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Temperature and Organism Size—A Biological Law for Ectotherms?

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I. SUMMARY

For plants, protists and that vast majority of animals that rely on external sources for body heat (ectotherms), temperature is a particularly important

and widespread correlate of differences in size between seasons and from one generation to the next. This includes the economically important differences between years in the yields of crops harvested at maturity such as cereals.

Laboratory studies under controlled conditions can isolate the specific effects of temperature and help identify just how similar is the relationship between organism size and (non-extreme) rearing temperature among different species. This chapter reviews the direct effects of rearing temperature on the size of ectotherms at any given stage of development, other environmental conditions being controlled, and within the range of temperatures which allow the organism to reach maturity but are not so stressfully high that an increase causes reduction in the rates of growth, differentiation or both. It thus considers phenotypic plasticity in organism size, and does not examine genetic variation related to temperature differences.

One hundred and nine studies, which included examples of animals, plants, protists and a bacterium, showed a significant effect of rearing temperature on size. In 83·5% of cases, increased temperature led to reduced size at a given stage of development. Only 11·9% of examples showed a size increase, and 4·6% showed a mixture of increases and decreases with temperature. Whilst some of these exceptions to the general size-reduction rule may result from unreported weaknesses in experimental protocol or inappropriate temperature conditions, several detailed studies still appeared to provide genuine exceptions. Because the rule applied to organisms of many different taxa, habitats and lifestyles, general, rather than ad hoc explanations were sought.

The explanation for the general rule offered by von Bertalanffy (1960)—that catabolism has a higher temperature coefficient than does anabolism, leading to faster growth and smaller ultimate size at high temperature—is shown strictly to be incorrect, though elaborations on the original hypothesis may be worth testing. No particular support was found for (and a little evidence was found against) the idea that, as size and temperature increased, growth became increasingly constrained due to oxygen shortage in aquatic and water-saturated habitats, or to desiccation in terrestrial habitats.

Of three hypotheses which considered the adaptive value of size at different temperatures, only the advantages for buoyancy in planktonic species could not be eliminated. But because this only applied to a group of aquatic species, other, more general explanations were sought.

Several correlates of temperature that should influence optimal rate of development and size have been identified. In particular, three promising areas require further study: (i) the relationship between temperature and individual growth rate, size at a given developmental stage and mortality. Mortality factors of particular interest are increased predation, accelerated ageing, future risks of drought (for terrestrial species), future risks of oxygen shortage (for aquatic species) and costs of rapid growth at different temperatures; (ii) the use of seasonal cues to adjust relative rates of growth and

development; and (iii) the extent to which size is affected by the rate of population growth at different temperatures. A hypothesis related to these latter two problems is based on the advantages of shortening the life cycle when conditions are favourable for population growth or when time available is constrained by season.

Some quantitative effects of temperature on size in natural and managed populations are briefly reviewed.

II. INTRODUCTION

For animals, plants, protists and bacteria, the ecological importance of organism size is clearly demonstrated by its effects on longevity, fecundity, metabolic rates, ability to migrate, competitive, predatory and anti-predator abilities, and ability to withstand starvation and desiccation (e.g. Dingle et al., 1980; Peters, 1983; Calder, 1984; Schmidt-Neilsen, 1984; Reiss, 1989). Its economic value is indicated by the effects of plant size on agricultural crop yields (Monteith, 1981; Warrick et al., 1986).

Temperature has an important effect on many functions relating to an organism's size. Metabolic rates, rates of gaseous exchange, risks of desiccation in terrestrial habitats or oxygen shortage in aquatic habitats are all affected by both temperature and size. This is sometimes because an increase in size without a change in shape decreases the ratio between surface area for exchange of heat, water and gases and the weight or volume of the body that produces or consumes those resources (Schmidt-Neilsen, 1984).

Over 30 years ago, following a series of experiments on a wide range of animals and protists together with a review of previous studies, Carleton Ray (1960) proposed that a general relationship existed between the temperature at which a poikilothermic organism is reared and its subsequent final size. (Body temperatures of poikilotherms vary according to environmental temperature; almost all these species are also ectothermic.) Specifically, he proposed that at increased rearing temperatures, a smaller body size is produced (see also reviews by Bělehrádek, 1935; von Bertalanffy, 1960; Precht et al., 1973). Much of the evidence, starting with the work of Standfuss (1895) on Lepidoptera, comes from laboratory studies and field comparisons over small distances.

This relationship appears to mirror that found for endotherms by Bergmann (1847). Bergmann proposed that, intraspecifically, body size decreases with average ambient temperature and hence tends to increase with latitude. However, since the evidence for the relationship in endotherms is based largely on geographical variation, differences may be largely genetic rather than a direct effect of rearing temperature as is observed for ectotherms. Moreover, the original explanation for "Bergmann's Rule", which invokes that large-bodied animals have a superior ability to conserve heat, is inappro-

priate for most poikilotherms whose body temperatures fluctuate rapidly and markedly as environmental temperatures change (von Bertalanffy, 1960; Calow, 1977). The only widely reported hypothesis for ectotherms is that of von Bertalanffy (1960) who proposed that growth becomes constrained at high temperatures because the rate of anabolism is fundamentally unable to keep up with that of catabolism.

But doubt still remains about whether a general relationship between rearing temperature and ectotherm size even exists. Some authors have produced arguments and data which appear to contradict the relationship, and have cited further counter examples (Calow, 1973; Roff, 1981; Lamb and Gerber, 1985). In one review of the effects of environmental temperature on final size of poikilothermic animals, Laudien (1973, p. 389) states that "individual animal species react in so many different ways that general statements cannot be made".

There is therefore a need to review the evidence critically and assess alternative hypotheses which may account for the effects of raising temperature on ectotherm size. This paper attempts to do this for protists, bacteria, ectothermic animals and plants and then examines the quantitative effect of temperature on size in some natural and managed populations.

III. PARAMETERS OF THE PROBLEM, AND METHODS

A. The Problem Defined

The problem under review here is concerned only with the direct ontogenetic effects of temperature on organism size, and not with genetically distinct strains showing different responses to temperature. Stressfully high or low temperatures or insufficient energy or other resources can obviously produce small size. Yet reviews have suggested that high temperature reduces size even in conditions favourable for growth (Ray, 1960). Also, size should be compared at the same stage of development. Therefore, the problem was defined so as to exclude unfavourable conditions for growth and inappropriate comparisons, thus:

The choice of upper temperature limits, indicated above, should exclude conditions stressful for growth. If organisms did not reach maturity at extreme low or high temperatures, or if daily mortality rate increased as temperature was reduced to very low values, despite reduced metabolic activity, these temperatures were considered stressful and were therefore also excluded from the review.

Not all studies recorded rates of differentiation, and very few recorded rates of growth. But, providing that energy and other resources are unlimiting, both these rates usually increase with temperature within the range
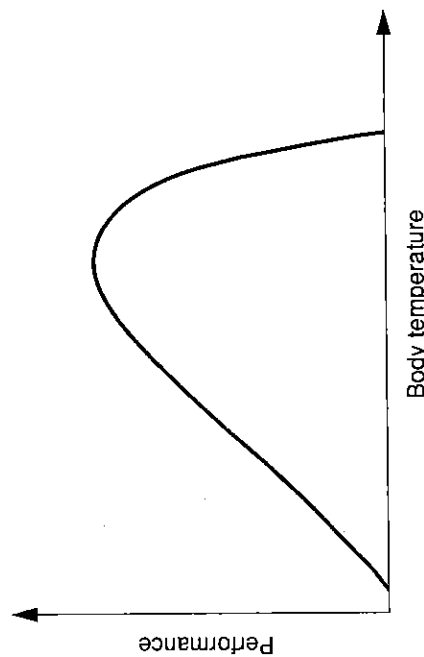
Fig. 1. The hypothetical asymmetric effect of temperature on ectotherm performance (after Huey and Kingsolver, 1989). "Performance" may apply to growth rates, rates of differentiation or other activities. At high temperatures enzyme systems start to break down.

normally encountered by the organism since physiological performance usually increases gradually until a sudden decline near the upper limits when enzyme systems become damaged (Fig. 1; Huey and Kingsolver, 1989). Therefore, the problem can be expressed thus:

Under controlled environmental conditions in which energy and other resources are not limiting, at temperatures which allow the organism to reach maturity but not so high that rates of growth, differentiation or both decline—how does rearing temperature affect organism size at a given stage of development?

Another way to consider the problem is: does an increase in temperature, whilst increasing rates of growth and differentiation, affect the latter more than the former so that body size at a given stage of development is reduced?

B. Scope of Review

The review focused on ectothermic animals, plants—most of which are ectothermic (Gates, 1980)—and protists. One bacterial example was found, so this was also included.

Besides the predominance of English-language references, apparent biases in the review may have arisen because size-at-stage data appear to be recorded particularly commonly in species with easily observed developmental stages and events (e.g. moults), and which cease growing in the adult stage.

Almost every study lacked at least some relevant data (e.g. mortality rates,

photoperiod, food quality), so analyses were also performed to investigate the effects of gaps in the data set.

C. Criteria for Inclusion of Studies

1. Size-at-stage Measures

Ideally, the dry or wet weights of an organism at the time of a particular developmental event (e.g. final metamorphosis) would precisely define both the size and developmental stage. However, other correlates of organism weight such as body length, measures of exoskeletal dimensions, insect wing-length and, in unicells, cell length or volume, were also accepted in cases where weight measurements were not made. Occasionally, in arthropods, when a paper did not indicate the particular time within a growing developmental stage in which size was measured, it was preferable to use exoskeletal measures rather than weights, since they reflect more accurately the size of the animal at the previous moult (a precise developmental event).

In species in which additional juvenile stages are optionally inserted according to environmental conditions (e.g. Bellinger and Pienkowski, 1987), the size of early stages may correlate particularly poorly with size when at the time of later (and necessary) developmental events such as reproductive maturity. Early stages will also have had less time growing under the experimental temperatures. For these reasons, in studies in which several developmental stages were examined, data from later stages, including adults, were preferentially selected.

In unicells, size at initiation of fission was only available from one study (Adolph, 1929). To increase sample size of protists, cruder measures such as average size over a period of several generations were also included.

2. Experimental Conditions

An experiment was excluded from the review if the amount of energy provided appeared to be limiting in any of the treatments (e.g. if all food was eaten between feeds; if light levels produced slower plant growth than at higher levels), or if treatments had different types of food provided or different photoperiodic regimes. This includes cases in which there was evidence that temperature itself may have altered food quality (e.g. Minkenberg and Helderman, 1990).

Results from animal studies were not included also if the food was both unnatural and caused a reduction in growth rate below that observed on natural food. An example of this is the mayfly, Leptophlebia intermedia, which, when reared on unnatural food, also experienced higher larval mor-

tality and produced significantly smaller adults at each temperature than on natural food (Sweeney et al., 1986).

If an excess amount of suitable food is provided for heterotrophs their growth should not be limited by energy supply. Yet for some unicellular algae growth is limited not only by low light intensities, and hence insufficient energy, but also by very high light intensities. Moreover, the high light intensity at which growth retardation starts to occur can increase with increasing temperature, as was found in the planktonic alga Cryptomonas erosa (Morgan and Kalff, 1979). Thus it may be impossible to find a single light intensity that will enable some species to grow at each of several temperatures without energy supply limiting growth at at least one of them. Studies which demonstrated that the light intensities which limited growth differed with temperature were not included in the analysis (Morgan and Kalff, 1979; Meeson and Sweeney, 1982).

3. Statistical Significance

Only experiments in which statistical tests had been performed were included in the initial data analysis.

In some studies in which no statistical tests had been performed by authors, it was still possible to perform a rank correlation of mean sizes against temperature using the Hotelling-Pabst statistic (Conover, 1980) or calculate 95% confidence limits, and hence test for significance. If these studies showed significant effects of temperature they were added to the data set for analysis.

Since statistical non-significance ($p > 0.05$) was sometimes associated with very small sample sizes, such results were noted but not considered in detail. Studies without statistical tests, but which showed trends with temperature, were noted in the discussion only.

IV. A BIOLOGICAL LAW FOR ECTOTHERMS?

A. Summary of Data

1. Overall Result

Of 69 experiments in which statistical tests were performed by the authors, only five (7.2%) showed no significant effect of rearing temperature (Ray, 1960; Poston et al., 1977; Palmer, 1984; Pechenik and Lima, 1984; Sims et al., 1984). At least two of these (Ray, 1960 [for Xiphophorus maculatus]; Palmer, 1984) had low sample sizes (fewer than nine per temperature).

The subsequent analysis combined the 64 results in which authors found significant effects of temperature, with the 45 others for which the investigation later was able to demonstrate statistical significance. Of these 109 studies (see Appendix), 91 (83.5%) showed a significant reduction in size with

an increase in rearing temperature (e.g. Fig. 3), 13 (11.9%) showed an increase (e.g. Fig. 4), and five (4.6%) showed a mixed effect (i.e. combinations of significant increases with significant decreases within the range; e.g. Fig. 5). Thus of the 104 experiments in which a simple significant effect
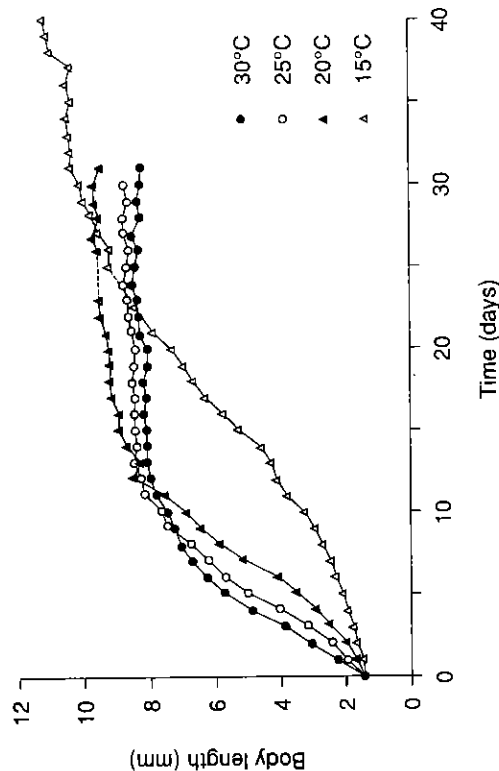

Fig. 2. Growth in mean body length of larvae of the midge *Chaoborus* at different temperatures (after Hanazato and Yasuno, 1989). This shows the typical effect of temperature when resources are not limiting; growth rate increases but final size is reduced with increasing temperature.

(an increase or a reduction) occurred, there is clearly a significantly greater number of reductions in body size than there are increases ($\chi^2 = 58.5$, $p < 0.001$). The proportion of cases giving reductions (83.5%) is similar to the 80% reported by Ray (1960) who applied less strict criteria for accepting studies for his review than were used here.

It is important to note that a decrease in temperature causes the majority of ectotherms to attain a larger size at a given stage of development despite their growing and developing slower. These temperatures which produce large size are often near the bottom of the range normally encountered and appear to be suboptimal (see also Figs. 1 and 2, and Section VI). Thus the widespread reduction in size with increased temperature appears not to be caused by increased stress or a deterioration in enzyme performance with temperature increase since temperatures are apparently well below these stressful levels.

2. Association with Taxonomic Group

A reduction (or increase) in size at a given stage of development caused by increased temperature may be confined only to certain taxa. To test this idea,
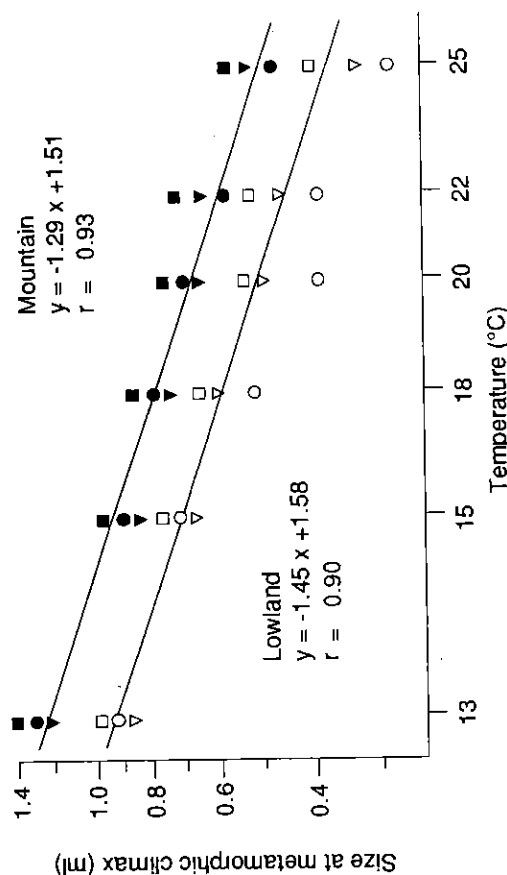
Fig. 3. Temperature dependence of size at metamorphic climax of mountain (closed symbols) and lowland (open symbols) wood frogs, *Rana sylvatica*. Each symbol equals the mean volumes of 24 larvae. Data are presented for frogs obtained from three lowland and three mountain ponds (after Berven, 1982b).

the results were analysed according to the taxonomic groups to which the organisms belonged.

Of the 109 studies, one was a bacterium, seven were of protists, six were of multicellular plants, and 95 were of animals (Fig. 6; Appendix). Of the seven protist examples five were autotrophs and two were heterotrophs. All but one of the protists showed a reduction in size with increased rearing temperature, as did the six plant examples and the bacterium *Pseudomonas*. The only protist exception was the marine diatom *Phaeodactylum tricornutum* which increased in size with increasing temperature (Fawley, 1984). The remaining 12 increases and five cases of mixed effect were found within the animal kingdom.

Eighty of the 95 animal examples were arthropods (Fig. 7). Among animals, only the arthropods showed instances of significant increases in, or significant mixed effects on body size with temperature (Fig. 7).

Effects of temperature on size of multicellular plants, at particular stages of development rather than at a fixed time of harvest, are not frequently cited. Examples are confined to crop plants belonging to the grass and pea families, so the sample is rather limited taxonomically. In addition to the studies of five plant species which followed the general rule (Appendix), Friend *et al.* (1962) found that the weight of wheat plants at anthesis generally decreased with increasing temperature, though statistical tests that might have confirmed the trend were not done. Similarly, whilst no significant tests were performed by
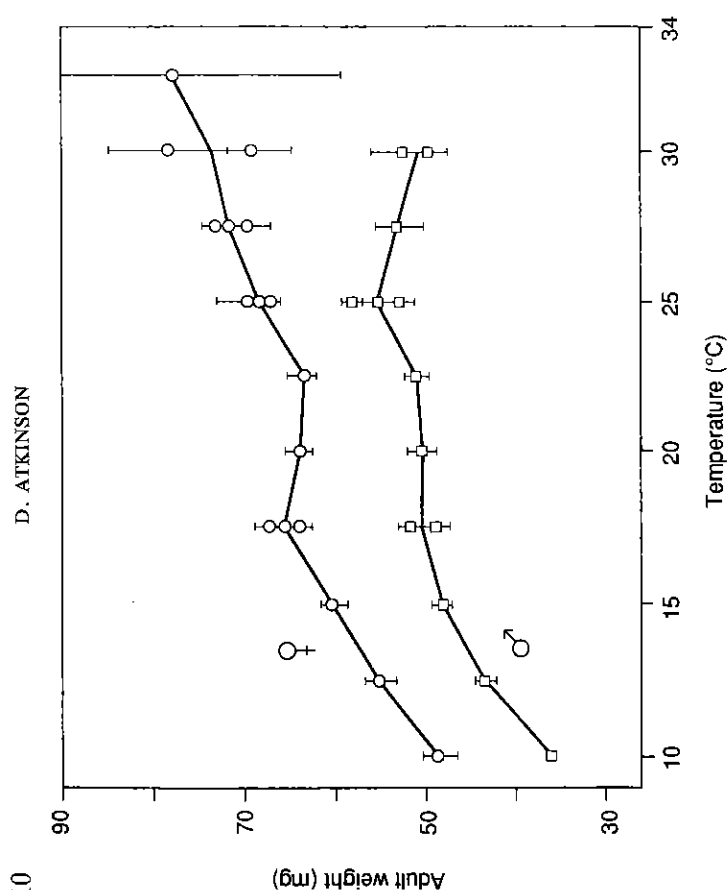
Fig. 4. Average adult weight (± SD) for the beetle *Entomoscelis americana* reared at different temperatures (after Lamb and Gerber, 1985).

Thorne *et al.* (1968), they found that dry weights of ears, shoots and roots at anthesis appeared to decline with increasing temperature, though no obvious effect on plant size was observed at spikelet initiation.

However, studies on maize, whilst most did not satisfy statistical criteria for inclusion in the Appendix, appear to show conflicting results. Consistent with the general rule were leaf weight at a particular developmental stage (determined by leaf number) measured by Brouwer *et al.* (1973) and plant size at anthesis recorded by Hunter *et al.* (1977). But Hardacre and Eagles (1986) and Hardacre and Turnbull (1986) found that plant size at each of three stages (determined by leaf number) was greatest at intermediate temperatures, and Gmelig Meyling (1969) showed that the effects of temperature on plant size at first flowering depended on sowing date.

Whilst all the plants were angiosperms, the animal phyla in which only significant reductions in size were reported, were represented by several classes or subphyla. The chordates included one fish and seven amphibian examples; the aschelminthes included two rotifers and a nematode; and the molluscs included two gastropods and two bivalves.

Two classes of arthropod were represented: the Insecta (67 of the 80 cases),
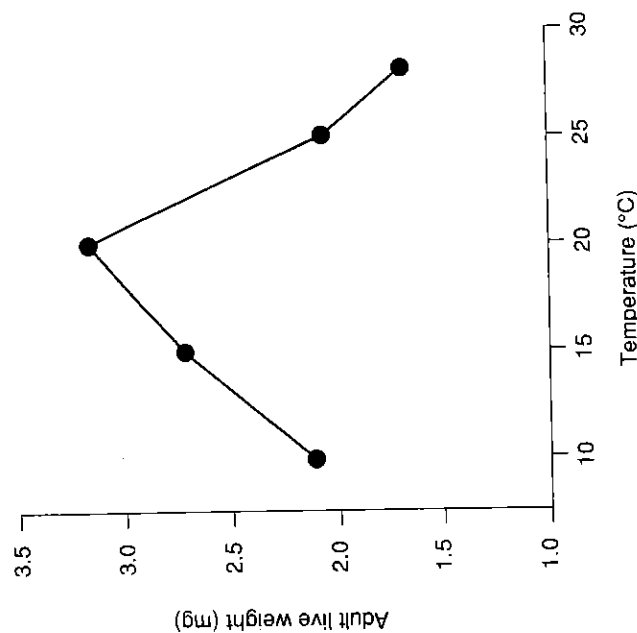
Fig. 5. Effect of rearing temperature on the live weight of apterous adults of the aphid *Acyrthosiphon pisum*. The data come from 15 Australian lines of the aphid (after Lamb and MacKay, 1988).
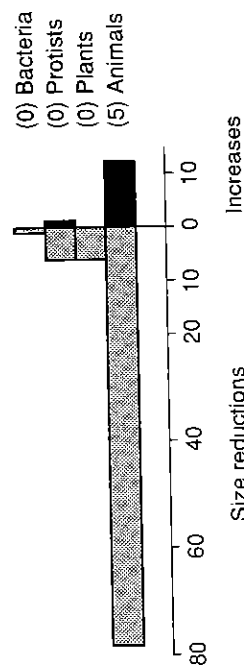
Fig. 6. Distribution of size reductions and increases in response to rearing temperature among four kingdoms (based on data in the Appendix). Numbers in parentheses represent the number of cases in which both size reductions and increases were recorded in the same study.

and the Crustacea (13 cases). Of these, 11 of the 12 cases of increase in size with temperature and all five cases of mixed effect were found among the insects. The only crustacean showing a significant increase in size with temperature was the parasitic copepod, *Salmincola salmoneus* (Johnston and Dykeman, 1987).

Increases in size or mixed effects of temperature were observed in six of the

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(0) Aschelminthes
(0) Mollusca
(0) Chordata
(5) Arthropoda

Size reductions — Increases

Fig. 7. Distribution of size reductions and increases in response to rearing temperature among four animal phyla (based on data in the Appendix). Numbers in parentheses represent the number of cases in which both size reductions and increases were recorded in the same study.

seven insect orders (Fig. 8). Only in the Orthoptera were there no examples of reductions in size found, but here the sample size was only two.
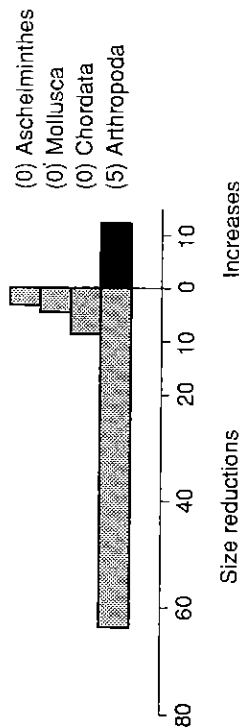
In each of the orders Orthoptera, Coleoptera and Ephemeroptera, more than a third of examples showed an increase in size. These belonged to two families of Orthoptera, three families of Coleoptera and four families of Ephemeroptera (Table 1), and were therefore not confined just to a single atypical family within each order. One family of the Lepidoptera, the Noctuidae, included two instances of a decrease in size, and also one of an increase.

Of the 32 dipteran examples, 30 showed reduced size, a figure which included 13 of the 14 studies of *Drosophila*. The discrepancy between Roff's (1981) claim that in *Drosophila* "phenotypic size increases with temperature" and the findings of the present review is due to his erroneous representation of the literature. Three of the references he cited (Eigenbrodt, 1930; Stanley, 1935; Tantawy and Mallah, 1961) actually found the opposite of what he claimed, and the fourth (McKenzie, 1978) did not examine size.

All simple increases in size except for an isolated diatom example, and all of the mixed effects of temperature were therefore confined to the Insecta. Even so, over three-quarters of insect examples still showed reductions in size with increasing temperature.

3. Association with Sex

If reductions or increases in size are confined mainly to one sex, then explanations related to sex differences at different temperatures may be involved.

In 37 of the 109 examples, statistical tests were performed on males and females separately. Table 2 shows that in 31 of these the effect was the same for both sexes. In no species was a significant increased found in one sex and a significant reduction or mixed effect found in the other. So there is no evidence that reductions or increases are confined mainly to one sex.

Page 13

(0) Orthoptera
(0) Hymenoptera
(1) Coleoptera
(0) Lepidoptera
(0) Ephemeroptera
(2) Hemiptera
(2) Diptera

Size reductions — Increases
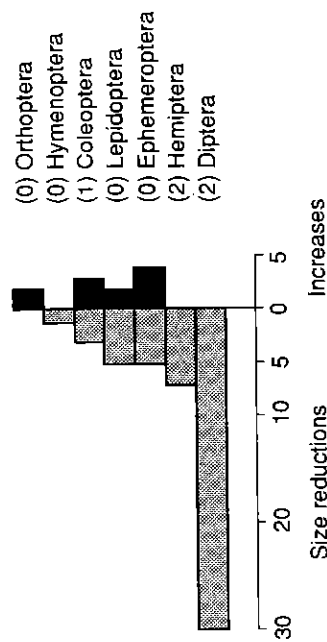
Fig. 8. Distribution of size reductions and increases in response to rearing temperature among seven insect orders (based on data in the Appendix). Numbers in parentheses represent the number of cases in which both size reductions and increases were recorded in the same study.

Table 1

Effects of temperature increase on size-at-stage in different families of three insect orders

ORDER	No. of cases with size:		
Family	reduction	increase	mixed response
COLEOPTERA			
Chrysomelidae		1	
Dermestidae		1	1
Cerambycidae		1	
Scolytidae	1		
Tenebrionidae	2		
EPHEMEROPTERA			
Ephemerellidae		1	
Caenidae		1	
Oligoneuriidae		1	
Tricorythodidae		1	
Leptophlebidae	1		
Baetidae	1		
Siphlonuridae	3		
ORTHOPTERA			
Acrididae		1	
Gryllidae		1	

4. Association with Cell Size

Laudien (1973) observed that an increased temperature can reduce cell size as well as size of the organism. The relationship between size and temperature found in most species may therefore be explained if the following two premises are true: (i) an increase in temperature causes a reduction in cell

Table 2

Significant effects of temperature increase on size-at-stage on different sexes

Sex	No. of significant size:			
	reductions	increases	mixed responses	Total
M (+ not F)	1	0	0	1
F (+ not M)	3	2	0	5
Both M + F	26	3	2	31
Total	30	5	2	37

M, males; F, females.

size; and (ii) for a given species, individuals at precisely the same stage in development contain the same or similar numbers of cells.

Consistent with the first premise are six of the seven protist examples (Adolph, 1929; Margalef, 1954; Ray, 1960) and the bacterium (Chrzanowski et al., 1988). Other studies of protists, whilst not backed up by statistical tests, are also consistent with the premise (Mučibabić, 1956; James and Read, 1957; James and Padilla, 1959; Johnson and James, 1960; Thormar, 1962; Donnan and John, 1984). Zeuthen (1964) reviewed work on *Tetrahymena pyriformis* (mainly by Thormar, 1962) showing that cells are smallest at an intermediate temperature which was the optimum for growth and division. Therefore, within the temperature limits considered in the present paper, cell size in protists and the bacterium reduced with increasing temperature.

No obvious effect of temperature was observed in cell size of the prokaryote *Salmonella typhimurium* (Schaecter et al., 1958). Like some unicellular eukaryotes, some prokaryotes exhibit increased cell sizes at temperatures which are so high that division is inhibited (Dowben and Weidenmuller, 1968).

Support for a reduction in cell size with temperature increase in multicellular animals is provided by the finding that *Drosophila* reared at lower temperature not only are heavier (Alpatov and Pearl, 1929; Eigenbrodt, 1930; Ray, 1960; Economos et al., 1982; Cavicchi et al., 1985; Masry and Robertson, 1979), but also have wings that are larger, due almost entirely to increased cell size rather than number (Alpatov, 1930; Robertson, 1959; Masry and Robertson, 1979; Cavicchi et al., 1985). However, Masry and Robertson (1979) also found that when larvae were shifted from 25°C to 29°C for a 12-hour period and then returned to complete their development at 25°C, the reduction in wing size compared with that observed at a constant 25°C was caused by either reduced cell size or reduced cell number depending on when during larval development the transfer took place. Whilst this does not negate the dual effect of temperature on cell and organism size, it does suggest that the potential exists for high temperature to

lead to the production of a smaller body by mechanisms other than a reduction in cell size.

The complexity of relationship between temperature, cell size and organism size is further illustrated by studies of other taxa. Evidence from multicellular animals and plants suggests that temperature affects the size of actively dividing cells differently from that of differentiated cells which they subsequently produce. For example, the coelenterate *Cordylophora* was larger and had larger cells in the growth zone when reared at 10°C than at 20°C, but other cells changed shape without a noticeable size change with temperature (Kinne, 1958). Cuadrado et al. (1989) described an increase in cell size with temperature increase in root meristem cells of *Allium cepa*, but observed no effect on cells of the differentiated portions of the root. Consistent with this difference between actively growing and mature cells is the apparent lack of effect of temperature on mature, fully differentiated root cells of *Zea mays* (Erickson, 1959), *Pisum* (Van't Hof and Ying, 1964), *Allium cepa* (Lopez-Saez et al., 1969) and *Helianthus* (Burholt and Van't Hof, 1971). Despite this, Burström (1956) reported that the final lengths of root cells of wheat decreased with increased temperature, though statistical tests were not performed. Moreover, Grif and Valovich (1973) are reported, by Francis and Barlow (1988), to have found no difference in meristematic cell length in roots of *Secale cereale* between 1°C and 23°C.

Overall, the idea that the effect of temperature on organism size is just a consequence of a universal effect on cell size, and that an explanation should be sought at the level of cell physiology, is not well supported by the data.

B. Possible Limitations of the Data Set

Non-significant results may be under-represented in the sample because of the following possibilities: (i) a reluctance of researchers to publish non-significant results; (ii) a reluctance to test for significant differences between individual temperatures if no overall trend appears evident; and (iii) a tendency for authors to overlook non-significant results when citing other studies that relate to their own statistically significant findings.

Even if a general relationship does exist, a figure of 100% reductions would hardly be expected given the inadequacies of the available data set. The following numbers of cases for which no values were available illustrate this: rates of differentiation, 25 (22·9%); rates of growth 81 (74·3%); and rates of mortality 80 (73·4%). In the absence of such data temperatures which, unknown to me, contravened the acceptance criteria (Section III.C) may have been included in the review. For example, cases in which small size was associated with high juvenile mortality may have been due to inadmissibly stressful temperatures (e.g. Tsitsipis, 1980).

Rank correlations are more likely to identify significant increasing or

There is thus no evidence that the increases or mixed size response to temperature resulted primarily from the choice of a small number of inappropriate size-at-stage measures.

Overall then, because the data available are so incomplete and their quality so variable, some apparent exceptions to a biological law may result from unreported weaknesses in experimental protocol or inappropriate temperature conditions. Yet a small number of detailed meticulous studies still appear to provide genuine exceptions to such a "law" (e.g. Guppy, 1969; Lamb and Gerber, 1985).

Whether or not the relationship turns out to be a universally applicable "law", rather than just a "rule" that can be demonstrated for the majority of cases (Mayr, 1956), the effect of temperature on size at a given stage of development still requires an explanation. Few have been offered hitherto. These will now be critically evaluated and new explanations will be proposed. Since the relationship is so widespread across different taxa, habitats and lifestyles, general rather than individual *ad hoc* explanations will be sought.

V. EXPLANATIONS INVOKING CONSTRAINTS ON GROWTH

A. A General Reduction in Growth

The present review is restricted to temperatures over which individual growth was observed or expected (see Fig. 2) to increase with temperature. Growth rate was actually observed to increase with temperature in 26% of cases. Despite this, it is still possible that the general trend was largely an artefact due to growth constraints at high temperature in the 74% of cases in which growth was not reported. To test this, the proportion of cases showing reductions in size at increased temperature was examined only among those studies in which growth rates were reported, and hence known to increase with temperature.

Of the 28 cases for which growth rates were known to increase, 22 (79%) showed a significant reduction in size at high temperatures, and six (21%) showed an increase—results not very different from the proportions in the whole data set. There is no evidence, therefore, that the high proportion of reductions in size at high temperature was due primarily to the inclusion of invalid studies in which growth rates were reduced at increased temperatures.

B. Von Bertalanffy's Hypothesis

Von Bertalanffy (1960) suggested that in general terms, catabolic processes were mainly of a chemical nature and would therefore have a high tempera-

decreasing trends rather than significant mixed size responses (significant increases *and* decreases between temperatures) over a range of several temperatures. Significant mixed size responses will thus be under-represented in the results.

Photoperiods were not stated in 44 cases (40·4%). Thus day length, which may affect the amount of time available for feeding or photosynthesis per day and which can provide information about the time of year, may not have been controlled in some cases. The effects of photoperiod and seasonality are discussed further in Section VI.C.

Animal studies in which the food both was unnatural and was observed to reduce growth rate below that found on natural food were excluded where possible. Yet since many studies did not indicate whether food quality was adequate, some invalid examples may have been included in the review. It is noteworthy that the mayfly *Leptophlebia intermedia* not only suffered higher juvenile mortality and slower growth on the poor diet (Section III.C), but produced larger adults at high rather than low temperatures: this is in contrast to the reduction with increasing temperature found on natural food (Sweeney et al., 1986). Other comparisons show similar effects of unnatural and poor quality food on size (Dixon et al., 1982; Galliard and Golvan, 1957).

Light energy was not demonstrated to be unlimiting in the studies of unicellular algae. Also, the effects of possible genetic adaptation to the temperature regimes were a possibility in studies in which the organism had spent several generations at the experimental temperatures.

Exceptions to the general trend may be caused by the inclusion of inappropriate measures of size-at-stage. Yet the proportions of exceptions found when indirect measures of size were used (e.g. body length, width or length of exoskeletal part) was never much greater, and often less, than when direct size measures (dry weight, live or wet weight) were made. Exceptions were also found over a wide range of developmental stages: reproductive maturity, final juvenile moult, pupa, other juvenile moult, adult, at maximum juvenile weight, average of all stages (in some unicells). Proportions of exceptions were not related to how early in the life cycle the measurements were taken. In addition, although no examples of hatchlings were included in the present analysis, the general reduction in size with increased temperature appears to hold for various fish fry hatching from eggs (reviews by Bělehrádek, 1935; Ray, 1960; Laudien, 1973). However, the size of hatchling locusts (*Schistocerca gregaria*) (as measured by hind femur length; Bernays, 1972) were significantly increased following incubation at high temperature, and effects on alligator hatchling size do not seem to show a simple trend (Deeming and Ferguson, 1988). So there is no evidence that exceptions to the general rule are particularly associated with a particular stage of development. When size and stage are considered together, the 18 exceptions comprised nine different types of size-at-stage measure.

ture coefficient. Conversely, he argued, anabolic processes ultimately depend on physical processes such as permeation and diffusion, which would likely have a low temperature coefficient. He also argued that anabolism was limited potentially by the rate of intake of substances such as respiratory gases and hence by the size of the areas through which they were absorbed. On the other hand, catabolism was proportional to body weight. Von Bertalanffy produced a growth equation which expresses the rate of growth as the difference between anabolism and catabolism:

$$dw/dt = mw^a - nw^b \qquad (1)$$

in which w is weight, t is time, and m, n, a and b are indices specific to particular combinations of genotype and environment: m, which affects anabolism, is almost constant in response to temperature, but n, which affects catabolism, increases with temperature. The value of a depends on the shape of the organism and specifically on the surface areas through which food or respiratory gases are absorbed. In the simplest case, the surface area of a spherical (say unicellular) organism will increase at a rate of 2/3 the power of body weight. In other species, such as insects, a appears to be nearer to 1 (von Bertalanffy, 1957, 1960). Von Bertalanffy asserted that if catabolism had a higher temperature coefficient (n) than did anabolism then an increase in temperature would increase growth rate and reduce final size. Yet, strictly speaking, the former cannot be true since if a rise in temperature increases catabolism more than anabolism then the rate of growth will decrease. A predicted decrease in final size does, however, follow logically from the above premises. Thus the explanation proposed by von Bertalanffy for a small final size at increased temperature does not strictly apply to the problem under investigation as defined in Section III.A.

Von Bertalanffy's argument can, however, be modified slightly to produce increased growth rates at moderately high temperatures (S. M. Wood, personal communication). If rate of anabolism increases linearly with temperature, and the rate of catabolism increases according to a power function, then growth rates may sometimes increase at first with temperature (Fig. 9). In such a case anabolism may be described algebraically as:

$$m = c + d(T - T_0) \qquad (2)$$

in which m is the same as in equation 1, c and d are constants, T is temperature and T_0 is a threshold growth temperature. Catabolism may be described as:

$$n = k(T - T_0)^i \qquad (3)$$

where k and i are constants. Assuming certain values for the parameters of
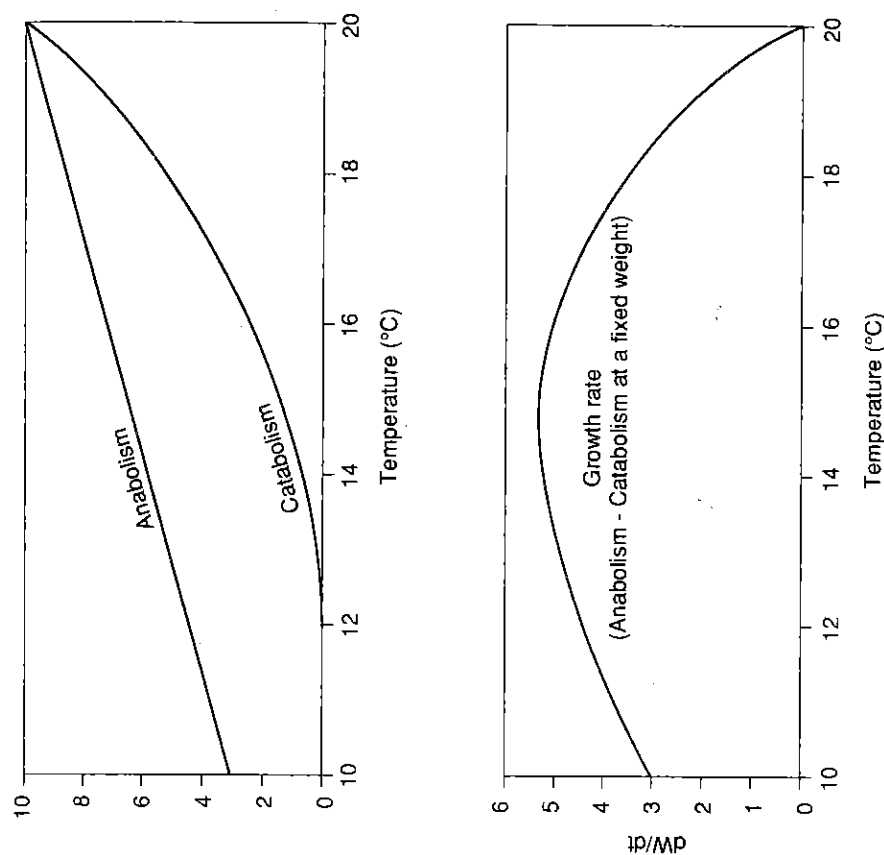
Fig. 9. Hypothetical effect of temperature on anabolism and catabolism (upper graph) based on equations (2) and (3), respectively. Anabolism (m) increases linearly with increasing temperature (T) above at threshold (10 °C) according to the equation $m = 3 + 0·7(T-10)$. Catabolism (n) increases according to the equation $n = 0·01(T-10)^3$. The lower graph shows the combined effect of these curves on growth rate (S.M. Wood, personal communication).

the equations, growth rate, which is the difference between anabolism and catabolism, may at first increase (Fig. 9).

More generally, the highly simplified growth equation (1) described by von Bertalanffy summarizes many different processes. Clearly, there are potentially many other ways in which temperature may constrain rates of growth. Thus whilst the overall effect of temperature increase may be to increase rates of both growth and differentiation, a physical or chemical constraint at high temperatures could still inhibit one activity more than the other.

However, constraints described by von Bertalanffy may be overcome if the

surfaces through which metabolites pass, the efficiency of their transport, or both (represented by a in equation (1)) are able to increase greatly at high temperatures. This still requires testing.

In conclusion, the explanation originally given by von Bertalanffy is not supported on theoretical grounds. Alternative explanations are possible, but these require testing.

C. Temperature and Plant Growth

Although plant growth rates are generally increased by increased temperature, this effect is confined mainly to early growth (van Dobben, 1962; Friend et al., 1962; Krol et al., 1984; Grace, 1988) and is due primarily to increased rates of leaf expansion rather than enhanced photosynthetic production per unit area of leaf (Monteith, 1981; Grace, 1988). Over a wide temperature range the rate of plant development increases approximately linearly with temperature (e.g. Roberts and Summerfield, 1987; Ellis et al., 1990). Consequently, increases in plant size at increased temperatures would be expected particularly at early developmental stages when leaf expansion is relatively important. This temperature sensitivity may explain some of the exceptions to the general trend found in early but not late stages of wheat and maize development (Section IV.A.2). However, no unavoidable physiological constraints on growth and development are known which might explain why the sensitivity of plant development rate to temperature prior to maturity is greater on average than is the rate of growth, thereby producing smaller mature plants. Adaptationist explanations (Section VI) which consider the adaptive significance of the relatively greater temperature sensitivity of development need also to be considered.

D. Oxygen Shortage

An oxygen shortage which limits growth at high temperature may be more likely in aquatic environments. The oxygen-carrying capacity of water is reduced as temperature is increased (Wiber, 1964) and may potentially limit growth. But if individual growth rate is still higher, on average, at increased temperature, then it must also be assumed that the oxygen shortage reduces growth rate increasingly as the size of aquatic organisms increases, so growth would slow down and cease at smaller sizes. This constraint would operate if oxygen requirements increase faster than does the rate of oxygen uptake which itself may be limited by the area through which respiratory gases pass.

Even terrestrial species may conceivably experience a shortage of oxygen at increased temperatures. Since cytoplasm and body fluids are aqueous, they will be less capable of holding onto dissolved oxygen, so more effort would

have to be directed to obtaining sufficient oxygen from the air. But since the air itself should not be particularly depleted of oxygen at increased temperatures, oxygen shortage should not be as acute as in aquatic environments. The oxygen shortage hypothesis assumes therefore that at increased temperatures, oxygen is in short supply, that (intraspecifically) large organisms are less able to meet their requirements, and that growth is affected more than is differentiation.

Sixty-eight of the 109 studies were on organisms in potentially water-saturated habitats such as ponds, streams and soil (Appendix): 61 of these showed a reduction in size with increased temperature and seven showed an increase. Potentially water-saturated habitats contained slightly but not significantly more of the reductions in body size than did terrestrial habitats (χ^2 = 0.73, $p > 0.20$). Thus, these results do not lend particular support to this oxygen-shortage hypothesis as the primary cause of size reductions. To test for the effects of oxygen shortage at increased temperatures, factorial experiments incorporating different temperatures and different oxygen concentrations (e.g. using an aquarium oxygenator) could be performed.

Again, this explanation assumes that respiratory activities and surface areas are unable to increase enough to compensate for increased oxygen requirements of large organisms at high temperature: and again, this requires testing.

E. Desiccation

In terrestrial habitats, growth may become constrained at high temperature due to desiccation. But if individual growth rate is still higher, on average, at increased temperature, then it must also be assumed that the water shortage reduces growth increasingly as organism size increases, so growth would slow down and cease at smaller sizes. If desiccation is an important part of the explanation for the general effect of temperature on size then terrestrial forms should show the effect more strongly than should aquatic ones. Of the 49 terrestrial examples in the Appendix, 37 (75·5%) showed a reduction in size with increased temperature: this is a lower proportion of the reductions than was found in the total sample. Thus there is no evidence that the main cause of size reductions at high temperature in the whole sample was the detrimental effects of desiccation on growth. Moreover, several studies of terrestrial species indicated that water was unlikely to be limiting (e.g. plants grown in nutrient solution (Brouwer et al., 1973), or said to be grown under conditions with "near optimum moisture content" (Gmelig Meyling, 1969); relative humidities controlled at levels of 80% or more (Muthukrishnan and Pandian, 1983; Wagner et al., 1987)).

In natural populations, whilst warm conditions may promote rapid growth at certain times, they may simultaneously be correlated with future drought or

oxygen shortage. This possibility will be considered in discussions of adaptive explanations (Section VI.C.1).

VI. ADAPTIVE EXPLANATIONS

A. The Nature of the Adaptation to Temperature

Adaptive explanations, which suggest *why* size should vary with temperature, can complement mechanistic explanations which suggest *how* growth and differentiation are affected by the immediate environment. Variations in life history between organisms can be produced by genetic differences and by environmentally induced differences among individuals of a given genotype. The latter phenomenon, phenotypic plasticity, is thus exhibited by organisms reared at different temperatures. Indeed, among members of a clone, it is the only source of observed variation. The set of phenotypes that a single genotype could develop if exposed to a specified range of environmental conditions is called a Norm of Reaction (Stearns and Koella, 1986). Phenotypic plasticity may allow an organism to utilize information present in prevailing environmental conditions to adjust its resource allocation in an adaptive manner between different activities (Atkinson, 1985; Atkinson and Thompson, 1987) though some of the phenotypic variation may be imposed by immediate environmental constraints. The adaptive nature of phenotypic plasticity, including attempts to model norms of reaction for age and size at maturity, have been the focus of considerable interest in recent years (Stearns and Crandall, 1984; Via and Lande, 1985; Stearns and Koella, 1986; Dodson, 1989; Stearns, 1989; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Gomulkiewicz and Kirkpatrick, 1992; Houston and McNamara, 1992; Kawecki and Stearns, 1993).

Within a species large size is often associated with high survivorship and fecundity (see Section II). But the increased sizes at reduced rearing temperatures are associated with low rates of population increase and low individual fitness, at least compared with individuals at increased temperatures which also increase rates of individual growth and differentiation (Cooper, 1965; Orcutt and Porter, 1984; Foran, 1986; Kindlmann and Dixon, 1992). This runs counter to the notion of an optimal thermal regime described by 'Sweeney and Vannote (1978) and Vannote and Sweeney (1980). In their thermal equilibrium hypothesis a thermal regime was considered optimal when an individual's weight and fecundity were maximized. In these terms there is a paradox because conditions seem to be favourable for individual growth and for fitness at high temperature, so why become small at a given developmental stage and suffer its apparently detrimental effects on fecundity and survivorship?

When trying to solve this problem, it is useful to recall that relevant selection pressures may act on different but correlated facets of the life cycle. Thus selection may operate directly not only on size at a given developmental stage, but also on the growth rate required to achieve this, and on the rate (or duration of previous stages) of development (Table 3). Size at one stage of the life cycle may also be closely correlated with sizes at other stages. For example, large offspring or dispersers may be favoured by natural selection but these sizes may also be correlated with size at maturity or, in animals, at the time of the last juvenile moult. Thus Berven (1982a) found that the large adult wood frogs occurring at high altitudes and low temperatures produced large offspring, and he hypothesized that adult size resulted indirectly from selection on offspring size in cold environments.

Possible general explanations for the rule relating temperature to size are provided by life-history theories. Those predictions which include potential likely effects of temperature are summarized in Table 3 and discussed in the following sections.

Other life-history predictions which currently lack a mechanism incorporating an effect of temperature are listed here to encourage the ingenious reader to seek mechanisms. An increase in final adult size is favoured when:

(i) the relationship between the development time and size becomes more nearly linear rather than convex (when viewed from below) (Sibly and Calow, 1986a);

(ii) the relationship between fecundity and size becomes more nearly linear rather than concave. Thus if an organism, by maturing at a large size can achieve a large increase in fecundity for a small increase in development time, then a large size would be favoured (Sibly and Calow, 1986a);

(iii) size-specific fecundity is reduced (Roff, 1981).

Two other hypotheses can be dismissed fairly promptly. Roff (1981) predicted, using a model which he applied to *Drosophila*, that an increase in rate of development would favour an increased body size. However, this hypothesis is clearly unimportant in the majority of ectothermic organisms since an increased temperature increases the rate of development yet usually reduces size at maturity. Likewise, the idea that in terrestrial habitats the effects of temperature on size are due primarily to the selective advantage of small size in desiccating conditions associated with high temperatures has no empirical support. Desiccating conditions favour large size: small individuals appear to suffer from desiccation more than large ones, at least in cricket frogs (Nevo, 1973), fruit flies (Barker and Barker, 1980), hatchling grasshoppers (Cherrill, 1987), and ants (J.H. Cushman, personal communication). This is probably due to their large surface area in relation to their volumes making them prone to losing a high proportion of their body water. It is this advantage of large size that Schoener and Janzen (1968) suggested could partly explain geo-

graphical interspecific variation in insect size. So desiccation stress at high temperature seems unable to account for the general reduction in size-at-stage in terrestrial ectotherms.

B. Temperature and Size

1. Size, Water Viscosity, and Buoyancy

The production of large individuals at low temperatures may be an adaptive response to the high viscosity and hence resistance of liquid media to movement by small organisms at these temperatures (Loosanoff, 1959). No data were found to test this hypothesis precisely. A quantitative analysis of this problem would also be useful, to help assess how important this selection pressure is likely to be. If the hypothesis is true and important there is likely to be selection pressure also to put a high proportion of resources into locomotory organs and streamlining at low temperatures. It has been speculated that this idea may explain why appendages found on species of dinoflagellates in tropical waters are longer than those on their counterparts in arctic waters (see Walsby and Reynolds, 1980). But Walsby and Reynolds (1980) also reported that no evidence for a direct effect of temperature on appendage length had been found from studies with cloned dinoflagellates in culture.

Another effect of increased size, at least among unicellular plankton, is that rates of sinking are increased (Eppley et al., 1967; Walsby and Reynolds, 1980). Also, since warm water is less dense than cold water, buoyancy will be reduced, although the importance of this needs to be ascertained (Walsby and Reynolds, 1980). Thus at high temperature, plankton may be able to offset some of the effects of reduced buoyancy caused by reduced water density (and also viscosity) by reducing their size. Even if the effect of temperature on water density is negligible, the explanation may be adapted to those unicellular algae which at low temperature cannot tolerate as high a light intensity as they can at high temperature (Morgan and Kalff, 1979; Meeson and Sweeney, 1982) though in other species no effect of temperature on size was evident (Yoder, 1979; Meeson and Sweeney, 1982). In these species, an increased size at reduced temperatures would allow the algae to sink to levels where light intensities are no longer too high. This is consistent with the effects of temperature on size of at least two species (Morgan and Kalff, 1979; Meeson and Sweeney, 1982). Also, no advantages to the pennate diatom *Phaeodactylum tricornutum* are evident from the greater sinking rate associated with large size when subjected to high temperatures (Fawley, 1984), since these gave the fastest rates of carbon fixation and cell division. Finally, since a separate explanation is still needed for terrestrial ectotherms, a more comprehensive explanation will be sought.

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Table 3

Conditions favouring changes in size-at-stage and in rate of development: potential effects of temperature

Trait	Conditions favouring increase in trait	Potential effects of temperature	Section of chapter
Size at a given stage of development	If survival, fecundity or both increase with size	Large individual plankton may be better able to: (i) move through cool water which is more viscous than is warm water; (ii) maintain a similar level of buoyancy at low as at high temperature (at high temperature, sinking rate can be increased by the relatively low density of the liquid medium; small size can help reduce sinking rate).	VI.B.1
		Risks of predation will vary with temperature: protection from this may be achieved by being big	VI.B.2
		Increased size may confer greater ability to achieve high body temperature when amount of solar radiation is low. (Conversely, small size in sunny conditions may help avoid overheating)	VI.B.3
Rate of development	High mortality associated with conditions during juvenile period	(i) Predation by ectotherms (but no endotherms) is likely to increase during an unseasonally warm period (ii) Total predation is generally higher in warm seasons (iii) Temperature increases rate of ageing (iv) High temperature may be associated with future drought (terrestrial species), oxygen shortage or habitat loss (aquatic species) (v) Rapid growth at high temperature may incur a cost	VI.C.1
	Rapid increase in population size	Fast individual growth when resources are unlimiting and temperature is high may correlate with population growth	VI.C.2
	Time constraints imposed by season or need for synchrony of developmental event	Slow-growing individuals (at low temperatures) which must reach a particular developmental stage by a particular time, will do so at the expense of size at that stage	VI.C.2 VI.C.3

But within a season, in ectotherm physiological time the amount of ectotherm predation may be relatively unaltered by temperature. The percentage juvenile mortality due to ectotherm predation thus may not differ substantially between high and low temperature since increased feeding by ectotherm predators at high temperatures may be balanced by the increased speed of passage through the juvenile period by the ectotherm prey. This argument still needs to be tested rigorously, however. Contrary to the rates of ectotherm predation, rates of predation by endotherms are likely to increase in both chronological and physiological time in conditions colder than the seasonal average: this is due partly to their increased metabolic requirements at low temperatures, and partly to the slowdown in ectotherm physiological time. So it is suggested that, in physiological time, risks of predation by endotherms are increased at low temperatures.

Examples in which large ectotherms appear to gain protection from ectotherm predation do exist (e.g. Paine, 1976), but little evidence has been found for this applying to predation by endotherms. Large cockles appear to be protected from predation by small wading birds but not from predation by oystercatchers (Seed and Brown, 1978): whether or not this represents a significant reduction in endotherm predation at large sizes is not known. There is little evidence that overall size of plants is closely related to size-selective grazing, though the size of parts, such as seeds, may be adaptations to size- and shape-specific predators (Janzen, 1971; Dodson, 1989).

Since endotherm predation appears to be relatively unimportant for many ectotherms (Zaret, 1980), this hypothesis is unlikely to be widely applicable.

But an additional argument is that increased size of predatory ectotherms caused by increased endotherm predation may favour an increase in size of their prey, thus allowing these prey to maintain their anti-predator protection. Larger fish fry are preferred less by their ectothermic predators (Miller et al., 1988) but small size provides a refuge for zooplankton experiencing mortality from size-selective predators such as fish and large insects (Zaret, 1980; Dodson, 1989). So even this further explanation is unable to account for the increase in size in planktonic species at low temperatures (e.g. Pechenik, 1984; Lonsdale and Levinton, 1985).

In conclusion, there appears to be little support for the idea that large sizes are produced at low temperatures mainly to provide protection from increased endotherm predation. However, the effect of predation risk on rate of juvenile development, and hence indirectly on size at maturity, still needs to be considered (see Section VI.C).

3. Size and Body Temperature

Two effects of size on body temperature are well recognized. First, for ectotherms absorbing solar radiation, heat transfer theory predicts that at thermal

2. Size and Predation Risk

Tests of hypotheses which predict how mortality rates affect optimal size (e.g. Williams, 1966; Wilbur and Collins, 1973; Roff, 1981; Stearns and Koella, 1986; Kozlowski and Wiegert, 1986; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Kawecki and Stearns, 1993) may be misleading if only data from laboratory studies which exclude natural predation are used.

If risk of predation varies according to environmental temperature, and if protection from predation can be gained by achieving a large size, then (all else being less important) organisms should grow faster in conditions with a high risk of predation. Conversely, if protection from predation is achieved by being small, then an organism under increased risk of predation should decrease growth rates, reproduce at a small size, or both. Chrzanowski et al. (1988) suggested that reduced cell size of planktonic bacteria at increased temperatures may reduce predation pressure which is more acute at warm times of year. This change in size might then affect the size of predators: Pace (1982) and Pace and Orcutt (1981) found that the zooplankton in Lake Oglethorpe was dominated by macroplankton in the cooler seasons, and by microplankton during the warmer seasons. To decide on the most likely selective effects of temperature-mediated predation on body size, the relationships between temperature and predation risk, and between predation risk and size need to be ascertained.

At high temperatures, predation by ectotherms, is likely to increase because of their increased energy demands, although that by endotherms may be unaltered or may even decrease due to a reduction in their energy demands. However, the ectotherm prey also feed, grow and develop faster at high temperatures. So in physiological time of the prey, rates of predation of ectotherms by endotherms may decrease. It is worth emphasizing, however, that this statement applies mainly to temperature variations away from seasonal averages. Between seasons, risks of predation are complicated by the following numerical responses of predators: (i) in temperate habitats both endotherms and ectotherms may be feeding offspring as well as themselves in the warm (breeding) season; (ii) at high latitudes, predation in summer is increased due to an influx of summer migrants and emergences from hibernation.

At low temperatures, rates of predation by ectotherms in chronological (daily) time appears generally to be reduced. Culver (1980) found that size at first reproduction in each of seven species of cladoceran declined as temperatures increased between spring and summer, and then sizes increased again in the autumn. He suggested that because small size usually provided protection from fish predation (Zaret, 1980) a rapid temperature change (or some close correlate) was used as a cue for altered predation rates by fish.

equilibrium larger organisms will have larger differences between body temperature and air temperature than will smaller organisms (Porter and Gates, 1969; Stevenson, 1985). Experimental work generally supports this theory (Willmer and Unwin, 1981). However, the second effect, in which heating and cooling of large bodies is too slow to follow the daily cycling of the thermal environment, becomes dominant for very large ectotherms. This "inertial homeothermy" (McNab and Auffenberg, 1976) reduces the range of body temperatures that they can experience. Evidence from experiments on reptiles illustrates the relatively slow rates of heating and cooling by large animals (Bartholomew and Tucker, 1964; McNab and Auffenberg, 1976). Large animals may also have a greater potential than small ones to reduce body temperature by evaporative cooling (Willmer, 1991).

Stevenson (1985), using a simple heat balance model which incorporated these two effects, calculated the relationship between body size and predicted maximum daily range of body temperature. The predicted daily body temperature excess above ambient temperature was found to increase at an increasing rate with body size up to about 0·1 kg when the effect then more or less levels off (Fig. 10). At body weights above 1 kg, the temperature excess then reduces rapidly. Thus for ectotherms below 1 kg, relatively large individuals may risk overheating in warm conditions (Willmer, 1991) but may also be better able to take advantage of limited amounts of solar radiation in less sunny conditions. This phenomenon may therefore help explain the smaller sizes at high temperature in species subject to heating from solar radiation. Yet if this is a major explanation, the increasing rate at which the temperature excess increases with body weight implies that temperature should cause the greatest reductions in size-at-stage in larger terrestrial animals weighing up to 0·1 kg.

No support for a greater reduction in live weight among larger species was found: the percentage reduction from the maximum weight over a 5°C temperature increase showed no trend with species size, except that the range of percentage weight losses was generally greater in the larger species (Fig. 11). No species weighed more than 1 kg, so effects due to inertial homeothermy could not be tested. In conclusion, the hypothesis that either a reduction in size at a given developmental stage at increased temperature is primarily to avoid overheating, or that an increased size is mainly to take advantage of limited amounts of solar radiation in less sunny conditions, has no empirical, albeit indirect support from this review. Moreover, another explanation would still be necessary for fossorial species and aquatic species which do not inhabit surface waters.
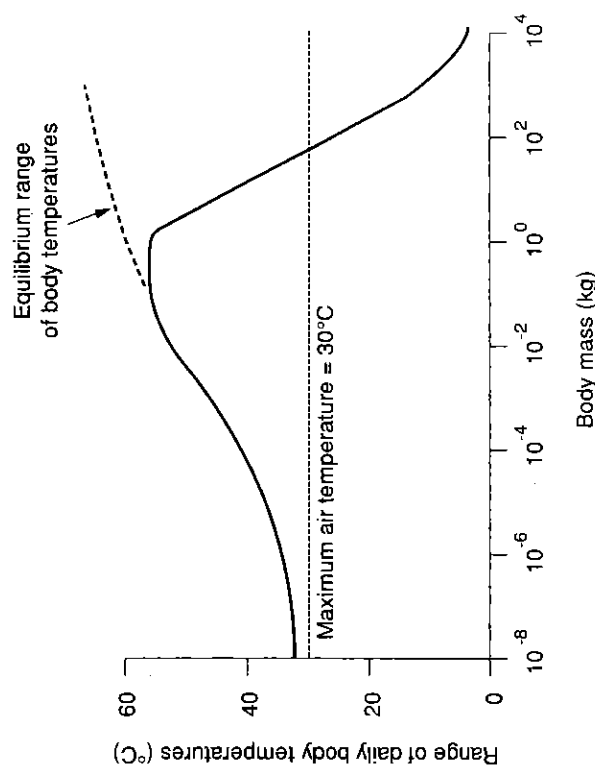

Fig. 10. The maximum daily range of available body temperature as a function of body mass, derived from the heat balance model of Stevenson (1985). For masses smaller than about 0·1 kg, the range of available body temperatures is the same as the range of body temperatures at equilibrium with environmental conditions. For masses greater than 1 kg the range of body temperatures rapidly decreases because of "inertial homeothermy".

C. Temperature and Developmental Rate

1. Mortality at Different Stages and Ages

(a) *Juvenile mortality.* For an organism with a particular growth rate, increases in size at any given stage can be achieved by slowing development and ultimately delaying maturity. If the benefits of increased size are negligible, the cost of delaying maturity is a delay in the production of offspring, which if the organism has a fixed length of life, will reduce lifetime fecundity. Under such conditions, early maturation and hence smaller size-at-maturity will be favoured. Another condition favouring early maturation is when risks of juvenile mortality are unavoidably high. Organisms should then minimize the time spent in the high-risk stage (Williams, 1966; Wilbur and Collins, 1973; Roff, 1981; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991). Only the life-history model of Stearns and Koella (1986) predicted a delayed maturation in response to an increased risk of juvenile mortality but their model included, for instance, the assumption that increased parental age and size reduces juvenile mortality: this effect, it is suggested here, is not likely to be

strong in the many ectotherms which do not provide parental care. This assumption also implies that some of the increased juvenile mortality is avoidable.

It may seem at first that when resources are unlimiting and individual growth rate is able to increase with temperature rises, mortality rates are unlikely to increase too. Yet daily risks of predation by other ectotherms will also likely increase. This increased selection pressure to mature early will need to be judged against the pressures to mature at a large size when juvenile growth is rapid (Wilbur and Collins, 1973; Rowe and Ludwig, 1991). The net effects on optimum size may not therefore be easy to predict. Further tests of effects of temperature on the ratio of individual growth to mortality, and more thorough theoretical analysis of the combined effects of individual growth and mortality risk on optimal size at maturity should help solve this problem.

It is important to recall, however, that endotherm predation risk is not likely to be any higher at unseasonally high temperatures since their energy requirements are likely to be less during warm spells. However, when the temperatures experienced are also strongly indicative of season, then in temperate latitudes expected mortality rates in physiological as well as chronological time may well be higher during the warm season due to increased *numbers* of both ectotherm and endotherm predators, as well as increased individual rates of ectotherm predation. Thus the selection pressure to mature early may be more intense during warm seasons than during unseasonal warm spells. Adaptations to season are discussed in detail in Section VI.C.3.

(b) Ageing and other future mortality. Another source of mortality may affect young adults and possibly juveniles, particularly at high, but not stressfully high, temperatures. It has been known for many decades that when resources are unlimiting, ectotherm lifespans are reduced at high temperatures (Loeb and Northrop, 1917; Shaw and Bercaw, 1962; review by Sohal, 1976). When resources are abundant, increased temperature causes rates of metabolism to increase (Sohal, 1986) and thereby brings ageing-related mortality forward in time (Fig. 12). Conditions that bring ageing and mortality risks earlier should generally favour precocious maturation. Indeed, a higher average risk of environmentally induced mortality throughout the whole of the life of an organism should also favour investment in rapid growth and
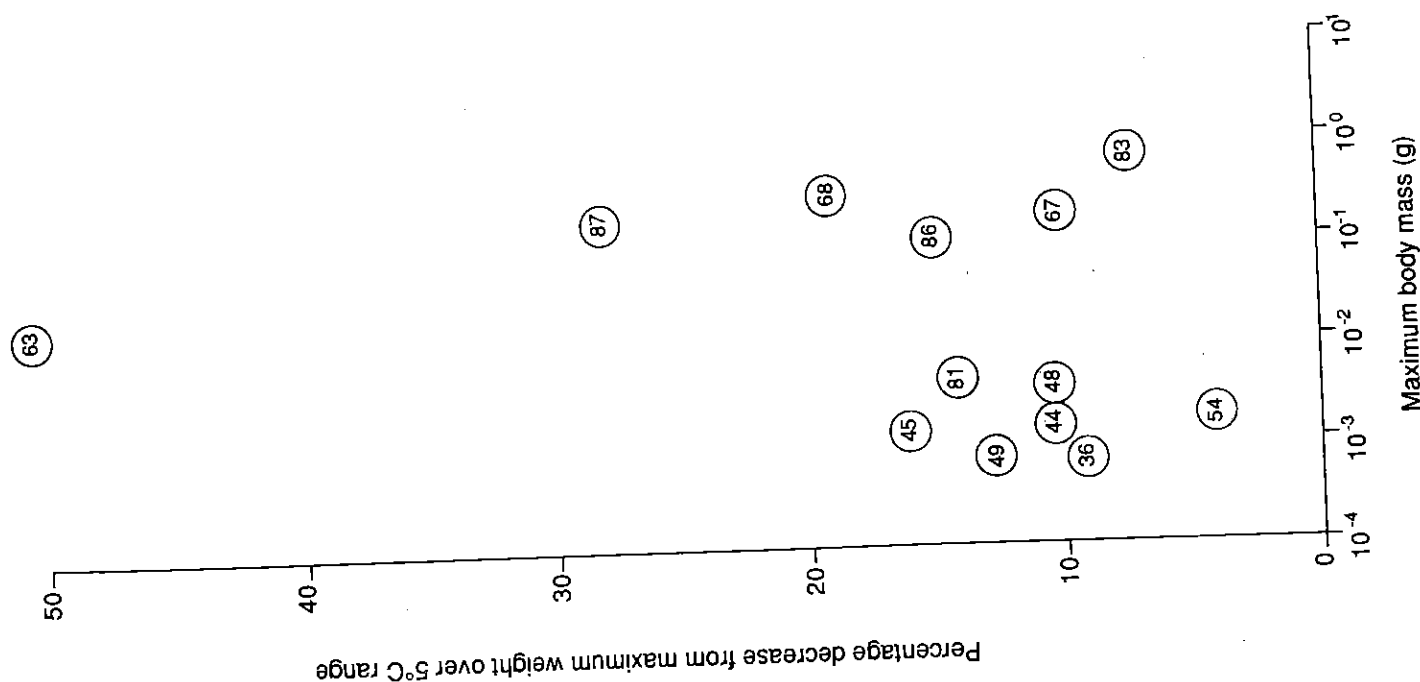

Fig. 11. The percentage decreases in weight below maximum over a 5 °C range, plotted against maximum recorded fresh weight. A consequence of the model of Stevenson (1985) is that temperature may be expected to cause greatest reductions in size in larger terrestrial animals weighing up to 0·1 kg. No such trend is observed. Numbers refer to studies listed in the Appendix.
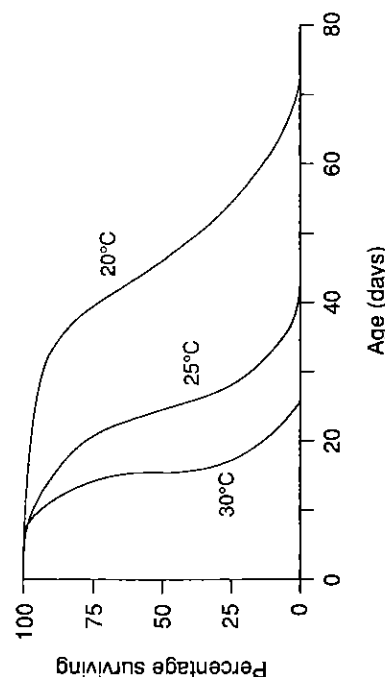
Fig. 12. Survivorship curves of male houseflies at different ambient temperatures (after Sohal, 1986).

reproduction at the expense of maintenance of somatic tissues (Kirkwood and Rose, 1991).

In addition to effects of ageing, future mortality in some terrestrial habitats might be increased following periods of high temperature if water shortage often ensues. In such a case the adaptive response would be to mature early to allow sufficient time for reproduction before the onset of a drought that may kill the organism or significantly reduce reproductive success. Since this correlation between present temperature and future drought is often likely to be very weak (e.g. in high rainfall areas) it at first appears unlikely to explain the majority of size reductions among terrestrial species. Yet even a rare drought can lead to early death and total failure of reproduction and hence local extinction, so genotypes should evolve that accelerate development rate in response to temperature, to allow at least some reproduction in drought years. According to this hypothesis, if organisms are reared under controlled experimental conditions with adequate amounts of water provided, temperature should especially accelerate developmental rate (compared with growth) in those with genotypes adapted to conditions in which a temperature rise correlates strongly with risk and intensity of future drought. This hypothesis remains to be tested.

Risks of future mortality in aquatic habitats may be increased at high temperatures if either oxygen shortage often ensues or the water body dries out. Of course neither of these effects necessarily follows periods of high temperature: exceptions to the general reduction in size at high temperature would therefore be expected under this hypothesis especially in organisms adapted to conditions in whch the correlation with these future mortality factors is very weak or non-existent. This too requires empirical testing.

An important distinction between these adaptationist hypotheses and those invoking constraints on growth due to oxygen shortage (Section V.D) or

desiccation (Section V.E) is that in the adaptationist case growth need not be constrained: instead the primary effect of rearing temperature on size-at-maturity is the provision of information about possible future conditions.

For each of these adaptationist hypotheses, the problem referred to in the discussion of juvenile mortality still remains: to what extent is the effect of increased mortality on optimal size balanced by that of increased individual growth at high temperatures?

(c) Cost of rapid growth. Another potential source of mortality at high temperatures is the cost incurred as a result of rapid growth. Sibly et al. (1985) and Sibly and Calow (1986a) provide support for the idea that organisms do not always maximize rates of growth but may optimize them. If rapid growth incurs a severe cost at particular temperatures, then selection may favour a reduction below the maximum possible. If the rate of differentiation is unaltered, the result will be a smaller size at a given developmental stage. Yet even an optimum growth rate probably would not eliminate the costs altogether. The benefits from reducing the costs of rapid growth will have to be weighed against the costs of not achieving particular sizes rapidly. Thus an optimum growth rate would be a compromise between the benefits of attaining a particular size in a given time period and the costs incurred directly from rapid growth per se. This compromise, between ends and means of achieving particular sizes in given periods of time, would be observed as a trade-off between growth rate and some other trait which affects fitness such as juvenile mortality.

Another slightly different view of optimal (cf. maximal) growth, which links it with ageing, arises if increased temperature increases the rate of molecular damage. Then more resources may need to be diverted from growth to repair (which involves molecular turnover; Calow, 1978) in order to reduce risks of mortality. Thus the costs of increased repair would be a reduction of growth below the maximum possible. If cumulative damage increases mortality risk, there would be selective pressure at high temperature not to slow down development but to bring forward the onset of reproduction. This argument thus assumes a mortality risk which can be reduced by diverting resources away from growth but maximizing the rate of development towards the stage at which offspring are produced.

(d) Adult mortality. For a growing juvenile, one particular set of risks of future mortality may be specifically associated with the adult period. Marked changes in mortality risk at adulthood will be particularly likely in organisms with complex life cycles such as amphibians and those insects that have aquatic larval and terrestrial adult phases (Rowe and Ludwig, 1991). Roff (1981) and Rowe and Ludwig (1991) predicted that an increased adult mortality would favour delayed maturity and hence large adult size. Organ-

ules, to predict mortality rates in a species of marine copepod. Their model successfully predicted the seasonal trend towards increased mortality rates in summer and a decrease in winter, whether mortality rates were assumed to be constant or dependent on size (i.e. visibility to fish predators increased at large sizes; Section VI.B.2). These data suggest that at least in one natural population, even when individual growth was accounted for, mortality rates in the warm season were apparently sufficiently increased to favour reduced adult size.

2. Temperature and Population Growth

In populations that are increasing in size, precocious reproduction should be favoured by natural selection since offspring born early will form a larger fraction of the total population than if they were born later, and hence will have a higher Darwinian fitness (Lewontin, 1965). Stearns (1976) explained this by analogy with compound interest in banking: "it will always pay to get your money in the bank as soon as possible so that the compounding interest rate will get to work most rapidly." Conversely, delayed reproduction may be favoured in populations that are decreasing in size (Charlesworth, 1980). However, this latter argument assumes that survival till the age of reproduction is the same even if reproduction is delayed, which seems improbable (Sibly and Calow, 1986b).

Within the temperature ranges in which an increase produces increased rates of growth and differentiation, it is suggested that an increased temperature should normally increase the rate of population growth, as found, for instance by Cooper (1965), Orcutt and Porter (1984) and Foran (1986). Since a temperature increase within the range normally experienced generally increases primary and secondary productivity, availability of food may not usually become limiting at high temperatures. If temperatures experienced by juveniles generally correlate positively with future population size, then especially rapid development, facilitating precocious reproduction, would be favoured by natural selection.

But this argument in favour of precocious reproduction, the "compound interest" hypothesis, does not apply to populations in which generation time is fixed (Meats, 1971). These populations lack the demographic pressure to mature especially early at high temperatures since no individual is capable of fitting in additional generations or parts of generations. Any other advantage from starting to reproduce early in the breeding season applies at low as well as high temperatures. In fact, if the length of growing season is limited, a faster growing individual of such a species should be expected to mature at a larger size, albeit still a little earlier, than one growing more slowly, thereby achieving the optimal compromise between large size and sufficient time for copious reproduction (Rowe and Ludwig, 1991).

isms which delay maturity would thus grow for a longer time into larger and hence generally more fecund adults.

This prediction appears to run counter to that for ageing-related and other future mortality, discussed earlier, in which higher adult mortality through ageing, desiccation or oxygen shortage favours earlier, not later, maturity. But the apparent discrepancy is resolved when it is realized that ageing-related and other future mortality is influenced by conditions experienced by juveniles as well as by adults, and may not therefore be delayed by spending longer in the juvenile period.

It is argued here that adult mortality (excluding ageing-related and other future mortality) is unlikely to be a major cause of the widespread reduction in size-at-stage of organisms growing at high temperatures. In many rapidly changeable and unpredictable environments, including terrestrial habitats and small water bodies, temperatures experienced during juvenile growth will be poor predictors of conditions that will be experienced by adults, especially when the adult stage is weeks or months away. Therefore the most likely explanations that involve temperature-dependent mortality are the effects of temperature on juvenile mortality and on mortality related to ageing and future risks of desiccation and oxygen shortage.

(e) Mortality evidence. The effects of mortality on size at a given developmental stage at increased temperatures cannot be predicted unless rates of individual growth are also taken into account (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991). In the absence of adequate data to examine this from studies in the Appendix, estimates of mortality in relation to development rate—a correlate of growth rate—were examined. Whilst this measure, which is equivalent to percentage juvenile mortality, is clearly inadequate for rigorous testing of the hypothesis, it will provide at least some idea of whether there is an overwhelmingly high mortality at high temperatures. In 29 cases in which juvenile mortality was measured, 23 showed no simple effect of temperature on percentage juvenile mortality so no overwhelming increase in stage-specific mortality was observed at high temperatures. Four studies did show an increase in mortality with temperature, and each of these showed reduced size-at-stage (Brust, 1967; Leffler, 1972; Economos et al., 1982; Hanazato and Yasuno, 1989). Moreover, whilst one of the two populations in which percentage juvenile mortality increased showed reduced size (Sweeney et al., 1986), the other showed an increase in individual size (Sweeney, 1978). So there is a suggestion that juvenile mortality risk in the absence of natural predators and parasites may affect individual size in some cases, but that no clear relationship is evident in most studies.

A model predicting that a higher mortality rate favours early maturation and smaller size was used by Myers and Runge (1983), together with measurements or estimations of adult size and growth and fecundity sched-

Another situation in which "compound interest" may be slight or even non-existent has been discussed recently by Houston and McNamara (1992) and Kawecki and Stearns (1993). These authors considered organisms which move freely among habitats or patches rather than remain as a largely isolated population within a habitat. They showed that the optimal life history for an individual in a given habitat or patch depends on the *overall* rate of increase (r, the Malthusian parameter) for the whole range of habitats and patches in which the organisms and their offspring occur. Thus for a highly mobile organism occurring in a patch which benefits greatly from increased temperature, the fitness benefits ("compound interest") accruing from early maturation may not be so great as would be calculated from just the local population growth rate in that patch. This would be especially true if there is free migration to and from surrounding patches, and if in these patches populations are at the same time shrinking. Not surprisingly, data are not currently available to test how important and widely applicable these ideas are. However, data on the flexibility of generation times should be easier to obtain.

Of the species listed in the Appendix, most appeared to have the capacity to alter their generation times. Under certain conditions, populations normally with a fixed number of generations a year may insert additional ones (e.g. Pullin, 1986). Therefore, only examples reported to be univoltine with an obligate diapause between generations were accepted as always having a fixed generation time. Based on the information given in the papers, only one definite example was found, the beetle *Entomoscelis americana* (Lamb and Gerber, 1985), in which adult size increased with increased temperature (see Fig. 4), and thus is consistent with the "compound interest" hypothesis.

Since environmental conditions can determine whether or not a population is univoltine (Pullin, 1986), it is possible that in some cases laboratory conditions may have indicated (falsely) conditions favouring univoltinism. This is discussed in the next section.

Whilst no generalizations can be made from the solitary example with fixed generation time, the hypothesis does need to be tested further. Recent results from work on a grasshopper with fixed generation time (K. Vosper, unpublished) also support this hypothesis.

A potential criticism of the hypothesis is: if increased (more favourable) temperatures account for small size because of advantages obtained from a shorter life cycle during periods of population growth, why aren't individuals that consume high quality food smaller than those that consume poor quality food (cf. Sweeney *et al.*, 1986)? One answer is that malnourished individuals are likely to be physically incapable of growing big because the size at which food intake fails to compensate for the costs of maintaining tissues will be less than for a well-fed individual: this would act against the prediction of the "compound interest" hypothesis. Achieving a large size should not be such a problem for (well-fed) individuals raised at low temperatures (cf. high tem-

peratures) since respiratory costs will be reduced as well as rates of food or energy uptake.

3. Seasonal Adaptation

The effects of temperature on size at a given developmental stage may also depend on the time of year. In some species of temperate latitudes, the timing of developmental events strongly correlate with photoperiod (Masaki, 1978; Tauber *et al.*, 1986; Roberts and Summerfield, 1987; Nylin *et al.*, 1989; Ellis *et al.*, 1990; Scott and Dingle, 1990)—a strong indicator of time of year. Long- and short-day photoperiods have been shown to affect the rate of development of the grasshopper *Melanoplus sanguinipes* (Scott and Dingle, 1990) and several crop plants (Ellis *et al.*, 1990) in different ways according to the temperature at which they are grown. Thus in populations with little time left before *having* to reach maturity or some other stage (e.g. before food deteriorates; Palmer, 1984), or in those which synchronize their adult emergence (e.g. some mayflies), faster juvenile growth at high temperatures could produce large rather than small adults since all would undergo the developmental event at similar times (or photoperiods).

Of only 15 species in the five studies reported to have been performed under natural rather than laboratory controlled photoperiods, ten showed a reduction in size-at-stage at high temperatures and five showed an increase. This relatively high proportion of increases (32%, compared with 11.9% in the total sample of 109; see Appendix) provides rather weak evidence that photoperiod may sometimes override the effects of temperature.

Four of the five increases and one of the reductions were shown by mayflies of temperate latitudes (Sweeney, 1978; Vannote and Sweeney, 1980) and the other increase was found in a parasitic crustacean of fish gills (Johnston and Dykeman, 1987). Six of the ten reductions were by chironomid midges, all in the same study (Rempel and Carter, 1987) and three were crop plants (Gmelig Meyling, 1969): in these cases photoperiod presumably did not override the general effects of temperature. However, further support for effects of photoperiod, though not supported by statistical tests, come from maize plants which were grown under high and moderate light levels at different constant temperatures, and sown at two different times of year (Gmelig Meyling, 1969). July-sown plants flowered at a reduced size at increased temperature and thus followed the general rule, but April-sown plants flowered at increased sizes at the higher temperature.

Another seasonal adaptation found in at least some organisms with several generations a year is the possession of specific generations adapted to particular seasons (Carvalho, 1987; Carvalho and Crisp, 1987). Thus some parts of the normal annual temperature range will be stressful to a given generation reared in the laboratory, whilst in nature relatively little stress would be

experienced since each generation is adapted to its own particular seasonal temperatures. This may explain why at temperatures below 15 °C which were nevertheless within the annual range experienced by a population of *Daphnia*, under a 16L/8D (summer) photoperiodic regime sizes at death were smaller and mortalities were higher than at higher temperatures (Orcutt and Porter, 1983). Photoperiod may also have been implicated in the production of small individual aphids at unseasonally but not exceptionally low temperatures (8·8–10·1 °C, Müller, 1966; 10–15 °C, Lamb and MacKay, 1988).

In some other studies, too (Vannote and Sweeney, 1980; Rempel and Carter, 1987), effects of temperature at natural photoperiods may have been partly caused by deviations from the ambient temperature to seasonally inappropriate levels.

VII. DEVELOPING NEW WORKING HYPOTHESES

A. Must Resources Be Unlimiting?

It is notable that the general relationship between size and temperature may be produced even when energy or other resources are not absolutely unlimiting; the general biological rule may therefore have wide application in natural populations. This is suggested by both empirical and theoretical studies. Empirical studies on legumes and grasses showed the reduction in size with increasing temperatures at intermediate and low, as well as high, light intensities (Gmelig Meyling, 1969). Theoretical work (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991) suggests that optimal size is strongly influenced by the ratio of individual growth to juvenile mortality rate. Growth rate can be higher at increased temperatures even when resources are not completely unlimiting. Therefore, the biological rule should still apply when the problem outlined in Section III.A is broadened to include organisms which have not experienced unlimited resources, so long as individual growth is still faster at increased temperature.

B. Favoured Hypotheses

Indirect evidence (Sections IV and VI.C.3) suggests that up to five of the 13 temperature increases and two of the mixed responses to temperature may be due to inadmissible temperatures (Müller, 1966; Vanotte and Sweeney, 1980; Tsitsipis, 1980; Lamb and MacKay, 1988). Lack of data may have prevented the identification of other inadmissible studies, so the proportion of significant reductions may be closer to 90%.

The relationship may conceivably be explained by constraints on growth using a modification of von Bertalanffy's hypothesis (Section V.B; Fig. 9).

But no evidence to support this modification is known to the author, and ways of overcoming constraints on growth may also exist.

The adaptationist hypotheses involving water viscosity and buoyancy (Section VI.B.1) have, of course, no explanatory power outside aquatic habitats. The review of mortality data and mechanisms suggests that increased ageing-related mortality, or mortality caused by predation, future desiccation, oxygen shortage or a cost to rapid individual growth are also possible candidates to explain the phenomenon. Further theoretical work is needed, however, to formulate clear testable hypotheses, appropriate to the wide range of life histories found in ectotherms. The "compound interest" hypothesis (Section VI.C.2), if it also incorporates time constraints on development due to season, also appears to be capable of explaining most of the reductions as well as at least one of the increases.

The reason for the very widespread occurrence of reduced size at increased temperature, may be that when the "compound interest" hypothesis does not operate, those involving high mortality may become important and *vice versa*. This is because high mortality generally favours *reduced size* but is likely to be associated with slow population growth (little or no "compound interest") whereas low mortality is more likely to be associated with increased population growth. However, before detailed and specific predictions can be made, these arguments need to be evaluated using a robust theoretical framework applicable to the vast majority of ectotherms.

In the meantime, empirical studies should identify and attempt to quantify mortality factors both in laboratory and field experiments using factorial experiments in which temperature and availability of predators and either water or oxygen are manipulated, together (where possible) with environmental or physiological information affecting developmental rates. Tests of the "compound interest" hypothesis in which population growth rates in natural populations are compared under different temperature regimes will be complicated by the variety of rates found in patchy environments (Kawecki and Stearns, 1993). However, if this is the primary cause of size reductions, exceptions to the general rule should be found in populations in which the generation time is fixed or when temperature is known not to be correlated with population increase.

VIII. TEMPERATURE AND SIZE IN NATURAL AND MANAGED POPULATIONS

Other environmental influences on organism size, besides temperature, include competition, water balance, photoperiod, and resource abundance and quality (Schoener and Janzen, 1968; Palmer, 1984; Honěk, 1986).

Most of the changes in size between seasons and between years will be ontogenetic responses to environmental change. Genetic variation will only

temperatures favours larger size at maturity (Rowe and Ludwig, 1991). Moreover, in at least one of these species, individuals are also larger when they experience higher average daily temperatures (K. Vosper, unpublished).

The effect of temperature on size can have considerable economic importance. The yield of cereals is positively correlated with the size of the plant, and annual yields of wheat (in tonnes ha^{-1}) between 1963 and 1978 in the east Midlands, England, were increased by up to 25% in the year with the coolest growing period compared with that with the warmest (Monteith, 1981). Mean temperature from May to July explained 38% of the annual variation in yield. Monteith described how the rate of development of wheat is also faster in warm years, and went on to argue that the effect on size was not due to dry conditions in such years.

The same response was demonstrated for the whole of England; and a similar effect has been found for barley yields in the east Midlands (Monteith, 1981) and for wheat yields in the United States (Bryson, 1978). In the latter, an average drop of 1 °C below normal during the month of July was shown to increase income from wheat in the United States by \$92M (1978 prices) due to increased yield.

However, if the "compound interest" hypothesis distinguishes between those with and without the capacity for flexible generation time, why aren't these annual crops exceptions to the usual trend? An answer is that under certain conditions barley can grow as a perennial and wheat can be occasionally biennial (Clapham et al., 1987), so they may have the capacity to alter generation time but are simply harvested before this potential is demonstrated. Another explanation is that crop development may be especially sensitive to temperature because of an historical (evolutionary) association between increased temperature and subsequent drought (Section VI.C.1).

B. Altitudinal Variation: A Well Studied Example

A particularly well studied example of altitudinal variation is provided by Berven (1982b) who separated environmental from genetic differences, and investigated temperature effects experimentally. Reciprocal transplantation experiments demonstrated that 73% of the altitudinal variation observed in the size of wood frogs at metamorphic climax could be explained by environmental rather than genetic differences. Results from laboratory experiments suggested that most of this was probably due to temperature differences (see Fig. 3; Berven, 1982b), producing large adults in the cool mountain sites.

IX. CONCLUSIONS

The conclusion of Ray (1960) is reaffirmed and given greater precision: in the vast majority of ectotherms (or poikilotherms) an increase in environmental

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be important between populations or temporally within populations evolving very rapidly (e.g. Carvalho, 1987; Carvalho and Crisp, 1987). For this reason geographical variation in size will not be discussed in this section except where genetic effects have been accounted for and effects of environmental rearing temperature investigated experimentally.

A. Temporal Variation

If temperature variation during the year is more important than that of other environmental variables, then seasonal changes in size should correlate strongly and negatively with temperature experienced during growth. Whilst size of emerging adults often decreases during a period of increasing temperatures (examples in Sweeney and Vannote, 1978; Atkinson and Begon, 1988) this result can also be explained by within-cohort competition (Atkinson and Begon, 1988).

Reductions in size between seasons, correlating with increased temperatures, have been found within populations of: copepods (Bogorov, 1934; Deevey, 1960; McLaren, 1963; Elbourn, 1966; Smith and Lane, 1987); cladocerans (Culver, 1980); amphipods (Nelson, 1980); dipterans (Mer, 1937; Golightly and Lloyd, 1939; Day et al., 1990); and mayflies (Macan, 1957; Elliott, 1967). These seasonal changes were sometimes substantial. For instance, weights of some aquatic insects may be reduced 50% in the summer relative to other seasons (Sweeney and Vannote, 1978).

However, counter-examples are known. First, Fahy (1973) found that the lengths of final-instar Baetis rhodani were greater in the winter-emerging than the summer generation in a subterranean isothermic stream as well as in one in which temperature fluctuated. And second, in two studies of chrysomelid beetles, adults were larger after a warm period of larval growth than after a cool one (Palmer, 1984; Sims et al., 1984). Moreover, in the laboratory, temperature was found to have no significant effect on size at adult emergence in these species. Deteriorating food quality best explained the size reduction in the field in one of these (Palmer, 1984).

Despite these exceptions and qualifications, the weight of evidence is consistent with the idea that variation in temperature is usually a major determinant of seasonal changes in size at a given life-cycle stage.

In annual species, temperature may influence differences in size between years. However, adult female hind femur length (a correlate of body weight) of each of two species of grasshopper were not shorter, but significantly (between 8 and 18%) longer in a warm year compared with a cool one (Atkinson and Begon, 1988). But these grasshoppers are univoltine with an obligate diapause only broken after cold winter temperatures have been experienced (Cherrill and Begon, 1989), so no gains in "compound interest" can be achieved from maturing especially early, and the faster growth at high

temperature which increases rates of growth and differentiation reduces size at a given stage of development. If conditions are otherwise controlled, this may well be a near-universal relationship, and most apparent exceptions may result from unreported weaknesses in experimental protocol or inadmissible temperature conditions. It would be useful, therefore, to repeat the experiments on these taxa but taking especial care to measure growth and mortality rates, and ensuring that controlled environmental conditions are maintained. Yet several apparently meticulous studies still appear to contradict the "law" (e.g. Lamb and Gerber, 1985).

When a single relationship applies to many different taxa from different habitats and with different trophic status, a single explanation would normally be sought. Yet authors have often proposed explanations, or used supporting evidence, specific to a given species or taxon.

In its search for one explanation or a very few wide-ranging ones, the present paper has highlighted the following promising areas which require further study:

(i) the effects of temperature on size when amounts of either supplementary water (for terrestrial species) or supplementary oxygen (aquatic species) are varied. This would investigate the effects of potential constraints on growth at high temperatures and could be combined with studies of anabolic and catabolic rates, the surface areas of organs responsible for the uptake of respiratory gases and nutrients from the environment, and the efficiency of their transport to the tissues;

(ii) the extent to which the relationship between temperature and size applies to populations in which generation time is fixed or in which temperature is not positively correlated with rate of population increases;

(iii) the effects of temperature on individual growth rates, size-at-stage and various mortality factors. Mortality at increased temperatures may be related to seasonal increases in predation, to ageing, to future desiccation (terrestrial species) or oxygen shortage (species in aquatic and water-saturated habitats), and to costs of rapid growth;

(iv) the use of seasonal cues to control relative rates of growth and differentiation.

A hypothesis has been proposed (Section VI.C.2) based on the advantages of shortening the life cycle when conditions are favourable for population growth: opposite predictions can be made depending on whether or not there is scope for variation in generation time between individuals in a population.

The effect of temperature experienced during a period of growth appears to be particularly important in explaining seasonal and between-year differences in size, including the economically important differences between years in the yields of crops harvested at maturity.

Knowledge of how and why temperature influences size-at-stage in so many species should help provide a universal biological basis for the production of predictive quantitative models of size-at-stage, especially and perhaps first of all in aquaculture, agriculture, and other closely controlled environments in which energy and nutrients are not usually limiting. But given the considerable and wide-ranging ecological importance of organism size, and the variability in both weather and climate, knowledge of this biological rule, and possible law, should prove valuable to ecologists in many different fields.

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REFERENCES

Abdullahi, B.A. and Laybourn-Parry, J. (1985). The effect of temperature on size and development in three species of benthic copepod. Oecologia 67, 295–297.

Adolph, E.F. (1929). The regulation of adult body size in the protozoan Colpoda. J. Exp. Zool. 53, 269–311.

Akey, D.H., Potter, H.W. and Jones, R.H. (1978). Effects of rearing temperature and larval density on longevity, size, and fecundity in the biting gnat Culicoides variipennis. Ann. Entomol. Soc. Am. 71, 411–418.

Alpatov, W.W. (1930). Phenotypical variation in body and cell size of Drosophila melanogaster. Biol. Bull. 58, 85–103.

Alpatov, W.W. and Pearl, R. (1929). Experimental studies on the duration of life. XII. Influence of temperature during the larval period and adult life on the duration of life of the imago of Drosophila melanogaster. Am. Nat. 63, 37–63.

Allsopp, P.G. (1981). Development, longevity and fecundity of the false wireworms Pterohelaeus darlingensis and P. alternatus (Coleoptera: Tenebrionidae) I. Effect of constant temperature. Aust. J. Zool. 29, 605–619.

Atkinson, D. (1985). Information, non-genetic constraints, and the testing of theories of life-history variation. In: Behavioural Ecology (Ed. by R.M. Sibly and R.S. Smith), pp. 99–104. Blackwell Scientific Publications, Oxford.

Atkinson, D. and Begon, M. (1988). Adult size variation in two co-occurring grasshopper species in a sand dune habitat. J. Anim. Ecol. 57, 185–200.

Atkinson, D. and Thompson, D.B.A. (1987). Constraint and restraint in breeding birds. Wader Study Group Bull. 49, 18–19.

Baker, J.E. (1983). Temperature regulation of larval size and development in Attagenus megatoma (Coleoptera: Dermestidae). Ann. Entomol. Soc. Am. 76, 752–756.

Barker, J.F. and Barker, A. (1980). The relation between body size and resistance to desiccation in two species of Zaprionus (Drosophilidae). Ecol. Entomol. 5, 309–314.

Bartholomew, G.A. and Tucker, V.A. (1964). Size, body temperature, thermal conductance, oxygen consumption and heart rate in Australian varanid lizards. *Physiological Zoology* **37**, 341–354.

Bayne, B.L. (1965). Growth and delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia* **2**, 1–47.

Beckwith, R.C. (1982). Effects of constant laboratory temperatures on the Douglas-Fir tussock moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* **11**, 1159–1163.

Bĕlehrádek, J. (1935). *Temperature and Living Matter. Protoplasma Monograph 8.* Borntraeger, Berlin.

Bellinger, R.G. and Pienkowski, R.L. (1987). Developmental polymorphism in the red-legged grasshopper *Melanoplus femurrubrum* (De Geer) (Orthoptera: Acrididae). *Environ. Entomol.* **16**, 120–125.

Bergmann, C. (1847). Ueber die Verhaeltnisse der Waermeoekonomie der Thiere zu ihrer Groesse. *Goett. Stud.* **1**, 595–708.

Bernays, E.A. (1972). Some factors affecting size in first-instar larvae of *Schistocerca gregaria* (Forskal). *Acrida* **1**, 189–195.

Berven, K.A. (1982a). The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution* **36**, 962–983.

Berven, K.A. (1982b). The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. II. An experimental analysis of larval development. *Oecologia* **52**, 360–369.

Berven, K.A. and Gill, D.E. (1983). Interpreting geographic variation in life-history traits. *Am. Zool.* **23**, 85–97.

Bogorov, B.G. (1934). Seasonal changes in biomass of *Calanus finmarchicus* in the Plymouth area in 1930. *J. Marine Biol. Assoc., UK* **19**, 585–612.

Brouwer, R., Kleinendorst, A and Locher, J. Th. (1973). Growth responses of maize plants to temperature. In: *Plant Responses to Climatic Factors* (Ed. by R.O. Slatyer), pp. 169–174. UNESCO, Paris.

Brust, R.A. (1967). Weight and development time of different stadia of mosquitoes reared at various constant temperatures. *Can. Entomol.* **99**, 986–993.

Bryson, R.A. (1978). The cultural, economic and climate records. In: *Climate Change and Variability* (Ed. by A.B. Pittock), pp. 316–327. Cambridge University Press, Cambridge.

Burges, H.D. and Cammell, M.E. (1964). Effect of temperature and humidity on *Trogoderma anthrenoides* (Sharp) (Coleoptera Dermestidae) and comparisons with related species. *Bull. Entomol. Res.* **55**, 313–325.

Burholt, D.R. and Van't Hof, J. (1971). Quantitative thermal induced changes in growth and cell population kinetics of *Helianthus* roots. *Am. J. Bot.* **58**, 386–393.

Burström, H. (1956). Temperature and root cell elongation. *Physiologia Plantarum* **9**, 682–692.

Calder, W.A. III. (1984). *Size, Function and Life History.* Harvard University Press, Cambridge, Massachussets.

Calow, P. (1973). On the regulatory nature of individual growth: some observations from freshwater snails. *J. Zool.* **170**, 415–428.

Calow, P. (1977). Ecology, evolution and energetics. *Adv. Ecol. Res.* **10**, 1–62.

Calow, P. (1978). The Ageing Process. In: *Life Cycles*, p. 120. Chapman & Hall, London.

Carvalho, G.R. (1987). The clonal ecology of *Daphnia magna* (Crustacea: Cladocera). II. Thermal differentiation among seasonal clones. *J. Anim. Ecol.* **56**, 469–478.

Carvalho, G.R. and Crisp, D.J. (1987). The clonal ecology of *Daphnia magna* (Crus-

tacea: Cladocera). I. Temporal changes in the clonal structure of a natural population. *J. Anim. Ecol.* **56**, 453–468.

Cavicchi, S., Guerra, D., Giorgi, G. and Pezzoli, C. (1985). Temperature-related divergence in experimental populations of *Drosophila melanogaster*. I. Genetic and developmental basis of wing size and shape variation. *Genetics* **109**, 665–689.

Charlesworth, B. (1980). *Evolution in Age-structured Populations.* Cambridge University Press, Cambridge.

Cherrill, A.J. (1987). *The Development and Survival of the Eggs and Early Instars of the Grasshopper* Chorthippus brunneus *(Thunberg) in North West England.* Unpublished PhD thesis, University of Liverpool.

Cherrill, A.J. and Begon, M. (1989). Timing of life cycles in a seasonal environment: the temperature-dependence of embryogenesis and diapause in a grasshopper (*Chorthippus brunneus* Thunberg). *Oecologia* **78**, 237–241.

Chrzanowski, T.H., Crotty, R.D. & Hubbard, G.J. (1988). Seasonal variation in cell volume of epilimnetic bacteria. *Microbial Ecol.* **16**, 155–163.

Clapham, A.R., Tutin, T.G. and Moore, D.M. (1987). *Flora of the British Isles*, 3rd edn. Cambridge University Press, Cambridge.

Coker, R.E. (1933). Influence of temperature on size of freshwater copepods (*Cyclops*) *Int. Rev. ges. Hydrobiol. Hydrographie* **29**, 406–436.

Conover, W.J. (1980). *Practical Nonparametric Statistics.* John Wiley, New York.

Cooper, W.E. (1965). Dynamics and production of a natural population of a freshwater amphipod, *Hyalella azteca. Ecol. Monogr.* **35**, 377–394.

Cuadrado, A., Navarrete, M.H. and Canovas, J.L. (1989). Cell size of proliferating plant cells increases with temperature: implications in the control of cell division. *Exp. Cell Res.* **185**, 277–282.

Culver, D. (1980). Seasonal variation in sizes at birth and at first reproduction in Cladocera. In: *Evolution and Ecology of Zooplankton Communities* (Ed. by W.C. Kerfoot), pp. 358–366. University of New England, Hanover.

David, J. and Clavel, M-F. (1967). Influence de la température subie au cours du développement sur divers caractères biométriques des adultes de *Drosophila melanogaster* Meigen. *J. Insect Physiol.* **13**, 717–729.

Day, J.F., Ramsey, A.M. and Shang, J-T. (1990). Environmentally mediated seasonal variation in mosquito body size. *Environ. Entomol.* **19**, 469–473.

Deeming, D.C. & Ferguson, M.W.J. (1988). Environmental regulation of sex determination in reptiles. *Philos. Trans. R. Soc. Lond. B* **322**, 19–39.

Deevey, G.B. (1960). Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham Oceanogr. Coll.* **17**, 54–86.

Dingle, H., Blakley, N.R. and Miller, E.R. (1980). Variation in body size and flight performance in milkweed bugs (*Oncopeltus*). *Evolution* **34**, 371–385.

Dixon, A.F.G., Chambers, R.J. and Dharma, T.R. (1982). Factors affecting size in aphids with particular reference to the black bean aphid, *Aphis fabae. Entomol. Exp. Appl.* **32**, 123–128.

Dodson, S. (1989). Predator-induced reaction norms. *Bioscience* **39**, 447–452.

Donna, L. and John, P.C.L. (1984). Timer and sizer controls in the cycles of *Chlamydomonas* and *Chlorella*. In: *The Microbial Cell Cycle* (Ed. by P. Nurse and E. Streiblova), pp. 231–251. CRC Press, Boca Raton, Florida.

Dowben, R.M. and Weidenmuller, R. (1968). Adaptation of mesophilic bacteria to growth at elevated temperatures. *Biochim. Biophys. Acta* **158**, 255–261.

Druger, M. (1962). Selection and body size in *Drosophila pseudoobscura* at different temperatures. *Genetics* **47**, 209–222.

Economos, A.C., Lints, C.V. and Lints, F.A. (1982). On the mechanisms of the effects of larval density and temperature on *Drosophila* development. In: *Advances in Genetics, Development and Evolution of Drosophila* (Ed. by S. Lakovaara), pp. 149–164. Plenum Press, New York.

Eigenbrodt, H.J. (1930). The somatic effects of temperature on a homozygous race of *Drosophila. Physiol. Zool.* **3**, 392–411.

Elbourn, C.A. (1966). The life-cycle of *Cyclops strenuus strenuus* Fischer in a small pond. *J. Anim. Ecol.* **35**, 333–347.

Elliott, J.M. (1967). The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. *J. Anim. Ecol.* **36**, 344–362.

Ellis, R.H., Hadley, P., Roberts, E.H. and Summerfield, R.J. (1990). Quantitative relations between temperature and crop development and growth. In: *Climatic Change and Plant Genetic Resources* (Ed. by M.T. Jackson, B.V. Ford-Lloyd and M.L. Parry), pp. 85–115. Belhaven Press, London.

Eppley, R.W., Holmes, R.W. and Strickland, J.D.H. (1967). Sinking rates of marine phytoplankton measured in a fluorometer. *J. Exp. Marine Biol. Ecol.* **1**, 191–208.

Erickson, R.O. (1959). Integration of plant growth processes. *Am. Nat.* **93**, 225–235.

Fahy, E. (1973). Observations on the growth of Ephemeroptera in fluctuating and constant temperature conditions. *Proc. R. Irish Acad., Sect. B* **73**, 133–149.

Fawley, N. (1984). Effects of light intensity and temperature interactions on growth characteristics of *Phaeodactylum tricornutum* (Bacillariophyceae). *J. Phycol.* **20**, 67–72.

Foran, J.A. (1986). A comparison of life history features of a temperate and a subtropical *Daphnia* species. *Oikos* **46**, 185–193.

Francis, D. and Barlow, P.W. (1988). Temperature and the cell cycle. In: *Plants and Temperature* (Ed. by S.P. Long and F.I. Woodward). pp. 181–201. Company of Biologists, Cambridge.

Friend, D.J.C., Helson, V.A. and Fisher, J.E. (1962). The rate of dry weight accumulation in Marquis wheat as affected by temperature and light intensity. *Can. J. Bot.* **40**, 939–955.

Galford, J.R. (1974). Some physiological effects of temperature on artificially reared oak borers. *J. Econ. Entomol.* **67**, 709–710.

Galliard, H. and Golvan, Y.J. (1957). Influence de certains facteurs nutritionels et hormonaux, a des températures variables, sur la croissance des larves d'*Aedes (S.) aegypti, Aedes (S.) albopictus, et Anopheles (M.) stephensi. Ann. Parasitol. Hum. Comp.* **32**, 563–579.

Gates, D.M. (1980). *Biophysical Ecology*. Springer, New York.

Gmelig Meyling, H.D. (1969). Effect of light energy in relation to temperature on the rate of development and growth of some agricultural crops. Report 403 of IBS. In: *Annual Report of IBS, 1969*, Wageningen.

Golightly, W.H. and Lloyd, L.I. (1939). Insect size and temperature. *Nature* **144**, 155–156.

Gomulkiewicz, R. and Kirkpatrick, M. (1992). Quantitative genetics and the evolution of reaction norms. *Evolution* **46**, 390–411.

Grace, J. (1988). Temperature as a determinant of plant productivity. In: *Plants and Temperature* (Ed. by S.P. Long and F.I. Woodward), pp. 91–107. Company of Biologists, Cambridge.

Grif, V.G. and Valovich, E.M. (1973). Effects of positive low temperatures on cell growth and division in seed germination. *Tsitologiya* **15**, 1362–1369. (In Russian.)

Guppy, J.C. (1969). Some effects of temperature on the immature stages of the

armyworm *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), under controlled conditions. *Can. Entomol.* **101**, 1320–1327.

Hanazato, T. and Yasuno, M. (1989). Effect of temperature in laboratory studies on growth of *Chaoborus flavicans* (Diptera, Chaoboridae). *Archiv. Hydrobiol.* **114**, 497–504.

Hardacre, A.K. and Eagles, H.A. (1986). Comparative temperature response of Corn Belt Dent and Corn Belt Dent × Pool 5 maize hybrids. *Crop Sci.* **26**, 1009–1012.

Hardacre, A.K. and Turnbull, H.L. (1986). The growth and development of maize at five temperatures. *Ann. Bot.* **58**, 779–788.

Harkey, G.A. and Semlitsch, R.D. (1988). Effects of temperature on growth, development and colour polymorphism in the ornate chorus frog *Pseudacris ornata. Copeia* (4) 1001–1007.

Honěk, A. (1986). Body size and fecundity in natural populations of *Pyrrhocoris apterus* L. (Heteroptera, Pyrrhocorida). *Zool. Jahrb. Abt. Syst.* **113**, 125–140.

Houston, A.I. and McNamara, J.M. (1992). Phenotypic plasticity as a state-dependent life-history decision. *Evol. Ecol.* **6**, 243–253.

Huey, R.B. and Kingsolver, J.G. (1980). Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* **4**, 131–135.

Hunter, R.B., Tollenaar, M. and Breuer, C.M. (1977). Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. *Can. J. Plant Sci.* **57**, 1127–1133.

Imai, T. (1937a). Influence of temperature on the growth of *Drosophila melanogaster. Sci. Rep. Tohoku Imp. Univ.* **11**, 403–417.

Imai, T. (1937b). The larval shell growth of *Lymnaea japonica* Jay. In special reference to the influence on temperature. *Sci. Rep. Tohoku Imp. Univ.* **11**, 419–432.

James, T.W. and Padilla, G.M. (1959). Physiological and size changes in protozoan cells in response to incubation temperatures. In: *Proceedings of the First National Biophysics Conference* (Ed. by H. Quastler and H.J. Morowitz), pp. 694–700. Yale University Press, New Haven, CT.

James, T.W. and Read, C.P. (1957). The effect of incubation temperature on the cell size of *Tetrahymena pyriformis. Exp. Cell Res.* **13**, 510–516.

Janzen, D.H. (1971). Seed predation by animals. *Ann. Rev. Ecol. Syst.* **2**, 465–492.

Johns, D.M. (1981). Physiological studies on *Cancer irroratus* larvae. I. Effects of temperature and salinity on survival, development rate and size. *Marine Ecol. Prog. Ser.* **5**, 75–83.

Johnson, B.F. and James, T.W. (1960). Alteration of cellular constituents by incubation temperature. *Exp. Cell Res.* **20**, 66–70.

Johnston, C.E. and Dykeman, D. (1987). Observations on body proportions and egg production in the female parasitic copepod (*Salmincola salmoneus*) from the gills of Atlantic salmon (*Salmo salar*) kelts exposed to different temperatures and photoperiods. *Can. J. Zool.* **65**, 415–419.

Johnston, N.T. and Northcote, T.G. (1989). Life-history variation in *Neomysis mercedis* Holmes (Crustacea, Mysidacea) in the Fraser River estuary, British Columbia. *Can. J. Zool.* **67**, 363–372.

Jones, R.E., Hart, J.R. and Bull, G.D. (1982). Temperature, size and egg production in the cabbage butterfly *Pieris rapae* L. *Aust. J. Zool.* **30**, 223–232.

Kawecki, T.J. and Stearns, S.C. (1993). The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. *Evol. Ecol.* **7**, 155–174.

Kindlmann, P. and Dixon, A.F.G. (1992). Optimum body size: effects of food quality

and temperature when reproductive growth rate is restricted, with examples from aphids. *J. Evol. Biol.* **5**, 677–690.

Kinne, O. (1958). Über die Reaktion erbgleichen Coelenteratengewebes auf verschiedene Aszalzgehalts- und Temperaturbedingungen. II. Mitteilung über den Einfluß des Salzgehaltes auf Wachstum und Entwicklung mariner, brackischer und limnischer Organismen. *Zool. Jahrb. Abt. Allgem. Zool. Physiol. Tiere* **67**, 407–486.

Kirkwood, T.B.L. and Rose, M.R. (1991). Evolution of senescence: late survival sacrificed for reproduction. *Philos. Trans. R. Soc. Lond. B* **332**, 15–24.

Kozlowski, J. and Wiegert, R.G. (1986). Optimal allocation of energy to growth and reproduction. *Theor. Pop. Biol.* **29**, 16–37.

Krol, M., Griffith, M. and Huner, N.P.S. (1984). An appropriate physiological control for environmental temperature studies: comparative growth kinetics of winter rye. *Can. J. Bot.* **62**, 1062–1068.

Lamb, R.J. and Gerber, G.H. (1985). Effects of temperature on the development, growth, and survival of larvae and pupae of a north-temperate chysomelid beetle. *Oecologia (Berl.)* **67**, 8–18.

Lamb, R.J. and MacKay, P.A. (1988). Effects of temperature on developmental rate and adult weight of Australian populations of *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae). *Mem. Entomol. Soc. Can.* **146**, 49–56.

Lamb, R.J., MacKay, P.A. and Gerber, G.H. (1987). Are development and growth of pea aphids, *Acyrthosiphon pisum*, in North America adapted to local temperatures? *Oecologia (Berl.)* **72**, 170–177.

Larsen, K.J., Madden, L.V. and Nault, L.R. (1990). Effect of temperature and host plant on the development of the blackfaced leafhopper. *Entomol. Exp. Appl.* **55**, 285–294.

Laudien, H. (1973). Changing reaction systems. In: *Temperature and Life* (Ed. by H. Precht, J. Christophersen, J. Hensel and W. Larcher), pp. 355–399. Springer-Verlag, Berlin.

Laybourn-Parry, J., Abdullahi, B.A. and Tinson, S.V. (1988). Temperature-dependent energy partitioning in the benthic copepods *Acanthocyclops viridis* and *Macrocyclops albidus*. *Can. J. Zool.* **66**, 2709–2714.

Lebedeva, L.I. and Gerasimova, T.N. (1985). Peculiarities of *Philodina rosleoa* (Ehrbg.) (Rotatoria Bdelloida). Growth and reproduction under various temperature conditions. *Int. Rev. Ges. Hydrobiol.* **70**, 509–525.

Leffler, C.W. (1972). Some effects of temperature on growth and metabolic rate of juvenile crabs, *Callinectes sapidus* in the laboratory. *Marine Biol.* **14**, 104–110.

Lewontin, R.C. (1965). Selection for colonizing ability. In: *The Genetics of Colonizing Species* (Ed. by H.G. Baker and G.L. Stebbings), pp. 77–91. Academic Press, New York.

Lints, F.A. and Lints, C.V. (1971). Influence of pre-imaginal environment on fecundity and ageing in *Drosophila melanogaster* hybrids, II. Pre-imaginal temperature. *Exp. Gerontol.* **6**, 417–426.

Lock, A.R. and McLaren, I.A. (1970). The effect of varying and constant temperature on the size of a marine copepod. *Limnol. Oceanogr.* **15**, 638–640.

Loeb, J. and Northrop, J.H. (1917). On the influence of food and temperature on the duration of life. *J. Biol. Chem.* **32**, 103–121.

Lonsdale, D.J. and Levinton, J.S. (1985). Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology* **66**, 1397–1407.

Loosanoff, V.L. (1959). The size and shape of metamorphosing larvae of *Venus (Mercenaria) mercenaria* grown at different temperatures. *Biol. Bull.* **117**, 308–318.

Lopez-Saez, J.F., Gonzalez-Bernaldez, F., Gonzales-Fernandez, A. and Garcia

Ferrero, G. (1969). Effect of temperature and oxygen tension on root growth, cell cycle and cell elongation. *Protoplasma* **67**, 213–221.

Ludwig, D. and Rowe, L. (1990). Life history strategies for energy gain and predator avoidance under time constraints. *Am. Nat.* **135**, 686–707.

Macan, T.T. (1957). The life histories and migrations of the Ephemeroptera in a stony stream. *Trans. Soc. Br. Entomol.* **12**, 129–156.

Margalef, R. (1954). Modifications induced by different temperatures on the cells of *Scenedesmus obliquus* (Chlorophyceae). *Hydrobiologia* **6**, 83–94.

Marian, M.P. and Pandian, T.J. (1985). Effect of temperature on development, growth and bioenergetics of the bullfrog *Rana tigrina*. *J. Thermal Biol.* **10**, 157–162.

Marks, E.N. (1954). A review of the *Aedes scutellaris* subgroup with a study of variation in *Aedes pseudoscutellaris* (Theo.). *Bull. Br. Mus. (Nat. Hist.) Entomol.* **3**, 349–414.

Masaki, S. (1978). Seasons and latitudinal adaptations in the life cycles of crickets. In: *Evolution of Insect Migration and Diapause* (Ed. by H. Dingle), pp. 72–100. Springer-Verlag, Berlin.

Masry, A.M. and Robertson, F.W. (1979). Cell size and number in the *Drosophila* wing. III. The influence of temperature differences during development. *Egypt. J. Genet. Cytol.* **8**, 71–79.

Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution* **10**, 105–108.

McKenzie, J.A. (1978). The effect of developmental temperatures on population flexibility in *Drosophila melanogaster* and *D. simulans*. *Aust. J. Zool.* **26**, 105–112.

McLaren, I.A. (1963). Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Bd Canada* **20**, 685–727.

McNab, B.K. and Auffenberg, W. (1976). The effect of large body size on the temperature regulation of the Komodo dragon. *Varanus komodoensis*. *Comp. Biochem. Physiol.* **55A**, 345–350.

Meats, A. (1971). The relative importance to population increase of mortality, fecundity and the time variables of the reproductive schedule. *Oecologia* **6**, 223–237.

Meeson, B.W. and Sweeney, B.M. (1982). Adaptation of *Ceratium furca* and *Gonyaulax polyedra* (Dinophyae) to different temperatures and irradiances: growth rates and cell volumes. *J. Phycol.* **18**, 241–245.

Mer, G. (1937). Variations saisonnières des caractères de *Anopheles elutus* en Palestine. II. *Bull. Soc. Pathol. Exot. Paris* **30**, 38–42.

Miller, T.J., Crowder, L.B., Rice, J.A. and Marschall, E.A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* **45**, 1657–1670.

Miller, W.E. (1977). Weights of *Polia grandis* pupae reared at two constant temperatures (Lepidoptera: Noctuidae). *Great Lakes Entomol.* **10**, 47–49.

Minkenberg, O.P.J.M. and Helderman, C.A.J. (1990). Effects of temperature on the life history of *Liriomyza bryoniae* (Diptera: Agromyzidae) on tomato. *J. Econ. Entomol.* **83**, 117–125.

Monteith, J.L. (1981). Climatic variation and the growth of crops. *J. R. Meteorol. Soc.* **107**, 749–774.

Morgan, K.C. and Kalff, J. (1979). Effect of light and temperature interactions on growth of *Cryptomonas erosa* (Chrysophyceae). *J. Phycol.* **15**, 127–134.

Mućibabić, S. (1956). Some aspects of the growth of single and mixed populations of flagellates and ciliates. The effect of temperature on the growth of *Chilomonas paramecium*. *J. Exp. Biol.* **33**, 627–644.

Mullens, B.A. and Rutz, D.A. (1983). Development of immature *Culicoides variipennis* (Diptera: Ceratopogonidae) at constant laboratory temperatures. *Ann. Entomol. Soc. Am.* **76**, 747–751.

Müller, H.J. (1966). Uber die Ursachen der unterschiedlichen Resistenz von *Vicia faba* L. gegenuber der Bohnenblattlaus *Aphis (Doralis) fabae* Scop. IX. Der Einfluss okologischer Faktoren auf das Wachstum von *Aphis fabae* Scop. *Entomol. Exp. Appl.* **9**, 42–66.

Murdie, G. (1969). Some causes of size variation in the pea aphid, *Acyrthosiphon pisum* Harris. *Trans. R. Entomol. Soc. Lond.* **121**, 423–442.

Muthukrishnan, J. and Pandian, T.J. (1983). Effect of temperature on growth and bioenergetics of a tropical moth. *J. Thermal Biol.* **8**, 361–367.

Myers, R.A. and Runge, J.A. (1983). Predictions of seasonal natural mortality rates in a copepod population using life history theory. *Marine Ecol. Prog. Ser.* **11**, 189–194.

Nayar, J.K. (1968). Biology of *Culex nigripalpus* Theobald (Diptera: Culicidae) Part 2. Adult characteristics at emergence and adult survival without nourishment. *J. Med. Entomol.* **5**, 203–210.

Nayar, J.K. (1969). Effects of larval and pupal environmental factors on biological status of adults at emergence in *Aedes taeniorhyncus* (Wied.). *Bull. Entomol. Res,* **58**, 811–827.

Nealis, V.G., Jones, R.E. and Wellington, W.G. (1984). Temperature and development in host-parasite relationships. *Oecologia (Berl.)* **61**, 224–229.

Nelson, W.G. (1980). Reproductive patterns of gammaridean amphipods. *Sarsia* **65**, 61–71.

Nevo, E. (1973). Adaptive variation in size of cricket frogs. *Ecology* **54**, 1271–1281.

Nylin, S., Wickman, P-O. and Wicklund, C. (1989). Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyrinae). *Biol. J. Linn. Soc.* **38**, 155–171.

Orcutt, J.D. and Porter, K.G. (1983). Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol. Oceanogr.* **27**, 720–730.

Orcutt, J.D. Jr. and Porter, K.G. (1984). The synergistic effects of temperature and food concentration on life history parameters of *Daphnia*. *Oecologia (Berl.)* **63**, 300–306.

Pace, M. (1982). Planktonic ciliates: their distribution, abundance and relationship to microbial resources in a monomictic lake. *Can. J. Fish. Aquat. Sci.* **39**, 1106–1116.

Pace, M. and Orcutt, J.D. (1981). The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. *Limnol. Oceanogr.* **26**, 822–830.

Paine, R.T. (1976). Size-related predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. *Ecology* **57**, 858–873.

Palanichamy, S., Ponnuchamy, R. and Thangaraj, T. (1982). Effect of temperature on food intake, growth and conversion efficiency of *Eupterote mollifera* (Insecta: Lepidoptera). *Proc. Ind. Acad. Sci. (Anim. Sci.)* **91**, 417–422.

Palmer, J.O. (1984). Environmental determinants of seasonal body size variation in the Milkweed Leaf Beetle *Labidomera clivicollis* (Kirby) (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* **77**, 188–192.

Pechenik, J.A. (1984). The relationship between temperature, growth rate and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L.). *J. Exp. Marine Biol. Ecol.* **74**, 241–257.

Pechenik, J.A. and Lima, G. (1984). Relationship between growth, differentiation,

and length of larval life for individually reared larvae of the marine gastropod, *Crepidula fornicata*. *Biol. Bull.* **166**, 537–549.

Pechenik, J.A., Eyster, L.S., Widdows, J. and Bayne, B.L. (1990). The influence of food concentration and temperature on growth and morphological differentiation of blue mussel *Mytilus edulis* L. larvae. *J. Exp. Marine Biol. Ecol.* **136**, 47–64.

Peters, R.H. (1983). *The Ecological Implications of Body Size.* Cambridge University Press, Cambridge.

Porter, W.P. and Gates D.M. (1969). Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 222–224.

Poston, F.L., Hammond, R.B. and Pedigo, L.P. (1977). Growth and development of the painted lady on soybeans (Lepidoptera: Nymphalidae). *J. Kansas Entomol. Soc.* **50**, 31–36.

Pourriot, R. (1973). Rapports entre la température, la taille des adultes, la longueur des oeufs et la taux de développement embryonnaire chez *Brachionus calyciflorus* PALLAS (Rotifère). *Ann. Hydrobiol.* **4**, 103–115.

Precht, H., Christophersen, J., Hensel, H. and Larcher, W. (1973). *Temperature and Life.* Springer-Verlag, Berlin.

Pullin, A.D. (1986). Effect of photoperiod and temperature on the life-cycle of different populations of the peacock butterfly *Inachis io*. *Entomol. Exp. Appl.* **41**, 237–242.

Ray, C. (1960). The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.* **106**, 85–108.

Reiss, M.J. (1989). *The Allometry of Growth and Reproduction.* Cambridge University Press, Cambridge.

Rempel, R.S. and Carter, J.C.H. (1987). Temperature influences on adult size, development and reproductive potential of aquatic Diptera. *Can. J. Fish. Aquat. Sci.* **44**, 1743–1752.

Roberts, E.H. and Summerfield, R.J. (1987). Measurement and prediction of flowering in annual crops. In: *Manipulation of Flowering* (Ed. by J.G. Atherton), pp. 17–50. Butterworths, London.

Robertson, F.W. (1959). Studies in quantitative inheritance XII. Cell size and number in relation to genetic and environmental variation of body size in *Drosophila*. *Genetics* **44**, 869–896.

Roe, R.M., Clifford, C.W. and Woodring, J.P. (1985). The effect of temperature on energy distribution during the last-larval stadium of the female house cricket, *Acheta domesticus*. *J. Insect Physiol.* **31**, 371–1378.

Roff, D.A. (1981). On being the right size. *Am. Nat.* **118**, 405–422.

Rowe, L. and Ludwig, D. (1991). Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**, 413–427.

Schaecter, M., Maaloe, O. and Kjeldgaard, N.O. (1958). Dependency on medium and temperature of cell size and chemical composition during balanced growth of *Salmonella typhimurium*. *J. Gen. Microbiol.* **19**, 592–606.

Schmidt-Neilsen, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge.

Schoener, T.W. and Janzen, D.H. (1968). Notes on environmental determinants of tropical versus temperate insect size patterns. *Am. Nat.* **102**, 207–224.

Scott, S.M. and Dingle, H. (1990). Developmental programmes and adaptive syndromes in insect life cycles. In: *Insect Life Cycles: Genetics, Evolution and Co-ordination*, pp. 69–85. Springer-Verlag, London.

Seed, R. and Brown, R.A. (1978). Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J. Anim. Ecol.* **47**, 283–292.

Seikai, T., Tanangonan, J.B. and Tanaka, M. (1986). Temperature influence on larval growth and metamorphosis of the Japanese flounder *Palalichthys olivaceus* in the laboratory. *Bull. Jap. Soc. Sci. Fish.* **52**, 977–982.

Shaw, R.F. and Bercaw, B.L. (1962). Temperature and life-span in poikilothermous animals. *Nature* **196**, 454–457.

Sibly, R.M. and Calow, P. (1986a). *Physiological Ecology of Animals: an Evolutionary Approach*. Blackwell Scientific Publications, Oxford.

Sibly, R.M. and Calow, P. (1986b). Why breeding earlier is always worthwhile. *J. Theor. Biol.* **123**, 311–319.

Sibly, R., Calow, P. and Nichols, N. (1985). Are patterns of growth adaptive? *J. Theor. Biol.* **112**, 553–574.

Simonet, D.E. and Pienkowski, R.L. (1980). Temperature effect on development and morphometrics of the Potato Leafhopper. *Environ. Entomol.* **9**, 798–800.

Sims, S.R., Marrone, P.G., Gould, F., Stinner, R.E. and Rabb, R.L. (1984). Ecological determinants of Bean Leaf Beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae), size variation in North Carolina. *Environ. Entomol.* **13**, 300–304.

Smith, S.L. and Lane, P.V.Z. (1987). On the life history of *Centropages typicus*: responses to a fall diatom bloom in the New York Bight. *Marine Biol.* **95**, 305–313.

Smith-Gill, S.J. and Berven, K.A. (1979). Predicting amphibian metamorphosis. *Am. Nat.* **113**, 563–585.

Söderström, O. (1988). Effects of temperature and food quality on life-history parameters in *Parameletus chelifer* and *P. minor* (Ephemeroptera): a laboratory study. *Freshwater Biol.* **20**, 295–303.

Sohal, R.S. (1976). Metabolic rate and lifespan. *Interdisc. Topics Gerontol.* **9**, 25–40.

Sohal, R.S. (1986). The rate of living. In: *Insect Aging* (Ed. by K.-G. Collatz and R.S. Sohal), pp. 23–44. Springer-Verlag, Berlin.

Squire, G.R. (1989). Response to temperature in a stand of pearl millet. *J. Exp. Bot.* **40**, 1391–1398.

Standfuss, M. (1895). On causes of variation in the imago stage of butterflies, with suggestions on the establishment of new species. *The Entomol.* **28**, 69–76.

Stanley, W.F. (1935). The effect of temperature upon wing size in *Drosophila*. *J. Exp. Zool.* **69**, 459–495.

Stearns, S.C. (1976). Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47.

Stearns, S.C. (1989). The evolutionary significance of phenotypic plasticity. *Bioscience* **39**, 436–445.

Stearns, S.C. and Crandall, R.E. (1984). Plasticity for age and size at sexual maturity: a life history response to unavoidable stress. In: *Fish Reproduction* (Ed. by G. Potts and R.J. Wootton), pp. 13–33. Academic Press, London.

Stearns, S.C. and Koella, J.C. (1986). The evolution of phenotypic plasticity in life history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**, 893–913.

Stevenson, R.D. (1985). Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.* **125**, 102–117.

Sweeney, B.W. (1978). Bioenergetic and developmental response of a mayfly to thermal variation. *Limnol. Oceanogr.* **23**, 461–477.

Sweeney, B.W. and Vannote, R.L. (1978). Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* **200**, 444–446.

Sweeney, B.W. and Vannote, R.L. (1984). Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly, *Cloeon triangulifer*. *Freshwater Biol.* **14**, 621–630.

Sweeney, B.W., Vannote, R.L. and Dodds, P.J. (1986). Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. *Can. J. Fish. Aquat. Sci.* **43**, 12–18.

Tantawy, A.O. and Mallah, G.S. (1961). Studies on natural populations of *Drosophila*. I. Heat resistance and geographical variation in *Drosophila melanogaster* and *D. simulans*. *Evolution* **15**, 1–14.

Tauber, M.J., Tauber, C.A. and Masaki, S. (1986). *Seasonal Adaptations of Insects*. Oxford University Press, Oxford.

Thormar, H. (1962). Cell size of *Tetrahymena pyriformis* incubated at various temperatures. *Exp. Cell Res.* **27**, 585–586.

Thorne, G.N., Ford, M.A. and Watson, D.J. (1968). Growth, development and yield of spring wheat in artificial climates. *Ann. Bot.* **32**, 425–446.

Tsitsipis, J.A. (1980). Effect of constant temperatures on larval and pupal development of Olive Fruit Flies reared on artificial diet. *Environ. Entomol.* **9**, 764–768.

Tsitsipis, J.A. and Mittler, T.E. (1976). Development, growth, reproduction and survival of apterous virginoparae of *Aphis fabae* at different temperatures. *Entomol. Exp. Appl.* **19**, 1–10.

van den Heuvel, M.J. (1963). The effect of rearing temperature on the wing length, thorax length, leg length and ovariole number of the adult mosquito *Aedes aegypti* (L.) *Trans. R. Entomol. Soc. Lond.* **115**, 197–216.

van Dobben, W.H. (1962). Influence of temperature and light conditions on dry matter distribution, development rate and yield in arable crops. *Neth. J. Agric. Sci.* **10**, 377–389.

van Dobben, W.H. (1963). The physiological background of the reaction of peas to sowing time. Report 214 of IBS. In: *Annual Report of IBS, 1963*, Wageningen.

Vannote, R.L. and Sweeney, B.W. (1980). Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* **115**, 667–695.

Van't Hof, J. and Ying, H.K. (1964). Relationship between the duration of the mitotic cycle, the rate of cell production and the rate of growth of *Pisum* roots at different temperatures. *Cytologia* **29**, 399–406.

Via, S. and Lande, R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**, 505–522.

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Q. Rev. Biol.* **32**, 217–231.

von Bertalanffy, L. (1960). Principles and theory of growth. In: *Fundamental Aspects of Normal and Malignant Growth* (Ed. by W.N. Nowinski), pp. 137–259. Elsevier, Amsterdam.

Wagner, T.L., Fargo, W.S., Flamm, R.O., Coulson, R.N. and Pulley, P.E. (1987). Development and mortality of *Ips calligraphus* (Coleoptera: Scolytidae) at constant temperatures. *Environ. Entomol.* **16**, 484–496.

Walsby, A.E. and Reynolds, C.S. (1980). Sinking and floating. In: *The Physiological Ecology of Phytoplankton* (Ed. by I. Morris), pp. 371–412. Blackwell Scientific Publications, Oxford.

Warrick, R.A. and Gifford, R.M. with Parry, M.L. (1986). CO_2, climatic change and agriculture. In: *The Greenhouse Effect, Climatic Change, and Ecosystems. Scope No. 29* (Ed. by B. Bolin, D. Doos and J. Jager), pp. 393–473. John Wiley and Sons, New York.

Whitman, D.W. (1986). Developmental thermal requirements for the grasshopper *Taeniopoda eques* (Orthoptera: Acrididae). *Ann. Entomol. Soc. Am.* **79**, 711–714.

Wilber, C.G. (1964). Animals in aquatic environments: introduction. In: *Handbook*

No.	KINGDOM PHYLUM Class (Subclass/Order) Species	Effect*	Reference
	KINGDOM		
	PHYLUM		
	Class		
	(Subclass/Order) Species		
	Magnoliopsida		
12	*Phaseolus vulgaris*	R	Gmelig Meyling (1969)
13	*Pisum sativum*	R	Gmelig Meyling (1969)
14	*P. sativum*	R	van Dobben (1963)
	ANIMALIA		
	ASCHELMINTHES		
	Nematoda		
15	*Cephalobus* sp.	R	Ray (1960)
	Rotifera		
16	*Brachionus calyciflorus*	R	Pourriot (1973)
17	*Philodina roseola*	R	Lebedeva and Gerasimova (1985)
	MOLLUSCA		
	Gastropoda		
18	*Crepidula fornicata*	R	Pechenik (1984)
19	*Lymnaea japonica*	R	Imai (1937b)
	Pelecypoda		
20	*Mytilus edulis*	R	Pechenik *et al.* (1990)
21	*M. edulis*	R	Bayne (1965)
	ARTHROPODA		
	Insecta		
	(Diptera)		
22	*Ablabesmyia mallochi*	R	Rempel and Carter (1987)
23	*Aedes aegypti*	R	van den Heuvel (1963)
24	*Ae. aegypti*	R	Galliard and Golvan (1957)
25	*Ae. nigromaculis*	R	Brust (1967)
26	*Ae pseudoscutellaris*	R	Marks (1954)
27	*Ae. taeniorhyncus*	R	Nayar (1969)
28	*Ae. vexans*	R	Brust (1967)
29	*Chaoborus flavicans*	R	Hanazato and Yasuno (1989)
30	*Conchapelopia aleta*	R	Rempel and Carter (1987)
31	*Culex nigripalpus*	R	Nayar (1968)
32	*Culicoides variipennis*	R	Mullens and Rutz (1983)
33	*C. variipennis*	R	Akey *et al.* (1978)
34	*Culiseta inornata*	R	Brust (1967)
35	*Dacus oleae*	M	Tsitsipis (1980)
36	*Drosophila equinoxalis*	R	Ray (1960)
37	*D. melanogaster*	R	Alpatov and Pearl (1929)
38	*D. melanogaster*	R	Imai (1937a)
39	*D. melanogaster*	R	Tantawy and Mallah (1961)

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of Physiology, Section 4: Adaptation to the Environment (Ed. by D.B. Dill), pp. 661–668. American Physiological Society, Washington, DC.

Wilbur, H.M. and Collins, J.P. (1973). Ecological aspects of amphibian metamorphosis. *Science* **182**, 1305–1314.

Williams, G.C. (1966). *Adaptation and Natural Selection.* Princeton University Press, Princeton, NJ.

Willmer, P. (1991). Thermal biology and mate acquisition in ectotherms. *Trends Ecol. Evol.* **6**, 396–399.

Willmer, P.G. and Unwin, D.M. (1981). Field analyses of insect heat budgets: reflectance, size and heating rates. *Oecologia* **50**, 250–255.

Yoder, J.A. (1979). Effect of temperature on light-limited growth and chemical composition of *Skeletonema costatum* (Bacillariophyceae). *J. Phycol.* **15**, 362–370.

Yu, D.S. and Luck, R.F. (1988). Temperature-dependent size and development of California red scale (Homoptera: Diaspididae) and its effect on host availability for the ectoparasitoid *Aphytis melinus* De Bach (Hymenoptera: Aphelinidae). *Environ. Entomol.* **17**, 154–161.

Zaret, T.M. (1980). *Predation and Freshwater Communities.* Yale University Press, New Haven, CT.

Zeuthen, E. (1964). The temperature-induced division synchrony in *Tetrahymena.* In: *Synchrony in Cell Division and Growth* (Ed. by E. Zeuthen), pp. 99–158. Wiley InterScience, New York.

APPENDIX: EFFECTS OF INCREASED TEMPERATURE ON SIZE-AT-STAGE

No.	KINGDOM PHYLUM Class (Subclass/Order) Species	Effect*	Reference
	BACTERIA (MONERA)		
1	*Pseudomonas* sp.	R	Chrzanowski *et al.* (1988)
	PROTISTA		
	CHLOROPHYTA		
2	*Chlamydomonas reinhardi*	R	Ray (1960)
3	*Chlamydomonas* sp. 1	R	Ray (1960)
4	*Chlamydomonas* sp. 2	R	Ray (1960)
5	*Scenedesmus obliquus*	R	Margalef (1954)
	BACILLARIOPHYTA		
6	*Phaeodactylum tricornutum*	I	Fawley (1984)
	CILIOPHORA		
7	*Colpoda* sp.	R	Adolph (1929)
8	*Tetrahymena gelei*	R	Ray (1960)
	PLANTAE		
	SPERMATOPHYTA		
	Liliopsida		
9	*Pennisetum typhoides*	R	Squire (1989)
10	*Triticum aestivum*	R	Gmelig Meyling (1969)
11	*Zea Mays*	R	Brouwer *et al.* (1973)

No.	KINGDOM PHYLUM Class (Subclass/Order) Species	Effect*	Reference
40	D. melanogaster	M	David and Clavel (1967)
41	D. melanogaster	R	Economos et al. (1982)
42	D. melanogaster	R	Lints and Lints (1971)
43	D. melanogaster	R	Stanley (1935)
44	D. persimilis	R	Ray (1960)
45	D. pseudoobscura	R	Ray (1960)
46	D. pseudoobscura	R	Druger (1962)
47	D. simulans	R	Tantawy and Mallah (1961)
48	Drosophila sp	R	Eigenbrodt (1930)
49	D. willistoni	R	Ray (1960)
50	Nilotanypus fimbriatus	T	Rempel and Carter (1987)
51	Parametriocnemus lundbecki	R	Rempel and Carter (1987)
52	Polypedilum aviceps	R	Rempel and Carter (1987)
53	Stempellinella brevis	R	Rempel and Carter (1987)
	(Hemiptera)		
54	Acyrthosiphon pisum	R	Murdie (1969)
55	A. pisum	R	Lamb et al. (1987)
56	A. pisum	M	Lamb and MacKay (1988)
57	Aonidiella aurantii	R	Yu and Luck (1988)
58	Aphis fabae	R	Dixon et al. (1982)
59	A. fabae	R	Tsitsipis and Mittler (1976)
60	A. fabae	M	Müller (1966)
61	Empoasca fabae	R	Simonet and Pienkowski (1980)
62	Graminella nigrifrons	R	Larsen et al. (1990)
	(Coleoptera)		
63	Attagenus megatoma	I	Baker (1983)
64	Enaphalodes rufulus	I	Galford (1974)
65	Entomoscelis americana	I	Lamb and Gerber (1985)
66	Ips calligraphus	R	Wagner et al. (1987)
67	Pterohelaeus darlingensis	R	Allsopp (1981)
68	P. alternatus	R	Allsopp (1981)
69	Trogoderma anthrenoides	M	Burges and Cammell (1964)
	(Orthoptera)		
70	Acheta domesticus	I	Roe et al. (1985)
71	Taeniopoda eques	I	Whitman (1986)
	(Ephemeroptera)		

No.	KINGDOM PHYLUM Class (Subclass/Order) Species	Effect*	Reference
72	Ameletus ludens	R	Vannote and Sweeney (1980)
73	Caenis simulans	I	Vannote and Sweeney (1980)
74	Cloeon triangulifer	R	Sweeney and Vannote (1984)
75	Ephemerella funeralis	I	Vannote and Sweeney (1980)
76	Isonychia bicolor	I	Sweeney (1978)
77	Leptophlebia intermedia	R	Sweeney et al. (1986)
78	Parameletus minor	R	Söderström (1988)
79	P. chelifer	R	Söderström (1988)
80	Tricorythodes atratus	I	Vannote and Sweeney (1980)
	(Hymenoptera)		
81	Apanteles rubecula	R	Nealis et al. (1984)
	(Lepidoptera)		
82	Achaea junta	R	Muthukrishnan and Pandian (1983)
83	Eupteroté mollifera	R	Palanichamy et al. (1982)
84	Inachis io	R	Pullin (1986)
85	Orgyia pseudotsugata	I	Beckwith (1982)
86	Pieris rapae	R	Jones et al. (1982)
87	Polia grandis	R	Miller (1977)
88	Pseudaletia unipuncta	I	Guppy (1969)
	Crustacea (Copepoda)		
89	Acanthocyclops vernalis	R	Coker (1933)
90	A. vernalis	R	Abdullahi and Laybourn-Parry (1985)
91	A. viridis	R	Abdullahi and Laybourn-Parry (1985)
92	A. viridis	R	Coker (1933)
93	A. viridis	R	Laybourn-Parry et al. (1988)
94	Cyclops serrulatus	R	Coker (1933)
95	Macrocyclops albidus	R	Abdullahi and Laybourn-Parry (1985)
96	M. albidus	R	Laybourn-Parry et al. (1988)
97	Pseudocalanus minutus	R	Lock and McLaren (1970)
98	Salmincola salmoneus	I	Johnston and Dykeman (1987)

No.	KINGDOM PHYLUM Class (Subclass/Order) Species	Effect*	Reference
	(Decapoda)		
99	*Callinectes sapidus*	R	Leffler (1972)
100	*Cancer irroratus*	R	Johns (1981)
	(Mysidacea)		
101	*Neomysis mercedis*	R	Johnston and Northcote (1989)
	CHORDATA		
	Amphibia		
102	*Pseudoacris ornata*	R	Harkey and Semlitsch (1988)
103	*Rana pipiens*	R	Smith-Gill and Berven (1979)
104	*R. sylvatica*	R	Ray (1960)
105	*R. sylvatica*	R	Berven and Gill (1983)
106	*R. sylvatica*	R	Berven and Gill (1983)
107	*R. sylvatica*	R	Berven and Gill (1983)
108	*T. tigrina*	R	Marian and Pandian (1985)
	Osteichthyes		
109	*Paralichthys olivaceus*	R	Seikai et al. (1986)

* R denotes a significant size reduction with increasing temperature; I denotes a significant size increase, and M denotes significant mixed effects (significant increases *and* reductions).