



The Respiration of *Geolycosa godeffroyi* (Araneae: Lycosidae) under Conditions of Constant and Cyclic Temperature

Author(s): W. F. Humphreys

Source: *Physiological Zoology*, Vol. 48, No. 3 (Jul., 1975), pp. 269-281

Published by: The University of Chicago Press

Stable URL: <http://www.jstor.org/stable/30160949>

Accessed: 25/05/2010 04:16

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ucpress>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *Physiological Zoology*.

<http://www.jstor.org>

THE RESPIRATION OF GEOLYCOSA GODEFFROYI (ARANEAE: LYCOSIDAE) UNDER CONDITIONS OF CONSTANT AND CYCLIC TEMPERATURE

W. F. HUMPHREYS¹

Department of Zoology, Australian National University, Canberra, A.C.T. 2600 Australia

INTRODUCTION

Measurements of respiration in the laboratory are invariably conducted under conditions of constant temperature. In the field however most terrestrial animals are subjected to irregular temperature fluctuations as well as diurnal and seasonal temperature cycles. In extrapolating results to the field, the assumption is normally made that the rate-temperature relationship derived from a series of constant temperature experiments in the laboratory are applicable to the field situation. The validity of this procedure is being increasingly questioned in the context of predicting development rates (Howe 1967; Baker 1971) but has remained largely unchallenged as a predictive method for field respiration. The respiratory response of animals to cyclic temperatures has intrinsic interest, but more important, it has wider implications in studies requiring the extrapolation of predictive models from the laboratory to the field as, for example, in ecological energetics.

The work reported here forms part of an investigation into the validity of using laboratory respirometry data in the field. The approach adopted has been to determine the respiration of the whole size range of the species covering the entire temperature range ex-

perienced by the species in the field. From these data the relationship between the respiration rate and temperature is derived in order to predict the expected level of respiration under cycling temperature conditions. These data are then compared with those found under conditions of cycling temperature.

MATERIAL AND METHODS

The species used was the wolf spider *Geolycosa godeffroyi* (L. Koch 1865). This species inhabits burrows and thermoregulates, mainly as a heliotherm, on sunny days throughout the year at about 35 C (Humphreys 1973, 1974, in press).

Oxygen consumption was measured in electrolytic respirometers using saturated copper sulphate solution as the electrolyte. The electrolysis of copper sulphate solution may produce traces of ozone; (Wager and Porter 1961; Woodland 1973), and this was prevented from reaching the animal chamber by a barrier of soda lime (Belew 1969) which also served to absorb carbon dioxide. The respirometers had interchangeable chambers so that the diameter could be changed to approximate the diameter of the burrow normally occupied by the spider under test. The volume of the compensation chamber was adjusted to equal the volume of air in the animal chamber. Ten respirometers were maintained at the

¹ Present address: Department of Zoology, La Trobe University, Bundoora, Victoria 3083 Australia.

required temperature in an incubator and each was connected in series with a direct-current power supply and a volumetric coulometer maintained in a separate incubator at 30 C. Following an equilibration period of 0.5 h, measurements were made for 24 h and adjusted to standard temperature and pressure (STP) before analysis.

EXPERIMENTAL CONDITIONS

1. *Resting metabolic rate*.—The spiders were adapted to the experimental conditions for from 7 to 10 days during which they were not fed. Experiments were conducted at 4, 10, 20, 30, and 40 C on spiders covering most of the size range found in the field, that is about 1–2,000 mg.

2. *Metabolic rate compensation or acclimation*.—Spiders were adapted for from 7 to 10 days at 4 C or 30 C and tested at 20 C and 40 C, respectively. Following Hochachka and Somero (1973), I will use the term "metabolic rate compensation" (MRC) when there is evidence that ectothermic animals are able to achieve a level of metabolic homeostasis at different temperatures.

3. *Cycling temperature*.—Spiders were adapted to the temperature cycle for from 7 to 10 days under a 14-h light, 10-h dark regime and without food. They were tested under the same conditions. The temperature cycled on a sine wave pattern between 11.7 C

($SD = 0.25, N = 25$) and 29.3 C ($SD = 0.54, N = 15$) with an arithmetic mean of 20.4 C and the mean determined by planimeter integration of 20.16 C. The full cycle covered 24 h with a peak temperature at 1300 hours; the lights were turned on at 0500 hours and off at 1900 hours.

Spiders weighing more than 100 mg were tested individually in the respirometers, but those weighing less than 100 mg were tested severally. In the latter case spiders of similar size were used and separated from each other to prevent interaction and cannibalism. The spiderlings from the back of the females were tested en masse as they were not cannibalistic at that stage.

RESULTS

The results for all the resting metabolic rate (RMR) experiments are initially presented as regressions against the live weight of the spider after double logarithmic transformation (table 1). These data are discussed in Humphreys (1973).

THE EFFECT OF THERMAL HISTORY ON RESPIRATION

The results of the experiments in which the spiders were tested at other than the adaptation temperature are presented in table 2 where they are compared with the corresponding RMR determinations in which the test and

TABLE 1
REGRESSION PARAMETERS RELATING RESTING OXYGEN CONSUMPTION ($\log_{10} Y \mu\text{l h}^{-1}$) TO LIVE
WEIGHT ($\log_{10} X \text{ mg}$) OF "GEOLYCOSA GODEFFROYI" AT VARIOUS TEMPERATURES

| TEMPERATURE (°C) | N | REGRESSION EQUATION | STANDARD ERROR | | CORRELATION COEFFICIENT | t_s | P |
|---------------------|----|-----------------------|----------------|-------|----------------------------|-------|-------|
| | | | Intercept | Slope | | | |
| 4 | 48 | $Y = 0.835 X - 1.052$ | .071 | .029 | .974 | 29.21 | <.001 |
| 10 | 67 | $Y = 0.795 X - 0.761$ | .061 | .028 | .963 | 28.83 | <.001 |
| 20 | 57 | $Y = 0.818 X - 0.434$ | .036 | .016 | .990 | 52.24 | <.001 |
| 30 | 61 | $Y = 0.847 X - 0.315$ | .086 | .035 | .952 | 23.94 | <.001 |
| 40 | 25 | $Y = 0.813 X - 0.051$ | .081 | .033 | .982 | 24.62 | <.001 |

TABLE 2

A. REGRESSION DESCRIBING RELATIONSHIP BETWEEN WEIGHT OF "GEOLYCOSA GODEFFROYI"
 $(\log_{10} X \text{ mg})$ AND RESTING OXYGEN CONSUMPTION ($\log_{10} Y \mu\text{l h}^{-1}$) IN SPIDERS
 PRECONDITIONED AT 4 C AND 10 C AND TESTED AT 20 C AND 40 C, RESPECTIVELY

| TEST TEMPERATURE (°C) | N | REGRESSION EQUATION | STANDARD ERROR | | CORRELATION COEFFICIENT | t_s | P |
|-----------------------------|----|-----------------------|----------------|-------|----------------------------|-------|-------|
| | | | Intercept | Slope | | | |
| 20 | 27 | $Y = 0.707 X - 0.213$ | .223 | .090 | .844 | 7.87 | <.001 |
| 40 | 22 | $Y = 1.369 X - 1.450$ | .035 | .130 | .921 | 10.53 | <.001 |

B. ANALYSIS OF VARIANCE COMPARING ABOVE REGRESSIONS WITH COMPARABLE DATA
 FROM SPIDERS PRECONDITIONED TO TEST TEMPERATURE

| | BARTLETT'S χ^2 TEST FOR RESIDUAL VARIANCE | | | TEST OF PARALLELISM | | | TEST OF IDENTITY | | |
|----------|---|----------|---------|---------------------|------|-------------|------------------|------|----------|
| | df | χ^2 | P | df | F | P | df | F | P |
| 20 | 1 | 8.79 | <.001 | 1, 51 | 2.44 | .25 — .1 | 2, 51 | 1.27 | .5 — .25 |
| 40 | 1 | 0.26 | .9 — .5 | 1, 29 | 9.33 | .005 — .001 | 2, 29 | 9.27 | <.001 |

adaptation temperature were the same. Both regressions are significant ($P < .001$), and they are compared with the RMR regressions after the data from spiders outside the weight range of the experiments using different test and adaptation temperatures had been excluded. Comparison of the two 20 C experiments showed that the data were heterogeneous so that the analysis of variance (table 2) must be treated with reserve. The regression coefficients were therefore compared using the appropriate modification given by Bailey (1959, p. 99) when $d = 0.467$ and is treated as t with 48.8 df (.9 > P > .5) indicating no significant difference between the coefficients. The regressions from the 40 C experiments are not parallel ($P < .001$), and the spiders adapted to the lower temperature had the higher metabolic rate.

The spiders exhibited MRC with an upward temperature transfer only at the higher temperatures and thus responded in a similar manner to *Lycosa lenta* (Hentz) and some other spiders. *Lycosa lenta* exhibited a 33% MRC when adapted to 10 C and tested at 30 C and the compensation occurred within 3 days. No reduction below the

expected rate was found when the spiders were tested at temperatures below the adaptation temperature (Anderson 1970). *Lycosa carolinensis* Walckenaer showed a 30% overshoot in respiration when transferred from 22 to 39 C and compensation was completed within 3 days. A small temperature change from 39 to 41 C did not produce an overshoot, and adjustment to the new temperature was slow, taking 2 days. This species exhibited higher respiration rates in winter than in summer, but the magnitude of the increase depended on the test temperature and ranged from 5% to 29.2% (Moeur and Eriksen 1972). The desert-living theraphosid *Aphonopelma* sp. failed to show temperature compensation in either the metabolic rate or its upper lethal temperature (Seymour and Vinegar 1973) and contrasts in both respects with *L. carolinensis*.

THE EFFECT OF TEMPERATURE ON THE RESTING METABOLIC RATE

The regression lines relating the RMR to the weight of the spiders at different temperatures were used to derive the relationship between respiration and temperature. The relationships

for selected spider weights are shown in figure 1 together with the 95% confidence intervals of the original regression line.

THE EFFECT OF CYCLING TEMPERATURE ON THE RESTING METABOLIC RATE

The experiments involving cycling temperatures were conducted throughout the period used to determine the RMR at 20 C to avoid any seasonal bias. The resulting regression of the spider weight against respiration (table 3, fig. 2) is significant ($P < .001$). An analysis of variance comparing these data with those obtained from the RMR experiments at 20 C constant temperature shows that the lines are parallel but displaced. The respiration under cycling conditions was 135% of that under constant conditions with the same mean temperature. The reality of this increase is supported by feeding experiments under constant and cycling temperatures in which the respiration was estimated from individual energy budgets (Humphreys 1973), and these will be reported elsewhere.

DISCUSSION

Various weighting factors have been used to compensate for the nonlinearity in rate-temperature (R-T) curves to make comparisons between growth data derived from constant and fluctuating temperatures (Messenger and Flitters 1959; Lamb 1961; review by Howe 1967; Baker 1971). Such adjustments are not required to compare the respiration rate of *Geolycosa godeffroyi* under constant and cycling conditions, for it was shown in figure 1 that the R-T curve was linear between 10 and 40 C. The curve describing the temperature cycle was close to a sine wave. Assuming a sine wave, the time

spent at temperatures on either side of the mean would be equal. Due to its linear properties in relation to temperature, the respiration rate would change equally but with opposite sign as the temperature departed from the mean in either direction. The expected respiration under the cycling temperature conditions should therefore be that of the mean temperature of the temperature cycle. The temperature cycle was not a sine wave but very close to it. Estimating the respiration over 24 h from the temperature at every 0.25 h of the temperature cycle gave a value 2.3% below that calculated using the mean temperature of the cycle. This slight departure from a sine wave could not account for the large increase observed in the respiration.

The reason for this increase in respiration under cycling conditions is not obvious. The simplest explanation is that there was an increase in orthokinetic activity by the spiders as the temperature departed from some preferred or adaptation temperature. Locomotory activity may be stimulated by both an increase and a decrease in temperature (Cloudsley-Thompson 1961). The tubular respirometer chambers used with *Geolycosa godeffroyi* encouraged the spiders' immobility due to their thigmotactic behavior. They were never seen to struggle within the chambers, and there was insufficient room for them to walk. Nevertheless, subtle changes in activity may have marked effects on the respiration of this spider (Humphreys 1973, p. 226). The scorpion *Euscorpius italicus* (Herbst) showed a distinct but transitory increase in respiration following a sudden change in light intensity (Dresco-Derouet 1961), and similar effects were observed with *G. godeffroyi*. The magnitude and duration of this effect could

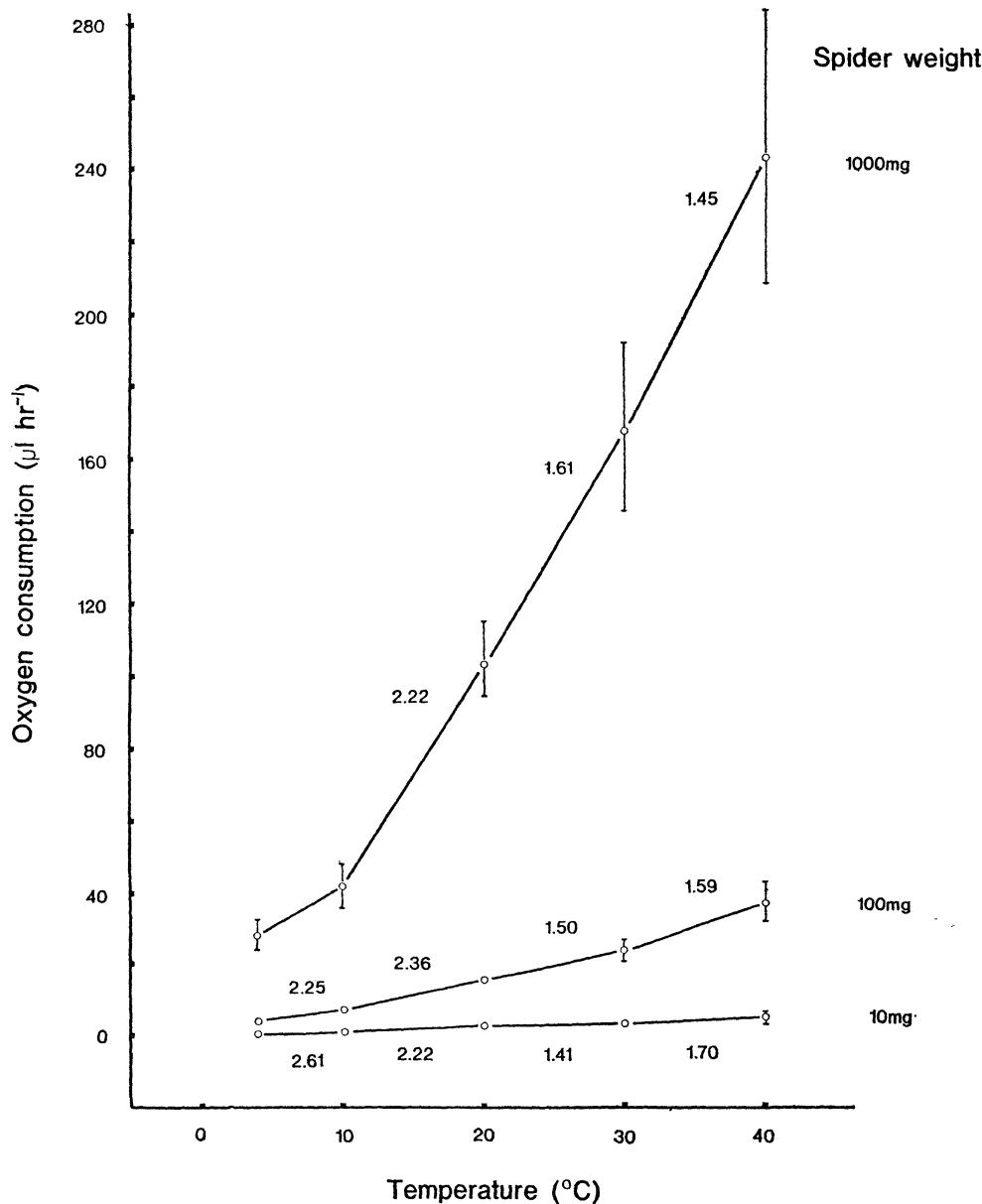


FIG. 1.—The relationship between oxygen consumption of *Geolycosa godeffroyi* at several weights and the experimental temperature. The vertical bars represent the 95% confidence intervals of the regressions in table 1. The numbers next to the lines are the Q_{10} values between the points.

not account for the observed increase in respiration under cycling conditions.

It is perhaps surprising that there is little work with which to compare the present results, for Macfadyen (1961) considered that his newly designed respirometers would be suitable for deter-

mining respiration under cycling conditions. Gromadska (1962) subjected the earthworm *Lumbricus castaneus* (Sav.) to respirometry combined with temperature transfers and compared the results with the respiration expected from the mean temperature of

TABLE 3

A. REGRESSION RELATING LIVE WEIGHT ($\log_{10} X$ mg) OF "GEOLYCOSA GODEFFROYI" TO OXYGEN UPTAKE ($\log_{10} Y \mu\text{l h}^{-1}$) UNDER FLUCTUATING TEMPERATURE CONDITIONS WITH TEMPERATURE CYCLING FROM 11.7 C TO 29.3 C

| TEMPERATURE (°C) | REGRESSION EQUATION | N | STANDARD ERROR | | CORRELATION COEFFICIENT | t_s | P |
|-----------------------|-----------------------|----|----------------|-------|----------------------------|-------|-------|
| | | | Intercept | Slope | | | |
| Cycling 11.7-29.3 ... | $Y = 0.808 X - 0.280$ | 53 | .098 | .040 | .943 | 20.22 | <.001 |

B. ANALYSIS OF VARIANCE COMPARING ABOVE REGRESSION WITH DATA FROM SPIDERS PRECONDITIONED TO CONSTANT TEMPERATURES

| CONSTANT | BARTLETT'S χ^2 TEST FOR RESIDUAL VARIANCE | | | TEST OF PARALLELISM | | | TEST OF IDENTITY | | |
|-----------|--|----------|--------------|---------------------|------|-------------|------------------|-------|----------|
| | df | χ^2 | P | df | F | P | df | F | P |
| 20 | 1 | 2.01 | .5 — .1 | 1, 106 | 0.06 | >.75 | 2, 106 | 11.91 | <.001 |
| 30* | 1 | 7.38 | 0.01 — 0.005 | 1, 110 | 0.44 | 0.75 — 0.50 | 2, 110 | 1.56 | .25 — .1 |

* Due to the significant Bartlett's test the regression coefficients are compared using the appropriate modification (Bailey 1959); $d = 0.208$ with 107.8 df, $.9 > P > .5$.

the temperature range. Macfadyen (1967) interpreted Gromadska's results as having shown an increase in respiration during the temperature transfer experiments, but Gromadska's results are ambiguous. He used three sets of conditions for the temperature transfers in which the minimum temperature was either 11, 14, or 17 C, and the temperature range from these minimum temperatures started with 3 C and increased by 3 C for each of four subsets, except the higher set which had only three subsets. While most of the conditions in the first two sets showed an apparent increase in respiration (no error values were presented), there was little effect in the last set, although the ranges overlapped with the previous sets and the upper limit did not fall outside the temperature tolerance of the species. While no conclusions can be drawn from his work the results are interesting enough to warrant further investigation.

There is, however, a large body of work in which the effects of fluctuating temperatures on growth or development rates have been examined. These studies have been concerned with the pre-

diction of development rates in the field and devote little discussion to the potential causes of the observed effects. Cloudsley-Thompson (1953), on reviewing the literature, concluded that it is impossible to estimate the rate of development of insects exposed to fluctuating temperatures using the mean temperature; the rate of development is normally enhanced unless the temperature cycles outside the optimum range. This must be considered an oversimplification, as the optimum temperature for development may change with different life stages (Bursell 1964) and is the result of a complex interaction between the temperature optima for such diverse parameters as respiration, assimilation efficiency, and feeding rates, all of which have been shown to have varying temperature optima (Brett and Higgs 1970). Andrewartha and Birch (1954) thought it incorrect to attribute the observed acceleration in development rates of insects to the "stimulating" effect of fluctuating temperatures or to acclimation, but that it should be considered as a manifestation of the diapause.

It has been shown that some reports

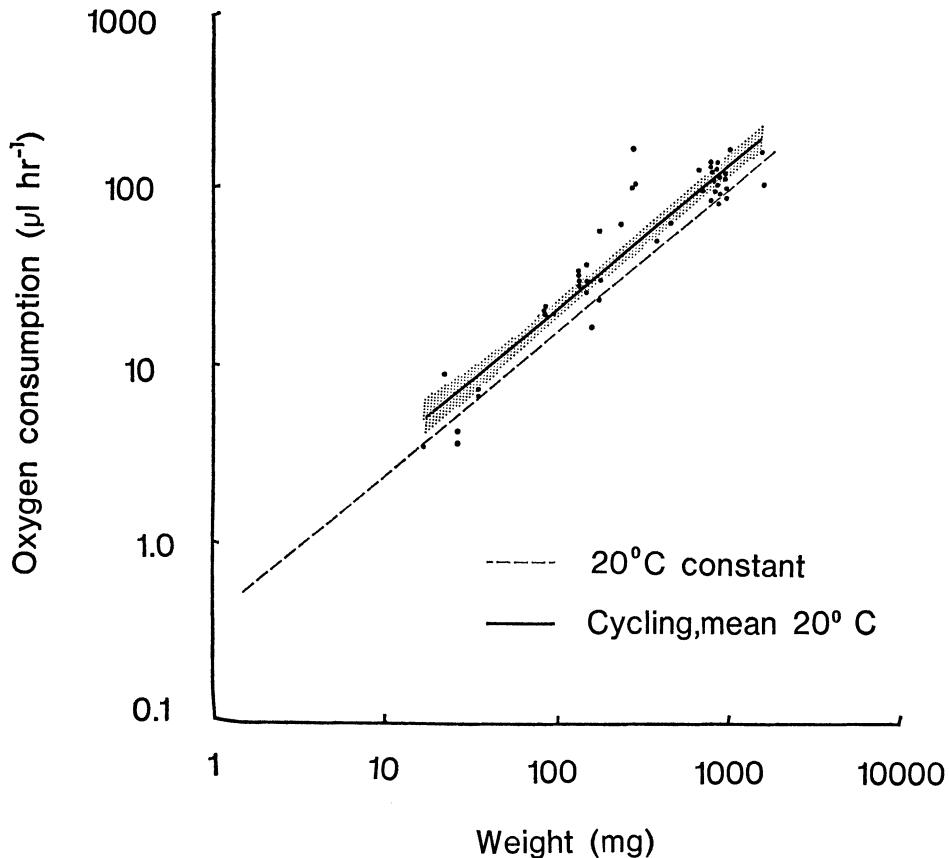


FIG. 2.—Regression relating the oxygen consumption of *Geolycosa godeffroyi* to its weight under cycling and constant temperature conditions. The shaded area represents the 95% confidence intervals of the regression and the fine broken line the regression obtained at 20°C constant temperature condition.

of accelerated development have resulted from lack of consideration of the nonlinear relationship between temperature and development rate (Johnson 1940; Lamb 1961; Bursell 1964; Greenham 1972). Temperature cycles did not affect the development rate of the mud-crab *Rithropanoeus harrisii* (Gould) but markedly increased the survival near the upper lethal temperature (Costlow and Bookhout 1971); the latter finding being in accord with that of Moeur and Eriksen (1972) for *Lycosa carolinensis*. Hagstrum and Hagstrum (1970) and Hagstrum and Leach (1973) reviewed much of the later literature on the effects of fluctuating

temperature on growth. They showed that there were seven cases of reported decreased rates, six with no effect; 36 of the 89 cases examined showed less than 10% acceleration, and there was a maximum acceleration of 82%. These authors ignored any nonlinearity in the form of the R-T curves and did not assess whether the reported acceleration could have resulted from this factor alone. A. H. Weatherley (personal communication) found differences in the development rates of turtle eggs (*Chelonia mydas* Linn.) when they were subjected to temperature transfer experiments and suggested that the later stages of de-

velopment of the embryos may be temperature independent. In the blaberid cockroach, *Panesthia australis* Brunn., the elimination rate of ^{65}Zn was greater at 25 C than at 15 C. When the temperature was cycled on a sine wave with a 24-h period between 15 and 25 C, the elimination rate was not different from that at 25 C constant temperature (T. G. Marples, personal communication). These latter results are interesting in the present context as they are similar to the respiration data from *G. godeffroyi* where the cycling temperature data are not different in level from those obtained under constant temperature conditions at 30 C (table 3).

Several of the authors who reported acceleration in development rates under cycling temperatures derived the expected rate from a knowledge of the form of the development R-T curve. The rates of development of three species of fruit fly were increased under certain cycling temperatures (Messenger and Flitters 1959). Messenger (1964) similarly found increased rates in the aphid *Therioaphis maculata* (Buckton) and concluded his paper by saying "not only does a fluctuating temperature environment stimulate more rapid development . . . but it also greatly enhances female fecundity and adult longevity. . . . In addition, such fluctuating conditions allow the aphid to complete its life cycle over a much wider range of temperature levels than do constant conditions. Such general findings are quite important when attempts are made to evaluate geographical distribution or development, reproduction, and longevity in field situations." He was perhaps understating the case, for Lewontin (1965), working with life-table statistics, produced mathematical models

which indicated that a small increase in development rate alone (about 15%) was equivalent to a doubling in fecundity.

The influence of fluctuating temperatures on ectotherms has been examined from few aspects and on a very limited range of species. The literature is often confused because various authors were looking for different effects. Applied biologists have generally been interested in methods to predict development rates in the field and considered that acceleration was shown if the species developed faster than would be expected from the mean temperature of the temperature cycle. Others have been interested in whether the acceleration that occurred under cycling conditions was greater than expected from the form of the development R-T curve. The former response to cycling temperatures seems to be widely applicable, but there are still few well-founded reports of the latter response.

Acute temperature changes have been shown to affect respiration and Grainger (1956) found that in various crustacea such changes were associated with an energy cost, both on and upward and downward transfer. Accompanying the overshoot in oxygen consumption he found a marked change in the respiratory quotient and calculated that the overall cost of a two-way transfer was $0.545 \mu\text{l O}_2 10 \text{ mg}^{-1}$ (wet weight). A similar cost in *G. godeffroyi* would increase respiration by 22.5% for a two-way transfer.

TOWARD A HYPOTHESIS

In this section the possible mechanism involved in the observed increase in respiration by *G. godeffroyi* under cycling conditions will be discussed.

Arthropods have been widely shown

to undergo MRC to some extent (Carlisle and Cloudsley-Thompson 1968; Anderson 1970; Moeur and Eriksen 1972), and such compensation may be brought about by factors other than temperature, for example, by current velocity in trichopteran larvae (Feldmeth 1970) and salinity (Kinne 1958). Several types of MRC have been distinguished (Prosser 1958) and may be summarized as no MRC, a vertical shift in the R-T curve with no change in the Q_{10} rotation of the R-T curve with a change in the Q_{10} , or a combination of the latter two. The time course of MRC may be evolutionary, seasonal, or immediate (Hochachka and Somero 1973), and in the present context the latter two are of interest.

The biochemical basis underlying metabolic rate compensation has been examined (Precht 1958; Hochachka 1967; Mutchmore 1967; Bishop and Gordon 1967; Hochachka and Somero 1973). The evidence indicates that MRC is the resultant of the interaction of numerous enzymes, each of which has a series of isoenzymes produced differentially at different temperatures and which have different thermal optima. The temperature optima of different enzymes are no longer considered to be a simple balance between the increase in rate due to temperature and a decrease in rate due to thermal denaturation of the protein (Wilson et al. 1964; Licht 1967). In consequence, the time course of MRC must be limited by that of protein synthesis.

The existence of MRC has important implications to the manner in which laboratory respirometry is conducted when it is required for predictive purposes in the field. In addition, it can explain the observed increase in respiration seen in *G. godeffroyi* under cycling temperatures and the observed

increase in growth and development rates reported in the literature. To illustrate the point I will use data from Anderson (1970) who studied MRC in a number of spiders. He adapted spiders to 10, 20, and 30 C and measured the respiration of each group at all three temperatures.

I have plotted his data for two of the species he studied in figure 3. The data for *Lycosa lenta* are included because they are the most comparable to *G. godeffroyi* and the data from *Phidippus regius* (C. L. Koch) because this species illustrated most clearly the effects I wish to discuss. It is clear from these figures that, when the spiders were tested at the temperatures to which they were adapted, the resulting R-T relationship was a straight line. Testing at temperatures greater than those to which they were adapted increased respiration, and the greater the difference between the test and adaptation temperature the greater the respiration at temperatures above 20 C. Conversely, testing the spiders at temperatures below the adapted temperature had little or no effect. Similar results were found for the blowfly *Calliphora erythrocephala* (Tribe and Bowler 1968).

The thermal history experiments indicate that the form of MRC in *G. godeffroyi* was similar to that found in *L. lenta*. As the RMR in *G. godeffroyi* was measured at the temperature to which it was adapted, the following would occur with cycling temperatures. As the temperature rose, the rate would increase above that expected from the constant temperature conditions, because it has been shown that MRC takes about 3 days to occur in spiders (Anderson 1970; Hagstrum, 1970; Moeur and Eriksen 1972). As the temperature fell the respiration would not

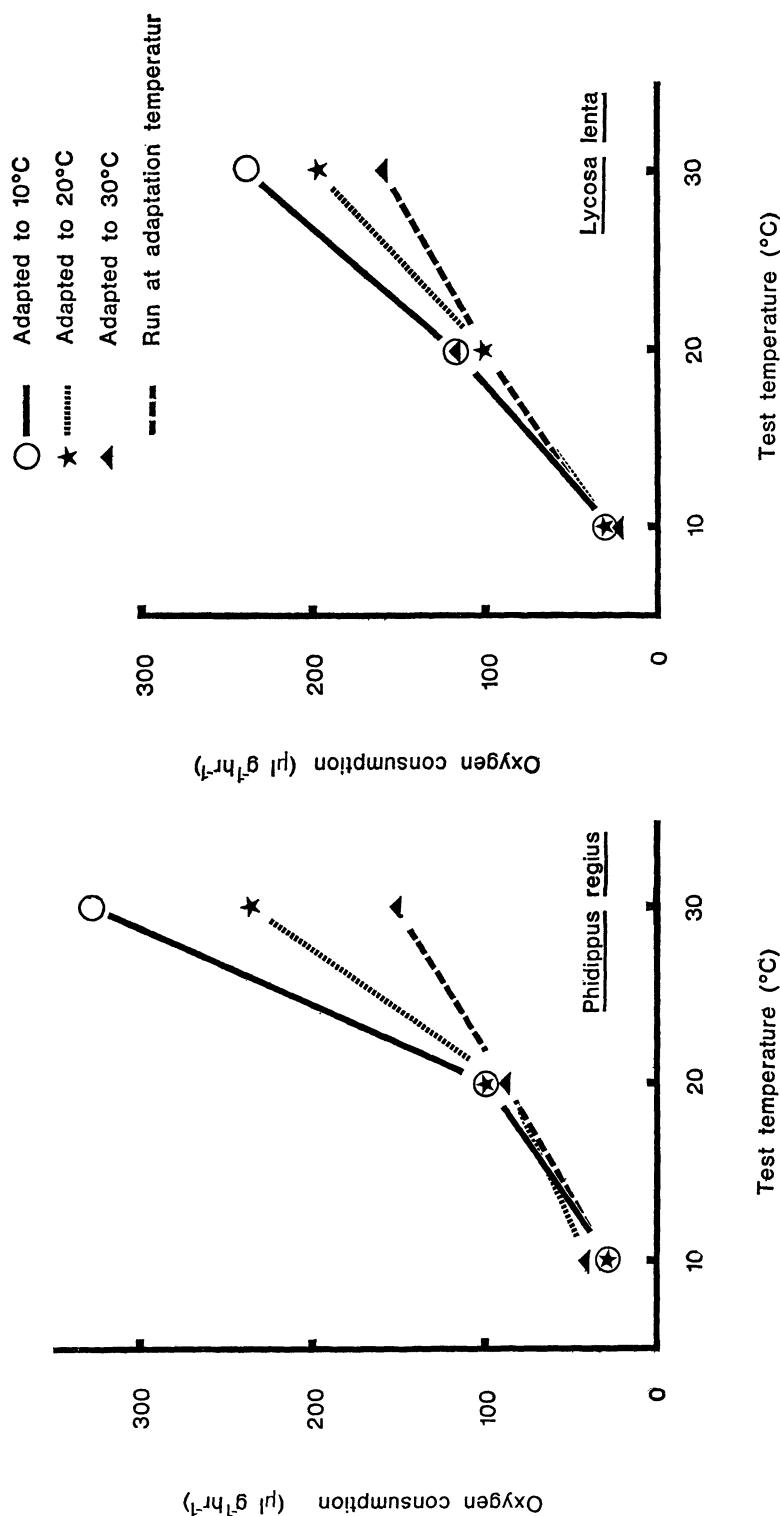


FIG. 3.—The respiration of *Phidippus regius* and *Lycosa lenta* under different adaptation and test temperatures. The figures were plotted from the data of Anderson (1970).

fall below that expected from the constant temperature experiments; the result would be an increase in respiration above that expected and due solely to the effects of MRC.

Using this argument one can roughly predict the increase in respiration expected under cycling temperature conditions above that expected from the mean temperature of the temperature cycle. This can be done for any species which has been subjected to MRC experiments of the type used by Anderson (1970) and Tribe and Bowler (1968). *Lycosa lenta* would be expected to show a 9.2% increase and *P. regius* a 28.5% increase. The spider *Filistratus hibernalis* (Hentz) (Filistatidae) was also examined by Anderson (1970) and should show an 8% increase, but the MRC response in this species was different from those of the other species and the compensation occurred when the measurements were made at temperatures below the adaptation temperature.

The previous argument can be applied in the same way to the acceleration of development rates observed under cycling temperatures and perhaps indicates why no explanation of the phenomenon has been proposed. In arthropods it is generally not possible to measure development rates at other than the adapted temperature due to the time course of MRC: development must be measured over a protracted period and MRC would occur within the experimental period. The types of measurements conducted on respiration by Anderson (1970), in which the measurement time was short

compared with the time required for MRC, consequently cannot be performed on arthropods with long development times. It may be possible to test the hypothesis by measuring division rates in some unicellular organisms due to their short generation time.

SUMMARY

Respiration was studied in the wolf spider *Geolycosa godeffroyi* at the temperatures to which they were adapted. The rate-temperature relationship was linear between 10 and 40 C. Respiration rates under a sine wave temperature cycle from 10 to 30 C would be expected to equal that at the mean of the temperature cycle. Under this variable temperature regime the respiration of the spiders was 135% of that at the mean temperature of the cycle.

These data are discussed with reference to other work relating cycling temperatures to biological rate processes. Using data from Anderson (1970), a hypothesis is developed suggesting that the increase in rate is due to the effects of metabolic rate compensation.

This study questions the validity of extrapolating rate-temperature curves, derived from a series of constant temperature experiments in the laboratory, to the variable thermal conditions in the field.

ACKNOWLEDGMENTS

I thank Dr. T. G. Marples and Prof. A. H. Weatherley for their helpful discussions and access to their unpublished data.

LITERATURE CITED

- ANDERSON, J. F. 1970. Metabolic rates of spiders. *Comp. Biochem. Physiol.* **33**:51-72.
- ANDREWARTHA, H. G., and L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- BAILEY, N. T. J. 1959. Statistical methods in biology. English Universities Press, London.
- BAKER, C. R. B. 1971. Egg and pupal development of *Spilosoma lubricipeda* in controlled temperatures. *Entomol. Exp. Appl.* **14**:15-22.
- BELEW, J. S. 1969. Ozonization. Pages 259-335 in R. L. AUGUSTINE, ed. Oxidation: techniques and applications in organic synthesis. Dekker, New York.
- BISHOP, L. G., and M. S. GORDON. 1967. Thermal adaptation of metabolism in anuran amphibians. Pages 263-280 in C. L. PROSSER, ed. Molecular mechanisms of temperature adaptation. Pub. 84. American Association for the Advancement of Science, Washington, D.C.
- BRETT, J. R., and D. A. HIGGS. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. *J. Fisheries Res. Board Can.* **27**:1767-1779.
- BURSELL, E. 1964. Environmental aspects: temperature. Pages 283-321 in M. ROCKSTEIN, ed. The physiology of insects. Vol. 1. Academic Press, New York.
- CARLYSLE, D. B., and J. L. CLOUDSLY-THOMPSON. 1968. Respiratory function and thermal acclimation in tropical invertebrates. *Nature* **218**:684-685.
- CLOUDSLY-THOMPSON, J. L. 1953. The significance of fluctuating temperatures on the physiology and ecology of insects. *Entomologist* **86**:183-189.
- . 1961. Rhythmic activity in animal physiology and behaviour. Academic Press, London.
- COSTLOW, J. B., and C. G. BOOKHOUT. 1971. The effect of cyclic temperatures on larval development in the mud-crab *Rhithropanopeus harrisi*. Pages 211-220 in D. J. CRISP, ed. Fourth European marine biology symposium. Cambridge University Press, London.
- DRESCO-DEROUET, L. 1961. Le métabolisme respiratoire des scorpions. I. Existence d'un rythme nyctéméral de la consommation d'oxygène. *Bull. Mus. Hist. Nat., Paris*. **32**:553-557.
- FELDMETH, C. R. 1970. The influence of acclimation to current velocity on the behaviour and respiratory physiology of two species of stream trichoptera larvae. *Physiol. Zoöl.* **43**:185-193.
- GRAINGER, J. N. R. 1956. Effects of changes of temperature on the respiration of certain crustacea. *Nature* **178**:930-931.
- GREENHAM, P. M. 1972. The effect of the temperature of cattle dung on the development of the larvae of the Australian bushfly, *Musca vetustissima* Walker (Diptera: Muscidae). *J. Anim. Ecol.* **41**:429-438.
- GROMADSKA, M. 1962. Changes in respiration metabolism of *Lumbricus castaneus* Sav. under influence of various constant and alternating temperatures. (In Polish.) *Stud. Soc. Sci. Torunensis* **6**:179-189.
- HAGSTRUM, D. W. 1970. Ecological energetics of the spider *Tarentula kochi* (Araneae:Lycosidae). *Ann. Entomol. Soc. Amer.* **63**:1297-1304.
- HAGSTRUM, D. W., and W. R. HAGSTRUM. 1970. A simple device for producing fluctuating temperatures, with an evaluation of the ecological significance of fluctuating temperatures. *Ann. Entomol. Soc. Amer.* **63**:1385-1389.
- HAGSTRUM, D. W., and C. E. LEACH. 1973. Role of constant and fluctuating temperatures in determining development time and fecundity of three species of stored product Coleoptera. *Ann. Entomol. Soc. Amer.* **66**:407-410.
- HOCHACHKA, P. W. 1967. Organisation of metabolism during temperature compensation. Pages 177-203 in C. L. PROSSER, ed. Molecular mechanisms of temperature adaptation. Pub. 84. American Association for the Advancement of Science, Washington, D.C.
- HOCHACHKA, P., and G. N. SOMERO. 1973. Strategies of biochemical adaptation. Saunders, London.
- HOWE, R. W. 1967. Temperature effects on embryonic development in insects. *Annu. Rev. Ent.* **12**:15-42.
- HUMPHREYS, W. F. 1973. The environment, biology and energetics of the wolf spider *Lycosa godeffroyi* (L. Koch 1865). Ph.D. diss. Australian National University, Canberra. 353 pp.
- . 1974. Behavioural thermoregulation in a wolf spider. *Nature* **251**:502-503.
- . In press. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (Koch 1865) (Araneae:Lycosidae). *J. Anim. Ecol.*
- JOHNSON, C. G. 1940. Development, hatching and mortality of the eggs of *Cimex lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature. *Parasitology* **32**:137-173.
- KINNE, O. 1958. Adaptation to salinity variations—some facts and problems. Pages 92-106 in C. L. PROSSER, ed. Physiological adaptations. American Physiological Society, Washington, D.C.
- LAMB, K. P. 1961. Some effects of fluctuating temperatures on the metabolism, development, and rate of population growth in the cabbage aphid, *Brevicoryne brassicae*. *Ecology* **42**:740-745.
- LEWONTIN, R. C. 1965. Selection for colonizing ability. Pages 77-94 in H. G. BAKER and G. L. STEBBINS, eds. Genetics of colonizing

- species. Academic Press, London and New York.
- LICHT, P. 1967. Thermal adaptation in the enzymes of lizards in relation to preferred body temperature. Pages 131-145 in C. L. PROSSER, ed. Molecular mechanisms of temperature adaptation. Pub. 84. American Association for the Advancement of Science, Washington, D.C.
- MACFADYEN, A. 1961. A new system for continuous respirometry of small air-breathing invertebrates under near natural conditions. *J. Exp. Biol.* **38**:323-341.
- . 1967. Methods of investigation of productivity of invertebrates in terrestrial ecosystems. Pages 383-412 in K. PETRUSEWICZ, ed. Secondary productivity of terrestrial ecosystems (principles and methods). Polish Academy of Sciences Institute of Ecology and International Biological Programme PT., Warsaw-Krakow.
- MESSENGER, P. S. 1964. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Theroaphis maculata*. *J. Econ. Entomol.* **57**:71-76.
- MESSENGER, P. S., and N. E. FLITTERS. 1959. Effect of variable temperature environments on egg development of three species of fruit flies. *Ann. Entomol. Soc. Amer.* **52**:191-204.
- MOEUR, J. E., and C. H. ERIKSEN. 1972. Metabolic responses to temperature of a desert spider, *Lycosa (Pardosa) carolinensis* (Lycosidae). *Physiol. Zoöl.* **45**:290-301.
- MUTCHMORE, J. A. 1967. Temperature adapta-
- tion in insects. Pages 165-176 in C. L. PROSSER, ed. Molecular mechanisms of temperature adaptation. Pub. 84. American Association for the Advancement of Science, Washington, D.C.
- PRECHT, H. 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold-blooded animals. Pages 50-78 in C. L. PROSSER, ed. Physiological adaptation. American Physiological Society, Washington, D.C.
- PROSSER, C. L. 1958. General summary: the nature of physiological adaptation. Pages 167-180 in Physiological adaptation. American Physiological Society, Washington, D.C.
- SEYMOUR, R. S., and A. VINEGAR. 1973. Thermal relations, water loss and oxygen consumption of a North American Tarantula. *Comp. Biochem. Physiol.* **44**:83-96.
- TRIBE, M. A., and K. BOWLER. 1968. Temperature dependence of "standard metabolic rate" in a poikilotherm. *Comp. Biochem. Physiol.* **25**:427-436.
- WAGER, H. G., and F. A. E. PORTER. An apparatus for the automatic measurement of oxygen uptake by electrolytic replacement of oxygen consumed. *Biochem. J.* **81**:614-618.
- WILSON, A. C., N. O. KAPLAN, L. LEVINE, A. PESCE, M. REICHLIN, and W. S. ALLISON. 1964. Evolution of lactic dehydrogenases. *Fed. Proc. Fed. Amer. Soc. Exp. Biol.* **23**:1258-1266.
- WOODLAND, D. J. 1973. The ozone problem in electrolytic respirometry and its solution. *J. Appl. Ecol.* **10**:661-662.