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Comparison of development and growth of nettle-feeding larvae of Nymphalidae (Lepidoptera) under constant and alternating temperature regimes

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Abstract. Mean development rates under cycling temperature regimes (both alternating and sinusoidal regimes) have been found to be either accelerated, decelerated or unaffected when compared to development at constant temperature regimes with equivalent means. It is generally accepted that this phenomenon is a consequence of the non-linearity inherent in the temperature-rate relationship of insect development and is known as the rate summation, or Kaufmann, effect. Some researchers invoke an additional physiological mechanism or specific adaptation to cycling temperatures resulting in a genuine alteration of development rate. Differences in development rates at constant and cycling temperatures may have important implications for degree-day (linear) population models, which are used in both pest management and ecological studies.

Larvae of *Aglais urticae* L. (small tortoiseshell), *Inachis io* L. (peacock), *Polygonia c-album* L. (comma) and *Vanessa atalanta* L. (red admiral) (Lepidoptera: Nymphalidae) were reared at constant (10, 15, 20, 25, 30°C) and alternating (20/10, 25/15, 30/10, 30/20°C) regimes. Development rates under the alternating regimes used were found to differ from those under equivalent constant temperatures in a pattern suggestive of the Kaufmann effect: in all species development at 20/10°C was faster than at 15°C, and for three species development at 30/20°C was slower than at 25°C. The exception was *A. urticae*. A similar pattern was found for growth rate and pupal weight. The results are discussed with respect to cycling temperature theory and degree-day modelling.

INTRODUCTION

The temperature-dependence of insect development has been well investigated, most often with the use of constant temperature experiments. To mimic field conditions more realistically, development under 24 h *cycling* temperature regimes has been studied (for reviews see Ratte, 1985; Beck, 1991; Liu et al., 1995), variations of which include *sinusoidal* regimes (e.g. Eubank et al., 1973; Hagstrum & Milliken, 1991), and, more commonly, as square-wave *alternating* regimes (e.g. Guppy, 1969; Siddiqui et al., 1973; Roltsch et al., 1990). Mean development rates under cycling regimes have been found to be either accelerated (e.g. Siddiqui et al., 1973; Beck, 1983), decelerated (e.g. Messenger, 1969; Hagstrum & Leach, 1973) or unaffected (e.g. Matteson & Decker, 1965; Butler & Lopez, 1980) when compared to development at constant temperature regimes with equivalent means. It is generally accepted that this phenomenon is a consequence of the non-linearity inherent in the temperature-rate relationship of insect development and is known as the rate summation effect, or the Kaufmann effect (after Kaufmann, 1932). Accelerated development is often observed when the majority of the cycling regime occurs at temperatures below the inflexion point of the temperature-rate curve, where the curve is positive. Retarded development is observed when the cycling temperatures occur mainly above the inflexion point, where the curve becomes negative. When the temperatures in a cycling regime occur within the approximately linear section of the temperature-rate relationship, little or no acceleration or retardation of development is observed.

Some researchers invoke an additional physiological mechanism or specific adaptation to cycling temperatures resulting in a genuine alteration of development rate, independent of the Kaufmann effect (e.g. Messenger, 1964; Ratte, 1985; Taylor & Shields, 1990), although this has never been proven (Worner, 1992). Physiological explanations for accelerated development under cycling temperatures include, for example, thermoperiodic stimulation of the neuro-endocrine system, diurnal organisation of behaviours and metabolic processes, circadian effects, and optimisation of enzyme functioning (see reviews by Beck, 1983; Ratte, 1985).

Whereas most studies have employed the more easily generated alternating temperature regimes, sinusoidal regimes more closely model natural temperature cycles and should thus be better expected to highlight any physiological responses, particularly in the majority of species for which body temperature is dependent on ambient. Some larval and nymphal insects, however, may gain independence of body temperature from ambient by basking (e.g. Porter, 1982; Begon, 1983; Knapp & Casey, 1986). On sunny days, the pattern of larval body temperature of thermoregulating species resembles the square-wave pattern of an alternating regime, over a 24 h period

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(Knapp & Casey, 1986; Bryant, 1998). It is possible, therefore, that specific physiological adaptation will be most pronounced in such species that thermoregulate at a specific temperature for at least part of the day, particularly for temperatures above the inflexion point when developmental retardation would otherwise be expected.

The purpose of this study was to investigate and compare the developmental responses of *Aglais urticae* L. (small tortoiseshell), *Inachis io* L. (peacock), *Polygonia c-album* L. (comma) and *Vanessa atalanta* L. (red admiral) larvae (Lepidoptera: Nymphalidae) to a series of constant and alternating temperature regimes. *Aglais urticae* and *I. io* larvae are gregarious, predominantly black, and have been shown to regulate body temperature at around 32.5°C and 31.5°C respectively when exposed to direct solar radiation (Bryant, 1998). They may thus be expected to show a greater developmental response under alternating regimes than *P. c-album* and *V. atalanta* larvae which are solitary and remain hidden from the sun most of the time, their body temperature being largely dependent on ambient. All four species share a common primary hostplant, common stinging nettle *Urtica dioica* L. Effects on pupal weight and growth rate were also investigated.

MATERIAL AND METHODS

At least ten adult females of each species were captured around the campus of the University of Birmingham (grid reference: SP0483) during spring 1995. They were placed in cages with potted *U. dioica* and kept in a well ventilated glasshouse. Natural sunlight was supplemented by a 200 watt UV light bulb above each cage for 18 h each day, providing a 18L : 6D photoperiodic regime. Ambient temperature was subject to external conditions during the day, and kept to a minimum of 15°C at night. Butterflies were fed from capillary matting soaked with 15% honey solution placed on the roofs of cages. Eggs were collected daily and placed at 20°C, 18L : 6D until they hatched.

On hatching, at least 50 larvae were placed into their experimental regime and reared through to adult eclosion. Five constant temperatures (10, 15, 20, 25 and 30°C) and four alternating temperature regimes [20/10, 25/15, 30/10 and 30/20°C, 12 h at the higher temperature (thermophase) and 12 h at the lower temperature (cryophase)] were chosen on the basis of previous work (Bryant et al., 1997). A photoperiod of 18L : 6D was used at each temperature; the 12 h thermophase of the alternating regimes occurred in the middle of the 18 h of the light (photo-) phase. Temperature in each incubator was recorded at 15 min intervals using a Grant Squirrel® data logger [SQ32-16U], to allow accurate estimation of temperatures experienced by the larvae for the duration of the experiment. Larvae were reared in sealed plastic boxes, to maintain constant humidity, and given freshly cut nettles each day excess to requirements. To minimise variation in the quality of the harvested nettles, leaves were taken from the same large nettle-bed throughout the experiment, and large mature leaves near the base of the stem were not used. Time to pupation and adult eclosion were recorded, and development rate calculated as 1 over time. Pupae were weighed 24 h after larval-pupal ecdysis.

Growth rate was calculated using the equation from Nylin (1992):

$$\log (\text{growth rate}) = [\log (W_i) - \log (W_f)] / D \qquad (1)$$

where W_i is initial larval weight, W_f is final weight and D is the number of days taken for the increase in weight (i.e. the duration of larval development). The equation returns a relative (multiplicative) measure of growth which can be expressed as per cent increase per day; i.e. a value of 1.0 represents no increase in weight per day (0% mean daily weight gain), and 1.25 represents 25% mean daily weight gain. Larvae were not weighed as part of the study, so pupal weight was taken as final weight, and initial weight was taken to be the same as mean egg weight (0.1 mg, *A. urticae*; 0.1 mg, *I. io*; 0.25 mg, *P. c-album*; 0.05 mg, *V. atalanta*; S.R. Bryant, unpublished data). This is not a measure of growth in the strict sense of Waldbauer (1968) or Scriber & Slansky (1981) but serves as a useful relative measure of growth that is comparable for each species over the range of temperatures.

If development rates under alternating temperature regimes differ from those at equivalent constant temperatures as a result of the Kaufmann effect, the predictable pattern of accelerated and retarded development should become apparent. Fig. 1 illustrates this for a "hypothetical insect" whose temperature-dependent development is described by the non-linear equation of Lactin et al. (1995) which has been manipulated to give an optimum temperature for development of 32°C and a linear developmental threshold of around 9°C, similar values to those of the study species (from Bryant et al., 1997). This hypothetical species was "reared" under the ideal conditions used in this study; the positions of the points were calculated by rate summation using the "typical developmental curve". Regression lines were fitted to both constant temperature "results" (solid line) and alternating temperature "results" (dotted line) to highlight the acceleration and retardation effects either side of the inflexion point of the temperature-rate curve. The point at which the two lines of regression cross corresponds to the inflexion point.

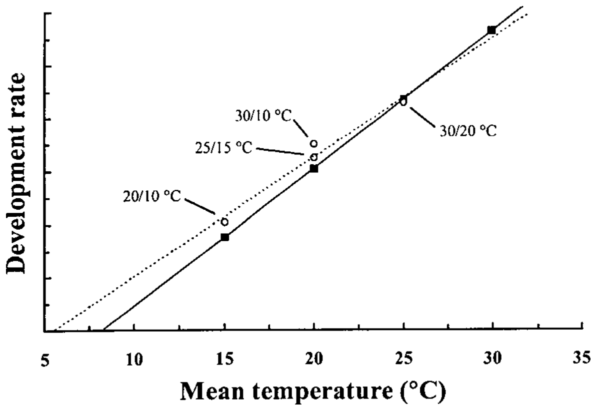

Fig. 1. Predicted pattern of mean development rates of a hypothetical insect under the constant and alternating temperature regimes used in this study. Black squares = constant temperatures, open circles = alternating temperatures. Lines fitted by least squares linear regression (solid line = constant temperatures, dotted line = alternating temperatures).

RESULTS

Development rate

Development rates under the alternating regimes used were found to differ from those under equivalent constant temperatures (Fig. 2; Table 1), in an overall manner suggestive of the Kaufmann effect: the per cent deviation column of Table 1 shows that in all species development at 20/10°C was faster than at 15°C, and for three species

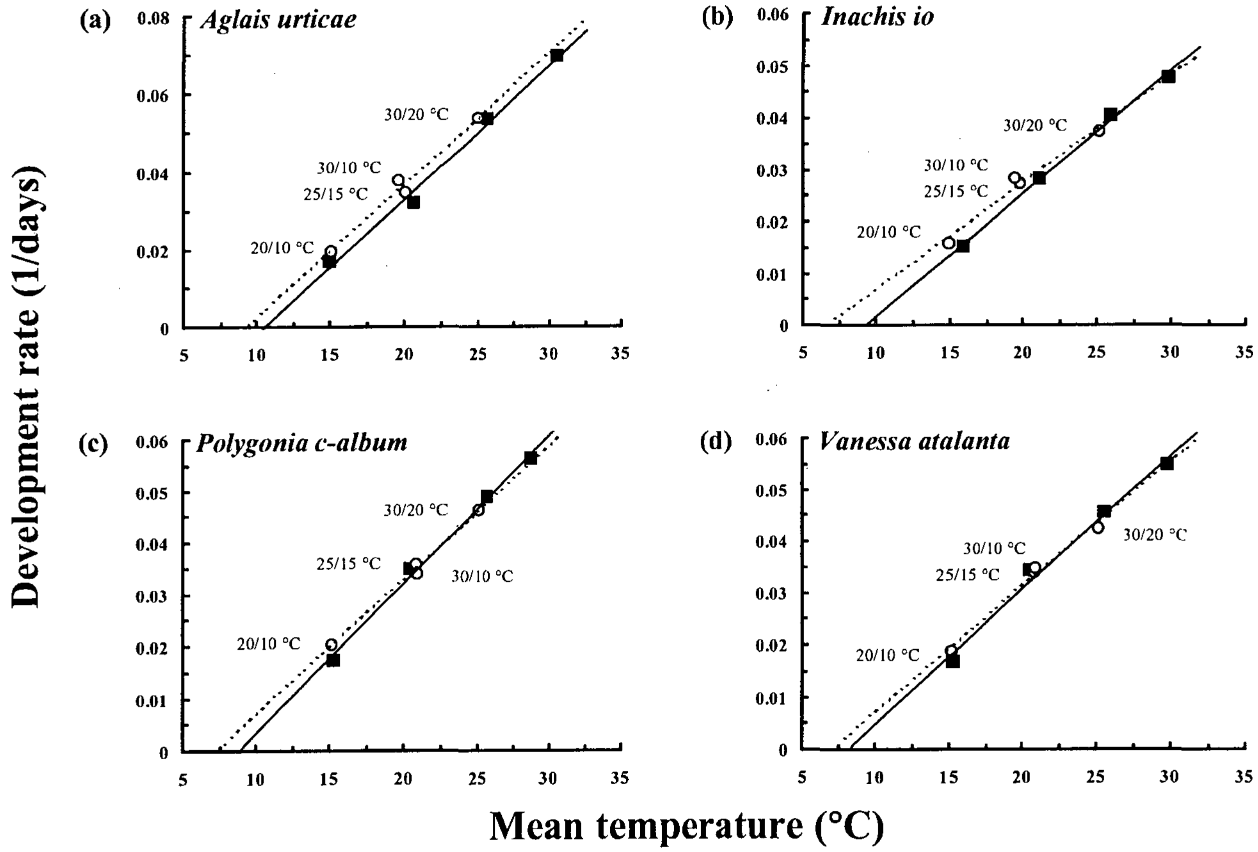

Fig. 2. The relationship between development rate and temperature from first instar to adult eclosion for (a) *Aglais urticae*, (b) *Inachis io*, (c) *Polygonia c-album* and (d) *Vanessa atalanta*. Black squares = mean development rates under constant temperature, open circles = mean development rates under alternating temperatures. Lines fitted by least squares linear regression (solid line = constant temperatures, dotted line = alternating temperatures).

development at 30/20°C was slower than at 25°C. The exception was *A. urticae*: development rate at 30/20°C was the same as at 25°C, although it occurred at a lower experimental mean temperature (25.0 and 25.7°C respectively) and as such represents an acceleration in development. This is the reason why the regression lines in Fig. 2a did not cross as predicted. The largest per cent deviation occurred with *A. urticae* at 30/10°C, again at a lower

TABLE 1. Summary of constant and alternating temperature effects on time taken to develop from first instar to adult eclosion.

Species	Constant temperatures				Alternating temperatures				% deviation[b]	Student's t-test	Level of significance
	Actual mean temp. (°C)	N	Days	± SE	Temperature regime (°C)[a]	N	Days	± SE			
Aglais urticae	15.0	36	58.50	0.36	20/10 (15.1)	52	51.33	0.16	+14.0	20.211	***
	20.6	43	31.42	0.13	25/15 (20.1)	50	29.14	0.08	+7.8	15.329	***
	"	"	"	"	30/10 (19.6)	48	26.58	0.07	+18.2	32.702	***
	25.7	43	18.60	0.16	30/20 (25.0)	55	18.60	0.11	0	0.032	NS
Inachis io	15.9	20	66.30	0.28	20/10 (14.9)	34	63.35	0.34	+4.7	5.926	***
	21.1	45	35.33	0.13	25/15 (19.8)	41	36.63	0.16	−3.5	−6.272	***
	"	"	"	"	30/10 (19.4)	26	35.38	0.21	0	−0.219	NS
	26.0	44	24.59	0.12	30/20 (25.2)	20	26.75	0.18	−8.1	−10.175	***
Polygonia c-album	15.3	42	57.69	0.35	20/10 (15.2)	42	49.14	0.13	+17.4	22.518	***
	20.5	52	28.69	0.15	25/15 (20.9)	40	27.98	0.19	+2.5	2.978	**
	"	"	"	"	30/10 (21.0)	28	29.61	0.26	−3.1	−3.232	**
	25.7	43	20.51	0.16	30/20 (21.5)	20	21.65	0.24	−5.3	−4.004	***
Vanessa atalanta	15.3	42	59.17	0.42	20/10 (15.2)	41	53.56	0.29	+10.5	10.882	***
	20.6	50	29.06	0.18	25/15 (20.9)	47	29.47	0.24	−1.4	−1.383	NS
	"	"	"	"	30/10 (20.9)	34	28.82	0.19	+0.8	0.888	NS
	25.6	43	21.98	0.15	30/20 (25.2)	31	23.53	0.26	−6.6	−5.501	***

[a] Actual mean temperatures shown in parentheses.

[b] Calculated as [(days at constant temp./days at alternating temp.) − 1] × 100. Positive values signify an acceleration in development, negative values a deceleration.

mean temperature than the corresponding mean constant temperature. Greater acceleration occurred under a 30/10°C regime compared to 25/15°C, except with *P. c-album*. This overall pattern was observed for the different developmental periods recorded, namely time to pupation and pupal duration. Comparisons of days to develop at alternating and constant temperatures were made (t-tests, Table 1) and were found to be significant in all but four cases.

Pupal weight and growth rate

Table 2 summarises pupal weights and growth rates. Note that the differences in actual mean temperatures between Tables 1 and 2 are due to their calculation over different periods. A two-way ANOVA was carried out to compare the effect of temperature and sex on pupal weight. Faster development at high temperature produced lighter (smaller) pupae (*A. urticae*, $F_{3,164} = 53.4$, $P \ll 0.001$; *I. io*, $F_{3,143} = 297.2$, $P \ll 0.001$; *P. c-album*, $F_{4,212} = 84.5$, $P \ll 0.001$; *V. atalanta*, $F_{4,193} = 68.6$, $P \ll 0.001$), in agreement with previous findings (Bryant et al., 1997). Females were significantly heavier than males for *A. urticae* ($F_{1,164} = 17.6$, $P \ll 0.001$) and *I. io* ($F_{1,143} = 95.5$, $P \ll 0.001$), but not for *P. c-album* ($F_{1,212} = 3.1$, $P > 0.05$), although at each temperature females were heavier than males. *Vanessa atalanta* males were just significantly heavier than females ($F_{1,193} = 4.2$, $P < 0.05$).

As with development rate, both pupal weight and growth rate were higher at 20/10°C than at 15°C for each species, although the difference in pupal weights was

TABLE 2. Summary of constant and alternating temperature effects on pupal weight and growth rate. Mean larval period is also shown.

Species	Actual mean temp. (°C)	Pooled mean larval period (days ± SE)	Male			Female			Pooled[b]			Relative growth rate (%/day)
			N	Weight (mg)	± SE	N	Weight (mg)	± SE	N	Weight (mg)[c]	± SE	
Aglais urticae	9.1	–	–	–	–	–	–	–	–	–	–	–
	15.3	36.4 ± 0.18	17	306.60	5.90	23	319.60	6.29	42	314.63	4.29	24.8
	20.4	20.5 ± 0.07	26	328.78	3.41	21	350.52	5.34	52	334.77	3.64	48.6
	25.7	12.3 ± 0.07	26	291.74	3.46	17	308.44	4.39	55	296.03	2.64	91.7
	30.5	9.3 ± 0.06	20	281.89	3.76	19	284.38	3.85	47	285.13	2.47	135.8
	15.2 (19.5/11.0)[a]	33.1 ± 0.15	27	320.86	4.42	25	328.51	5.52	56	325.76*	3.41	27.7
	20.1 (25.2/14.9)	18.9 ± 0.06	27	319.64	3.44	23	345.88	5.18	53	330.76^{NS}	3.40	53.6
	19.5 (29.0/9.9)	17.2 ± 0.09	27	294.64	4.17	21	309.01	4.86	51	301.16***	3.18	59.4
	24.8 (30.3/19.3)	12.3 ± 0.10	25	320.76	4.37	30	334.11	4.91	60	327.51***	3.60	93.2
Inachis io	9.3	–	–	–	–	–	–	–	–	–	–	–
	15.4	45.6 ± 0.28	10	461.01	7.22	11	542.33	10.14	30	497.37	9.93	20.5
	20.8	25.2 ± 0.11	21	486.84	8.22	25	545.62	7.36	52	512.63	7.15	40.3
	25.9	17.5 ± 0.10	22	358.47	5.44	24	418.87	6.22	53	384.74	6.08	60.3
	29.7	15.1 ± 0.17	13	290.10	8.43	22	322.42	9.64	42	304.95	6.67	70.0
	14.6 (18.0/9.9)	43.8 ± 0.27	15	492.13	14.37	20	528.41	9.04	44	515.21^{NS}	7.61	21.6
	19.9 (25.6/14.3)	25.3 ± 0.07	23	442.72	8.77	18	521.40	10.33	52	471.22***	8.13	39.6
	19.4 (28.5/10.3)	24.7 ± 0.14	11	413.68	8.13	15	472.39	10.63	37	449.13***	8.37	40.5
	25.0 (30.3/19.7)	18.5 ± 0.18	11	451.03	10.46	9	535.61	11.57	24	285.87***	11.26	58.2
Polygonia c-album	11.8	52.1 ± 0.22	18	362.40	8.21	26	373.88	6.55	50	368.27	4.59	15.0
	15.1	35.7 ± 0.18	18	350.57	4.56	24	355.90	5.10	47	351.11	3.67	22.5
	20.4	18.2 ± 0.13	28	341.04	5.69	24	357.04	5.48	53	348.13	4.02	48.8
	25.9	13.3 ± 0.14	25	311.77	3.88	18	302.24	5.00	46	306.62	3.16	70.9
	28.7	12.0 ± 0.16	18	274.63	5.88	19	279.94	6.01	40	277.65	4.75	79.4
	15.2 (20.4/10.0)	30.5 ± 0.16	18	347.79	4.67	24	357.90	3.87	50	358.81^{NS}	2.77	26.9
	20.8 (26.2/15.4)	18.3 ± 0.13	17	322.81	5.23	23	344.11	4.78	50	333.79*	3.79	48.0
	20.9 (30.4/11.5)	19.5 ± 0.18	13	316.27	6.62	15	334.12	4.44	41	328.32***	4.02	44.5
	24.8 (30.3/19.3)	13.3 ± 0.23	11	268.71	8.98	9	286.78	8.02	24	274.87***	5.62	69.4
Vanessa atalanta	11.8	63.9 ± 0.30	13	701.96	12.96	11	716.76	12.92	25	708.90	8.75	16.1
	15.1	37.5 ± 0.31	24	604.55	9.62	18	575.74	14.39	42	592.20	8.45	28.4
	20.5	18.9 ± 0.15	34	620.40	7.06	16	611.40	16.64	50	617.52	7.09	64.7
	25.9	14.4 ± 0.10	21	543.90	9.47	15	541.54	13.86	44	552.07	8.84	91.1
	29.7	12.0 ± 0.17	19	520.71	10.81	21	500.06	15.15	42	511.60	8.51	116.2
	12.2 (20.4/10.0)	34.5 ± 0.20	21	609.59	9.63	20	596.32	8.00	42	603.58^{NS}	6.16	30.4
	20.8 (26.2/15.4)	19.9 ± 0.21	22	578.42	11.37	25	550.19	8.59	47	563.40***	7.24	59.8
	20.9 (30.4/11.5)	20.1 ± 0.23	13	503.99	17.66	21	485.56	9.71	34	492.61***	9.01	58.0
	24.9 (30.0/19.5)	15.3 ± 0.17	21	466.38	13.93	11	465.09	21.83	37	458.44***	10.84	81.1

[a] Mean temperature (mean thermophase temperature/mean cryophase temperature).

[b] Includes pupae that formed successfully, but which failed to hatch.

[c] Results from t-test comparing pupal weight from alternating regimes with those from the corresponding constant temperature are given in superscript.

only significant for *A. urticae* (Table 2). At higher mean temperatures, however, alternating regimes had a significant negative effect on pupal weight and growth rate. The exceptions to this rule were significantly heavier *A. urticae* and *I. io* pupae at 30/20°C than at 25°C, and higher growth rates shown by *A. urticae* at all alternating temperatures. Each species produced heavier pupae at 25/15°C than at 30/10°C (*A. urticae*, $t = 6.397$, $P < 0.001$; *I. io*, $t = 1.807$, $P < 0.05$; *P. c-album*, $t = 1.330$, $P > 0.05$; *V. atalanta*, $t = 6.182$, $P < 0.001$).

DISCUSSION

There was no evidence in the patterns of observed development rates to suggest the presence of a physiological mechanism or adaptation acting to increase development rates notably under alternating regimes, in addition to those responsible for the Kaufmann effect: accelerated development was observed at low temperatures, retarded development at high temperatures. The possible exception was *A. urticae* which achieved equal development rates under a 30/20°C regime (actual mean of 25.0°C) and the equivalent constant temperature regime (actual mean of 25.7°C). However, sources of error in such experiments are numerous and may arise, for example, from inaccurate determination or measurement of actual temperatures experienced by larvae, genetic variability (confounded by small sample sizes), nutritional and humidity effects, and, in the case of describing temperature/rate relationships, too few rearing temperatures used (e.g. Howe, 1967). Simple comparison of development under alternating and constant regimes is likely to show up only gross differences even with accurate measurement of rearing temperatures (Liu et al., 1995), and rate summation using complete temperature/rate descriptions is necessary to show unequivocally specific physiological adaptations, if present. Certainly in this study, lack of constant temperature data at both upper and lower thresholds prevented calculation of expected development rates under alternating regimes for each species.

Like development rates under cycling regimes, reports of increased, decreased or unaffected pupal weights and/or growth rates under thermoperiodic regimes can be found in the literature (e.g. Beck, 1983, 1986; Behrens et al., 1983; Ratte, 1985; Brakefield & Mazzotta, 1995). Unlike development rate, however, rigorous rules accurately describing the temperature-dependence of growth rates have not yet been deduced (Ratte, 1985), although it is generally considered that growth rates show a similar response, and one might expect them to be affected under cycling temperatures in a similar way to development rates. The results support this to some extent in that, as for development rates, growth rates were higher at 20/10°C compared to at 15°C in all species, and the general trend at higher alternating temperatures was towards retardation (Table 2). An increase in growth rate, however, will result in heavier pupae only if the developmental period allows, and vice versa [from equation (1)]. Thus the effect of increased growth at 20/10°C was offset by a reduced development period, and pupal weights, although slightly higher than those at 15°C, were only significantly so in *A. urticae*. Conversely, *I. io* larvae grew more slowly at 30/20°C than at 25°C but produced heavier pupae because they developed over a longer period. This was due in part to a difference in the actual mean temperature experienced, and it follows that comparisons of growth indices between cycling and constant temperature regimes should be made with the same caution exercised when comparing development rates.

Aglais urticae was the only species where growth rates were higher at alternating compared to constant temperatures for all regimes tested. This was particularly remarkable considering the retardation of growth rate shown by the other species at 25/15, 30/10 and 30/20°C (apart from a very slight increase for *I. io* at 30/10°C). Growth rates for *A. urticae* larvae have previously been shown to be similar to those of *I. io*, *P. c-album* and *V. atalanta* larvae between constant 10 and 25°C, following an approximately linear relationship, but a great deal higher between 30 and 34°C; this was thought to be associated with the larval thermoregulatory strategy of *A. urticae* (Bryant et al., 1997). An envisaged growth effect analogous to the Kaufmann effect would presumably be responsible for accelerated growth only at low temperatures. It remains unclear, therefore, whether the observed accelerations of growth rate in *A. urticae* are a consequence of (a) temperature alternation per se, or (b) a summation effect brought about by abnormally high rates of growth at temperatures included in the alternating regimes used in this study. Ratte (1985) considered development rate to be coincidental to growth rate; the relative increase in development rate at 30/20°C compared to 25°C in *A. urticae* may be a real effect, but more a consequence of increased growth rate.

The results highlight the potential for growth at temperatures around or below the theoretical threshold. The consequence of this in terms of modelling the phenology of the study species and other insects will depend on the technique employed. Integration of an *adequate* nonlinear description of the temperature/rate relationship (rate summation) would, by definition, incorporate developmental responses attributable to the Kaufmann effect. Rearing insects at low constant temperature(s), however, is difficult and time consuming, and thus more open to experimental error. The degree-day approach (thermal summation) requires development data for intermediate constant temperatures only, and, although it fails to consider development at low temperatures, is widely used. By including low temperatures within cycling regimes, however, observed rates incorporate low temperature development effects attributable to the Kaufmann effect, and thus two possibilities exist for the improvement of degree-day modelling in the light of cycling temperature experiments: (1) calculation of degree-day requirements and the developmental threshold could be made using rates observed under *both* constant and cycling regimes together, or (2) degree-day requirements and the developmental threshold could be calculated using *only* those rates observed under cycling regimes. Such cycling temperature experiments are easier to implement than constant low temperature experiments, and as such could provide an alternative for including the inherent non-linearity of insect development within degree-day models.

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