul, D.B., Beatty, J. (Eds.), *Thinking about evolution: historical, philosophical, and political perspectives*, vol. 2. Cambridge University Press, Cambridge, UK, pp. 309–321.
- Sun, R., 2001. *Principles of Animal Ecology*, third edition, Beijing Normal University Press, Beijing (pp. 178–190).
- Uvarov, B.P., 1931. Insects and climate. *Trans. Entomol. Soc. London* 79, 1–232.
- van der Have, T.M., de Jong, G., 1996. Adult size in ectotherms: temperature effects on growth and differentiation. *J. Theor. Biol.* 183, 329–340.