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Arthropods life cycle and temperature: beyond isomorphy hypothesis

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ABSTRACT

In poikilotherms, developmental time and adult lifespan are biological traits driven by temperature although their underlying physiological mechanisms differ. The developmental theory of ageing predicts a positive correlation between these two traits without confirming a genetic or causal relationship. The developmental rate isomorphy hypothesis established that the proportionality in the duration of each pre-imaginal stage with respect to total developmental time does not vary with temperature. This may have important evolutionary implications. We conducted an analysis with arthropods of agronomic interest to study if the hypothesis could be extended to the total lifespan of poikilotherms, including adult lifespan. We showed that isomorphy could be acceptable for a global description of this relationship. However a general model of power law type is more appropriate for characterizing the relationship between developmental time and adult lifespan. In this model, the shape of the curve is a constant characteristic, but the parameters that control it depend on the functional type of the arthropod (phytophagous, predator or parasitoid). Presumably this power law could be extended to all arthropods of agricultural interest, and more generally to all arthropod.

Keywords Ageing, Developmental constraints, life-history traits, thermal requirements, power law

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1. Introduction

Ectotherms are directly affected by environmental temperature conditions because they do not regulate their body temperature, which consequently is very close to the atmospheric temperature (May 1979). Ambient temperature is one of the environmental factors that strongly influences the fitness of ectotherms in particular through its direct effect on developmental rate (Gillooly et al. 2002). Jarosik et al. (2002) established a general rule regarding the dependence on temperature of the developmental rate of poikilotherms. According to this hypothesis, called developmental rate isomorphy, within the temperature range for which the relationship between developmental rate and temperature is linear, the proportionality in the duration of each stage with respect to total developmental time does not vary with temperature. This was shown for 426 non-diapausing populations of 342 insect species (n= 417) and of 7 mite species (n=9) (Jarosik et al. 2002) and was later extended to 22 other representative groups of animals, including vertebrates (Jarosik et al. 2004). This invariance in proportionality when the temperature changes implies the existence of a lower thermal threshold common to all developmental stages (Jarosik et al. 2002). The existence of this common thermal threshold physiologically links all pre-imaginal stages between them. Indeed, adaptation of a particular stage to the temperature of its environment can not be realized independently of the other stages of development. In other words, a particular stage can not adapt to the temperature of its environment without affecting the thermal adaptation of all the other stages of development. (Jarosik et al. 2002).

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Development is not the only trait driven by temperature; all functional life-history traits involving physiological processes are affected. Adult Lifespan is one of these. Although the physiological mechanisms of aging are different from those involved in development, both are strongly temperature dependent. The temperature responses of developmental and adult lifespan rates are unimodal and asymmetric (left-skewed): they increase gradually from a lower temperature threshold to an optimum temperature and then rapidly decrease to the upper temperature threshold. According to the developmental theory of ageing (Lints 1978,1988; Lints and Lints 1969) a link between development and ageing exists, as shown by the positive correlation between developmental time and adult lifespan (Lints and Lints 1969; Muller 1963). Although, experimental work seems to confirm the genetic relationship between development and lifespan (Lints 1978), this relation is not necessarily a causal one (Zwaan et al. 1991). Development is a continuous process in which senescence forms the last stage (Muller 1963), and the lifespan of an organism could be lengthened as a whole by stretching the development programme in the immature stages (Comfort 1968).

Given that developmental time and adult lifespan exhibit the same response to temperature, could isomorphy, i.e. the general rule developed by Jarosik et al. (2002) for pre-adult development, be extended to the total lifespan of ectotherms? Thus, is there a common lower thermal threshold at all stages, including the adult stage? Grouping together lifespan and developmental time in an analysis raises another important question about proportionality. It is well known that arthropods invest more in the juvenile phase or in the adult phase depending on their lifestyle as phytophagous, predator or parasitoid (Nylin and Gottard 1998, Boggs 2009). What impact the lifestyle could therefore have on the proportionality between development time and lifespan, knowing that under the assumption of isomorphism this relationship is considered to be

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invariant? To answer this question, we conducted an analysis using the same test as carried out by Jarosik, with arthropods of agronomic interest belonging to different functional types (phytophagous, predator or parasitoid). This group is well studied in terms of number of species, experiments carried out and geographic locations. Further, we tested whether the isomorphy hypothesis' understanding of the proportional relationship between development time and lifespan was true and proposed a power law type for characterizing this relationship. More precisely we considered a power law model for which the functional groups are fixed factors, and the species (inside groups) are random factors. With this model, a reduced number of parameters is enough for estimating the functional group effect and for summarizing the random species effect with a good statistical power.

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2. Materials and methods

2.1. Materials

The data used in this study were compiled from the available literature on arthropods (mites or insects) of agronomic importance. In order to reduce experimental bias, only studies for which development and adult lifespan have been characterized in the same experiment and at least for 3 different temperatures, were selected. The final data used in the analysis concerned 72 species belonging to 20 families, of which 44 were pest (10 mites and 34 insects), and 28 were natural enemies (17 predators and 12 parasitoids) (Table 1). After a graphical inspection, only data falling within the range of the linear relationship between the rate of population increase and temperature were used.

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2.2. Methods

2.2.1. Rate isomorphy (Jarosik's approach)

In this first analysis, the existence of isomorphism between pre-imaginal development time and adult lifespan was tested following the method used by Jarosik, Honek and Dixon (2002). For this, Z , the angular transformation of the proportion of time spent in the pre-imaginal period (D) with respect to the total lifespan (pre-imaginal (D) + adult lifespan (L)) was analysed as the dependent variable with rearing temperature (T) as the independent variable, i.e., $Z = a + bT + \varepsilon$. Under the isomorphy hypothesis, Z does not depend on temperature (T). Thus the regression slope (b) should not significantly differ from zero. Conversely, significant deviation ($p<.0.05$) from the zero slope of the regression line violates the isomorphy hypothesis. To test for variation among species at the same time, we performed ANCOVA additionally entering arthropod species (i), $Z(i, T) = a_i + b_i T + \varepsilon$. Nested sub-models including arthropod family or functional type (phytophagous, predator or parasitoid) were additionally tested against the general model using a Fisher-Snedecor F test.

2.2.2. Power law (beyond Jarosik's approach).

In a second analysis, we examined the relationship between adult lifespan and developmental time in a more general context than a strict proportionality. For this, a linear regression between Log(lifespan) and Log(developmental time) was performed.

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Following the hypothesis of Jarosik et al. (2002), if the proportion of time spent developing is independent of temperature (T), then $\frac{D(T)}{D(T)+L(T)} = K$, and the lifespan (L) is equal to $L(T) = \frac{D(T)*K}{(1-K)}$). Thus, L(T) should be proportional to developmental time (D(T)). For each species and each temperature, adult lifespan was plotted against pre-imaginal developmental time.

$$L = K * D_T^b * e^{\varepsilon} \qquad (1)$$

which, after a log transformation, results in the following ANCOVA model:

$$\mathrm{Log}\,(L) = b * \mathrm{Log}(D) + \mathrm{Log}(K) + \varepsilon \qquad (2)$$

Note that under the isomorphy hypothesis, b = 1 and $K' = \frac{1}{E(e^{\varepsilon})}\frac{K}{1-K}$

As in the rate isomorphy test above, we additionally entered functional type, family or species. Therefore covariance analysis was performed to test whether the slopes (b_i) for various groups differ from 1, as assumed by the isomorphy hypothesis of Jarosik et al. (2002) and/or from each other.

2.2.3. Modelling functional group effects

In a third analysis, a linear mixed model was used to describe the relationship between lifespan and development which gives:

$$\mathrm{Log}(L_{i,n}) = a_n + (b_n + \beta_i)\mathrm{Log}(D_{i,n}) + \alpha_i + \varepsilon \qquad (3)$$

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where $D_{i,n}$ (respectively $L_{i,n}$) is the development time (respectively lifespan) of arthropod species i belonging to type n, both at the same temperature, a_n and b_n are constants depending on the functional type, α_i and β_i are random effects linked to the species of variance σ_1^2 and σ_2^2 and ε is a residual random effect of variance σ^2.

3. Results

3.2 Rate isomorphy

For the 72 arthropod species tested, the proportional relationship between the total pre-adult developmental time and the temperature is shown in Figure 1. The data points are evenly spread around the mean curve and no general trend can be observed. However, grouping the points by functional type (phytophagous, predator or parasitoid) suggests that at least a type effect exists. The Fisher-Snedecor F test showed a significant effect among arthropods (species level: F=13.19, df1=142, df2=197, p-value<10^{-7}; Functional type level: F=7.86, df1=138, df2=197, p-value<10^{-7}; Family level: F=5.54, df1=116, df2=197, p-value<10^{-7}). The statistical tests also rejected the assumption of a common intercept or slope for the model as they showed an effect at the type level (Common slope: F=1.80, df1=71, df2=197, p-value=0.008; Common intercept: F=2.25, df1=71, df2=197, p-value=6.10^{-5}). For each species, the p-values of the test assuming a value of the slope equal to zero vary between 0.0028 and 0.9758, but most are higher than 0.05; only 11 out of 72 are lower than 0.05. A Bonferroni correction was used to take into account that the 72 tests were performed simultaneously. They showed no significant differences. Thus, although the isomorphy hypothesis was rejected overall,

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this was due to the low number of species showing a low p-value, leading to non-significance after Bonferroni correction.

3.2. Power law

Figure 2 shows the relationship between the two variables L(T) and D(T), for each functional type (phytophagous, predator or parasitoid) after logarithmic transformation. The dispersion of points observed in Figure 2 suggests that using a linear relationship between the logarithms of development time and lifespan is the most appropriate. Note that in this case the isomorphy hypothesis corresponds to a regression coefficient equal to one. As in the above analysis (isomorphy test), among the levels at which data can be grouped, the species level is more significant than the family and the type levels (species level: F=12.16, df1=142, df2=197, p-value<10^{-7}; Functional type level: F=7.30, df1=138, df2=197, p-value<10^{-7}; Family level: F=5.15, df1=116, df2=197, p-value<10^{-7}). The statistical tests of a common intercept or slope for the model including an effect at the arthropod level are also rejected (Common slope: F=1.76, df1=71, df2=197, p-value=0.0012; Common intercept: F=2.66, df1=71, df2=197, p-value=4.10^{-8}). Only 13 intercept p-values (respectively 12 slope p-values) of the test of a common intercept (respectively common slope equals to one) out of 72 were lower than 0.05. The Bonferroni correction showed that no slope was statistically different from 1 and that only two intercepts (out of the 72) were significantly different than the common intercept.

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Only one species displayed an intercept and slope value largely different from the others. If this species is not considered, the slope distribution is unimodal with a mode value closed to 0.8, whereas the intercept distribution showed three modes that might correspond to the regression slope built from each of the three functional types.

3.3. Modelling functional group effects

When the different functional types are taken into account, the sum of squares decreases strongly, even if the species level remains significant. Thus, we put forward the mixed model above (eq. 3).

The estimates of the fixed effects (a_n and b_n) are presented in Table 2. The fixed effects between phytophagous and predators were not significantly different, so they were grouped together for further analysis against parasitoids. No significant difference was found between parasitoids and the group (phytophagous + predators) (Khi2=5.78, df=2). The random effect due to species was very low at the slope level ($\sigma_\alpha^2 = 0.005$), but relatively high at the intercept level ($\sigma_\beta^2 = 0.138$). The residual variability was also very low (σ^2=0.075).

Thus, a common power-law shape can describe the relationship between the developmental times of all species tested. The exact shape of this power law is common to phytophagous and predator. The species effect observed at the intercept level is no longer present in the regression coefficient, thus almost no species effect on the power coefficient is observed when considering the parasitoids.

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4. Discussion

After analysing the data using the same procedure and tools as Jarosik et al. (2002), the isomorphy hypothesis can be seen as a good approximation as our results were similar to those of Jarosik et al. (2002) and Jarosik et al., (2004), with very few species showing a significant slope. However, the Jarosik's approach uses the arcsine transformation that was originally defined for proportions based on counts rather than continuous variables. A further analysis showed that the relationship is more complex than that predicted by Jarosik's model: the proportionality between pre-adult development and adult lifespan had to be replaced by a general power relationship that, nevertheless, remains quite close to the proportionality in the range of temperatures studied. While this relationship held true for all arthropods we tested, the parameters of the model change according to the functional type of the species: phytophagous, predator or parasitoid. For a given total lifespan at a given temperature, we observed that adult lifespan is often longer than pre-imaginal developmental time for predators and phytophagous. The opposite was observed for parasitoids, for which, at a given temperature, pre-adult developmental time was always greater than adult lifespan. For each functional type, the slopes of the model vary; the slopes for phytophagous and predators are not significantly different, reflecting a common response with a varying "species" coefficients, but the slopes for parasitoids are different from the others (predators and phytophagous). However, the intercepts are significantly different among the groups.

Why do parasitoids invest more in development than lifespan as compared to predators?. Part of the answer may lie in metabolism and energetic needs. Insects' body fat is central to energy storage and utilization (Carnovoso et al. 2001). It is mainly

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composed of lipids, which are the main source of metabolic fuel, essential for growth and reproduction (Arrese and Soulages 2010). The majority of adult parasitoid species are unable to synthesize lipids. The loss of lipogenesis is an evolutionary consequence of a parasitoid lifestyle. Parasitism facilitates the redundancy of traits involved in lipid production (Visser et al. 2010). Some parasitoids show lipogenic ability, but these are all host species generalists. Having a large range of host species may impede effective host manipulation in which the host is forced to synthetize lipids for the benefit of the parasitoid (Visser et al. 2010). Giron and Casas (2003) report that all parasitoid species for which lipogenesis has been investigated are unable to synthesize lipids from sugars in significant amounts, although these species are able to cover all their functional energetic needs. These authors showed that a parasitoid female invests more in the production of eggs than what she obtains from food and must therefore draw continuously on her reserves. Yet, these reserves are set at adult emergence and do not increase due to the high demand of maintenance and the inability to ensure lipogenesis. Parasitoids are holometabolous insects, so the storage of body fat, especially lipids, is essential to their survival. Reserves carried over from the larval stage are also crucial for oogenesis (Arrese and Soulages 2010). Over a lifespan of duration equal to that of predators or phytophagous, a higher investment in pre-adult developmental time rather than adult lifespan would therefore be justified in parasitoids because fat reserves are accumulated during this period.

In contrast, predators can maximize their energetic gains by increasing the number of prey or selecting more nutritious prey (Visser et al. 2010). Predators are not dependent on their immature phase to increase their fat reserves and, more importantly, predation is much more effective when performed by adults (Dostalkova et al. 2002). This may

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explain why for a given lifespan, the period corresponding to lifespan in predators is always longer than that of pre-imaginal development. Following Jafferty and Kunis (2002), phytophagous could be defined as micro-predators of plants, thus it is not surprising that their accumulation of fat reserves is also more efficient during the adult phase. As observed in predators, for a given lifetime, the proportion relative to adult lifespan of phytophagous is greater than that relative to pre-imaginal development.

We show here for arthropods of economic importance that the proportional relationship between lifespan and development period can be formalized mathematically. The resulting slope is an average group characteristic, but the parameters depend on the functional type of the arthropod (phytophagous, predator or parasitoid). If we consider the type as a random effect, then the mathematical relationship can be expressed as Lifespan= (Developmental time /(Developmental time + Lifespan)*Developmental time$^{0.78}$. Note that the existence of a common lower thermal threshold for all stages of development of a given insect species (Jarosik et al. 2002) remains valid when switching from the linear relationship to a power law. Presumably this power law could be extended to all arthropods of agricultural interest, and more generally to all arthropods. Further studies on a larger number of poikilothermic species are needed to explore the potential universality of this law.

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Figure legends

Figure 1. Isomorphy rate, i.e., proportional relationship between the total pre-adult developmental time and rearing temperature (in °C) for 72 arthropod species grouped by functional type: *Phytophagous* (◯,___), *Predator* (△, ---) and P*arasitoid*. (●,....). Symbol = data points, curve = regression line.

Figure 2. Relationship between lifespan and developmental time after logarithmic transformation of both variables to stabilize the variance for 72 arthropod species of agronomic importance grouped by functional type: *Phytophagous* (◯,___), *Predator* (△, ---) and P*arasitoid*. (●,....). Symbol = data points, curve = regression

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Table 1: List of 72 species considered in the analysis, with their bibliographic source, temperatures to which they were tested by the authors and our estimate of the slope of isomorphy rate.

PHYTOPHAGOUS

		Temperatures	Slope estimate
Aleyrodidae			
Bemisia tabaci Gennadius	Takalloozadeh HM. 2012. *Mun. Entomol. Zool.* 7, 893-898	20 – 24 – 28 - 32	0.0015(
Bemisia tabaci Gennadius	Ahn KS. *et al*. 2001. *Korean J. Appl. Entomol*. 40, 203-209	15 – 20 - 25 – 30	0.0015
Bemisia tabaci Gennadius	Bonato O. *et al*. 2007. *Physiol. Entomol*. 32, 50-55	17 – 21 – 25 – 30 - 35	0.0015
Trialeurodes vaporariorum (Westwood)	Manzano M and van Lanteren J. 2009. *Neotrop. Entomol*. 38, 452-458	19 – 22 - 26	0.0333
Aphididae			
Aphis gossypii Glover	Xia JY. *et al*. 1999. *Entomol. Exp. Appl*. 90, 25-35	10 - 15 – 20 - 25 – 30 - 35	0.0032
Aphis gossypii Glover	Kersting U. *et al*. 1999. *J. Appl. Entomol*. 123, 23-27	15 – 20 - 25 – 30 - 35	0.0032
Brevicoryne brassicae L.	Salman AMA. 2006. *Ann. Agric. Sci. Univ. Cairo*. 51, 271-281	15 – 18 – 21 - 24	0.0064
Cinara sp nov	Kairo MTK. and Murphy ST. 1999. *Entomol. Exp. Appl*. 92, 147-156	10 - 15 – 20 - 25	-0.0035
Macrosiphum rosae L.	Mehrparvar M. and Hatami B. 2007. *Eur. J. Entomol*. 104, 631-634	15 – 18 – 22 - 25	-0.0069
Myzus persicae (Sulzer)	Rodrigues BLR. *et al*. 2006. *Acta Sci. Agron*. 28, 221-225	15 – 20 - 25 – 30	0.0034
Rhopalosiphum maidis (Fitch)	Kuo MH. *et al*. 2006. *Appl. Entomol. Zool*. 41, 171-177	6 – 10 – 15 – 20 – 25 – 30 - 35	-0.0068
Sipha flava (Forbes)	Oliveira de S. *et al*. 2009. *Neotropical Entomol*. 38, 311-316	12 – 16 – 20 – 24 – 28 - 32	-0.0062
Tuberolachnus salignus (Gmelin)	Collins CM. and Leather S. 2001. *Eur. J. Entomol*. 98, 177-182	10 - 15 – 20 - 25	-0.0112
Cicadelidae			
Cicadulina bipunctata (Melichar)	Tokuda M and Matsumura M. 2004. Appl. Entomol. Zool. 40, 213-220	16.5 – 19.2 – 22.1 – 25.3 – 28.4 – 31.4 - 34	0.0018
Chrysomelidae			
Gastrophysa viridula (De Geer)	Honek A. *et al*. 2003. *Eur. J. Entomol*. 100, 295-300	18.0 – 21.5 – 25.0 - 28	-0.0002
Miridae			
Adephocoris fasciaticollis (Reuter)	Lu YL. *et al*. 2009. *Physiological Entomol*. 34, 318-324	10 - 15 – 20 - 25 – 30 - 35	-0.0109
Adephocoris lineolatus (Goeze)	Lu YL. *et al*. 2009. *Physiological Entomol*. 34, 318-324	10 - 15 – 20 - 25 – 30 - 35	-0.0068
Adephocoris suturalis (Jakovlev)	Lu YL. *et al*. 2009. *Physiological Entomol*. 34, 318-324	10 - 15 – 20 - 25 – 30 - 35	-0.0035
Apolygus lucorum (Meyer-Dür)	Lu YL. *et al*. 2010. *Appl. Entomol. Zool*. 45, 387-393	15 – 20 - 25 – 30 - 35	-0.0070
Creontiades dilutus (Stal)	Khan M. *et al*. 2009. *Australian J. Entomol*. 48, 201-216	20 – 23 – 26 – 30 - 32	-0.0058
Lygus elisus Van Duzee	Bommireddy PL. et al. 2004. *Environ. Entomol*. 33, 1549-1553	15 – 20 - 25 – 30 - 35	0.0030

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Lygus hesperus Knight	Mueller AJ., Stern VM. 1973. *Ann. Entomol. Soc. Am*. 66, 593-597	20 – 23 – 26	0.0044
Lygus lineolaris (Palisot de Beauvois)	Ugine TA. 2012. *Environ. Entomol*. 41, 1-10	17 – 18 – 21 – 25 – 25 – 27 – 30 - 32	-0.0054
Pseudococcidae			
Phenacoccus madeirensis Grenne	Chong JH. *et al*. 2003. *Ann. Entomol. Soc. Am*. 96, 539-543	15 – 20 - 25 – 30 - 35	-0.0058
Phenacoccus solenopsis Tinsley	Kumar S. *et al*. 2013. *Florida Entomol*. 96, 19-28	20 - 25 – 30 - 35	0.0018
Planococcus citri Risso	Goldasteh S. *et al*. 2009. *Arch. Biol. Sci. Belgrade*. 61, 329-336	15 – 18 – 20 – 23 – 25 – 28 – 30 – 32	-0.0085
Pseudococcus cryptus Hempel	Kim SC. et al. 2008. *J. Asia Pacific Entomol*. 11, 149-153	16 – 20 – 24 – 28 - 32	-0.0044
Tetranychidae			
Amphitetranychus viennensis (Zacher)	Kasap I. 2003. *Exp. Appl. Acarol*. 31, 79-91	20 – 30 - 35	-0.0063
Eotetranychus sexmaculatus (Riley)	Jamieson LE. and Stevens PS. 2007. *New Zealand Plant Prot*. 60, 72-77	10 – 13 – 18 – 21 – 25 - 30	-0.0019
Mononychellus progresivus Doreste	Bonato O. *et al*. 1995. *Entomol. Exp. Appl*. 75, 119-125	16 – 22 – 26 – 31 - 36	0.0066
Oligonychus gossypii (Zacher)	Bonato O. *et al*. 1995. *Entomol. Exp. Appl*. 75, 119-125	16 – 22 – 26 – 31 - 36	0.0004
Tetranychus abacae Baker & Pritchard	Vasconcelos GJN. *et al*. *Neotrop. Entomol*. 33, 149-154	20.0 – 23.0 – 25.5 – 30.0	0.0022
Tetranychus evansi Baker & Pritchard	Moraes G. and McMurthry JA. 1987. *Exp. Appl. Acarol*. 3, 95-107	15 – 20 - 25 – 30 - 35	-0.0017
Tetranychus evansi Baker & Pritchard	Bonato O. 1999. *Exp. Appl. Acarol*. 23, 11-19	21 – 26 -31 - 36	-0.0017
Tetranychus lintearius Dufour	Stone C. 1986. *Exp. Appl. Acarol*. 2, 173-186	15 – 20 – 23 - 25	-0.0174
Tetranychus ludeni Zacher	Domingues da Silva CA. 2002. *Pesq. Agropec. Bras*. 37, 573-580	20 – 23 – 25 – 28 - 30	-0.0039
Tetranychus pueraricola Ehara & Gotho	Gotho T. *et al*. 2004. *Appl. Entomol. Zool*. 39, 675-682	15.0 – 17.5 – 20.0 – 22.5 – 25.0 – 27.5 – 30.0	-0.0100
Tetranychus urticae(Koch)	Osman MA. *et al*. 2012. *Acarines*. 6, 25-30	15 – 20 - 25 – 30 - 35	0.0052
Tingidae			
Gargaphia torresi Lima	Domingues da Silva CA. 2004. *Rev. Brasileira Entomol*. 48, 547-552	20 – 23 – 25 – 28 - 30	0.0133
Corythucha ciliata (Say)	Ju RT. *et al*. 2011. *J. Insect Sci*. 2011, 11-16	16 – 19 – 22 – 26 – 30 – 33 - 36	-0.0051
Stephanitis takeyai Drake & Maa	Tsukada M. 1994. *Appl. Entomol. Zool*. 29, 571-576	15 – 18 – 20 - 25	-0.0121
Thripidae			
Ceratothripoides claratris (Shumsher)	Premachandra WT *et al*. 2004. *Bull. Entomol. Res*. 94, 377-384	22 – 25 – 27 – 30 – 34 – 35 - 40	0.0030
Dichromothrips smithi (Zimmermann)	Ahn KS. *et al*. 2003. *Korean J. Apl. Entomol*. 42, 211-216	15 – 20 – 25 - 30	-0.0114
Frankliniella occidentalis (Pergande	Zhang ZJ. *et al*. 2012. *Acta Entomol. Sin*. 55, 1168-1177	15 – 20 - 25 – 30 - 35	-0.0017

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Frankliniella occidentalis (Pergande)	Katyama H. 1997. *Jpn. J. Appl. Zool.* 41, 225-231.	15 – 20 - 25 – 30	-0.0017
Megalurothrips sjostedti (Trybom)	Ekesi S. *et al*. 1999. *Entomol. Exp. Appl*. 93, 149-155	14 – 17 – 20 – 23 – 26 - 29	-0.0065
Pezothrips kellyanus (Bagnall)	Varikou K. *et al*. 2009. *Ann. Entomol. Soc. Am*. 102, 835-841	15.0 – 20.0 – 25.0 – 30.0 – 32.5 - 35	0.0031
Thrips tabaci Lindeman	Murai T. 2000. *Appl. Entomol. Zool*. 35, 499-504	15 – 20 – 23 – 25 - 30	0.0121

PREDATORS

Miridae

Cyrtorhinus lividipennis Reuter	Do Bae S. *et al*. 2002. *Korean J. Appl. Entomol*. 41, 91-97	24 – 28 - 32	0.0029
Deraeocoris brevis (Uhler)	Kim DS., Riedl H. 2005. *BioControl*. 50, 881-897	21.7 – 24.0 – 30.1 – 32.0	0.0109
Macrolophus pygmaeus Rambur	Perdikis DC., Lykouressis DP. 2002. *Bio. Control*. 17, 55-60	15 – 20 - 25 – 30	-0.0099
Pilophorus typicus Distant	Nishikawa H. *et al*. 2010. *Jpn. Appl. Entomol. Zool*. 45, 313-318	17.5 – 20.0 – 22.5 – 25.0 – 27.5	0.0171

Anthocoridae

Orius albidipennis Reuter	Cocuzza GE. *et al*. 1997. *Entomol. Exp. Appl*. 85,189-198	15 – 25 – 35	-0.0020
Orius laevigatus Fieber	Cocuzza GE. *et al*. 1997. *Entomol. Exp. Appl*. 85,189-198	15 – 25 – 35	0.0040
Orius naivashae (Poppius)	Bonte J. *et al.* 2012. *Environ. Entomol*. 41, 989-996	15 -19 -25 - 33	0.0003
Orius sauteri (Poppius)	Nagai K., Yano E. 1999. *Appl. Entomol. Zool*. 34, 223-229	15 – 20 - 25 – 30	-0.0038
Orius strigicollis Poppius	Kim JH. *et al*. 1999. *Korean J. Appl. Entomol*. 38, 29-33	15 – 20 - 25 – 30	-0.0040
Orius thripoborus (Hesse)	Bonte J. *et al.* 2012. *Environ. Entomol*. 41, 989-996	15 -19 –25 –33	0.0091

Nabidae

Nabis roseipennis Reuter	Nadgauda D. and Pitre H. 1986. *Environ. Entomol*. 15, 536-539	20 - 25 – 30	0.0055

Coccinellidae

Adalia bipunctata L.	Jalali MA. *et al*. 2009. *J. Appl. Entomol*. 133, 615-625	19 – 23 - 27	-0.0059
Axinoscymmus cardilobus	Huang Z. *et al*. 2008. *Biol. Control*. 46, 209-215	14 – 17 – 20 – 23 – 26 – 29 - 32	-0.0017
Clitostethus arcuatus (Rossi)	Adriano Mota J. et al. 2008. *BioControl.* 53, 603-613	15 – 20 - 25 – 30	0.0050
Hippodamia variegata (Goeze)	Mandour NS. *et al*. 2011. *Egyp. J. Bio. Pest Control*. 21, 305-312	15 – 20 - 25 – 30	-0.0019
Scymnus levaillanti (Mulsant)	Uygun N. and Atlihan R. 2000. *BioControl*. 45, 453-462	15 – 20 - 25 – 30 - 35	-0.0035

PARASITOIDS

Aphelinidae

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Encarsia acaudaleyrodis Hayat	Zandi-Sohani N. and Shishelbor P. 2011. *BioControl*. 56, 257-263	20 - 25 – 30 - 32	0.0005
Encarsia inaron (Walker)	Malekmohammadi A. *et al*. 2012. *Crop Protection*. 34, 1-5	20 - 25 – 30 - 32	0.0199
Eretmocerus sp. nr *furuhashii*	Qiu BL. *et al.* 2007. *BioControl.* 52, 733-746	20 – 23 – 26 – 29 - 32	-0.0050
Braconidae			
Apanteles taragamae Viereck	Dannon EA. *et al.* 2010. *BioControl*. 55, 363-378	20 – 24 – 26 – 28 - 30	0.0148
Eucoilidae			
Gronotoma micromorpha (Perkins)	Abe Y. and Tahara M. 2003. *J. Appl. Entomol*. 127, 477-480	15 – 18 – 20 – 25 - 30	-0.0037
Eulophidae			
Quadrastichus haitiensis (Gahan)	Castillo J. *et al*. 2005. *Biol. Control*. 36, 189-196	15 – 20 – 25 – 30 - 33	-0.0161
Ichneumonidae			
Campoletis chlorideae Uchida	Dhillon MK. and Sharma HC. 2009. *BioControl*. 54, 743-750	18 – 23 - 27	0.0035
Venturia canescens Gravenhorst	Spanoudis CG. and Andreadis SS.2012. *J. Pest Sci*. 85 :75-80	15.0 – 17.5 – 20.0 – 22.5 – 32.5 -25 – 27.5 – 30.0 –	0.0093
Platygastridae			
Amitus fuscipennis McGown & Nebeker	De Vis RMJ. *et al*. 2002. *J. Appl. Entomol*. 126, 24-33	15 – 20 – 25 – 30	-0.0054
Scelionidae			
Telenomus cyamophylax Polaszek	Foerster LA. and Butnariu AR. 2003. *Biol. Control*. 29, 1-4	15 – 20 – 25 – 30	0.0162
Trissolcus semistriatus (Nees)	Kivan M. and Kilic N. 2006. *Entomol. Sci*. 9, 39-46	17 – 20 – 26 - 32	-0.0136
Trichogrammatidae			
Trichogramma aurosum Sugonjaev & Sorokina	Samara R. *et al*. 2011. *Phytoparasitica*. 39, 109-119	15 – 20 – 25 – 30	0.0066

Table 2 : Fixed effect estimates of the mixed model describing the relationship between lifespan and developmental time for the 72 arthropods tested.

	Estimate	Std. Error	*t* value
a (*Parasitoid*)	-0.61304	0.27044	-2.267
a (*Predator*)	0.96762	0.22635	4.275

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a (*Phytophagous*)	0.88140	0.14088	6.256
b (*Parasitoid*)	1.05384	0.08523	12.365
b (*Predator*)	0.85853	0.06853	12.528
b (*Phytophagous*)	0.78863	0.04614	17.094

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Figure 1

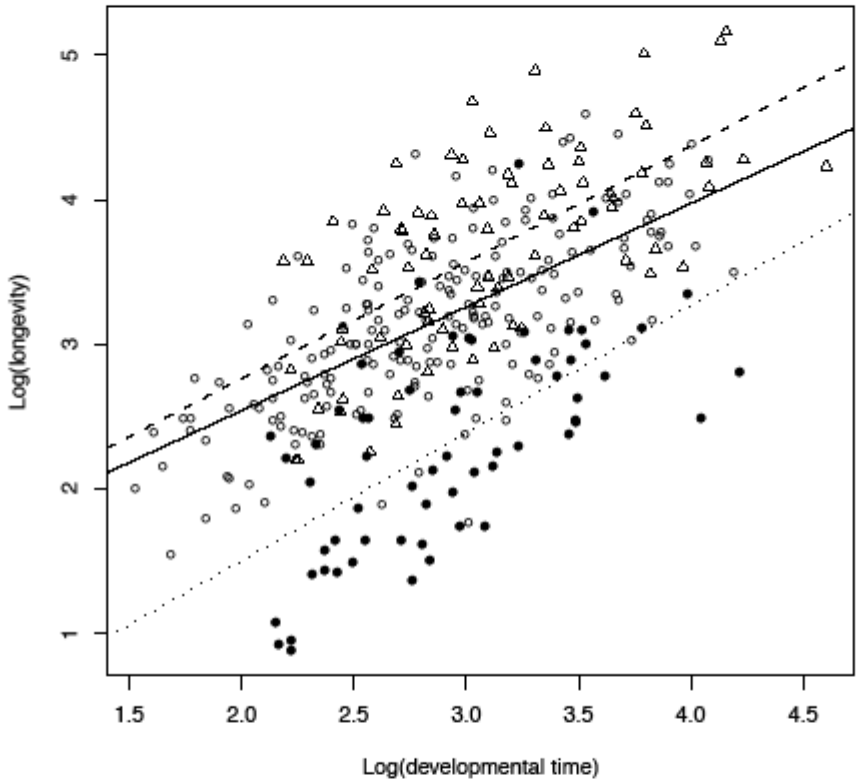

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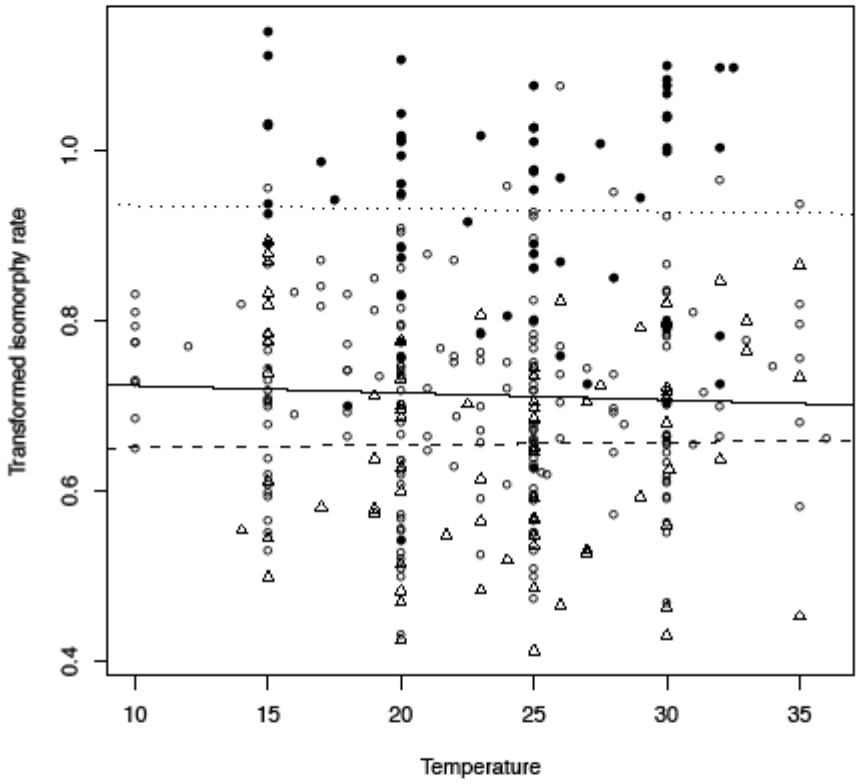
Figure 2



Highlights :

Relationship between lifespan and development time is more complex than that predicted by rate isomorphy hypothesis

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A power law can describe the relationship of proportionality between development time and lifespan

This power law is applicable to all arthropods tested but the parameters depend on their functional type: phytophagous, predator or parasitoid

The hypothesis of a lower thermal threshold common to all developmental stages of a same species remains valid

This power law could be extended to all arthropods of agricultural interest

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