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Respiratory Physiology of the Scorpion Paruroctonus Aquilonalis

Wayne A. Riddle

RESPIRATORY PHYSIOLOGY OF THE SCORPION - RIDDLE

THE UNIVERSITY OF NEW MEXICO
ALBUQUERQUE, NEW MEXICO 87106

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RESPIRATORY PHYSIOLOGY OF

THE SCORPION PARUROCTONUS AQUILONALIS

Title

Wayne A. Riddle

Candidate

Biology

Department

Bernard Spolsky

Dean

November 23, 1976

Date

Committee

Clifford S. Crawford

Chairman

M. F. Riedesel

J. David Ligon

James R. Gosz

RESPIRATORY PHYSIOLOGY OF
THE SCORPION _PARUROCTONUS_ _AQUILONALIS_

By

Wayne A. Riddle

B.S., Utah State University, 1968
M.S., University of New Mexico, 1973

DISSERTATION

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ABSTRACT OF DISSERTATION

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ABSTRACT

The scorpion Paruroctonus aquilonalis (Stahnke) was studied to better understand the influence that six potentially important factors (size, sex, temperature, nutrition, season, and humidity) have on its respiratory metabolism. Respiratory rate: temperature relations of oxygen consumption from 5°C to 36°C, and standard metabolism estimates at 20°C and 25°C were employed. Respirometry was performed on both freshly collected mature and immature scorpions and on laboratory-maintained animals.

Inverse weight: metabolism relationships were noted for males and females above 24°C, but below 24°C live weight did not influence metabolic rate among females. For mature males positive weight: metabolism patterns were found below 24°C due to seasonally elevated levels of oxygen consumption. Respiratory temperature coefficient (Q_{10}) values were found to vary with live weight, demonstrating a general trend of lower Q_{10} with larger size.

Prolonged starvation of adult females lowered the slope of metabolic rate: temperature (R:T) curves, and also depressed standard metabolic rates at 20°C. These changes were considered as highly adaptive means of conserving energy during starvation periods.

R:T curves for scorpions previously exposed for about 2 weeks to either 10°C or 24°C differed significantly at most test temperatures. These changes, however, were probably complicated by starvation effects, so that evidence for thermal acclimation through changes in R:T curves was inconclusive.

Seasonal changes in R:T curves were found for mature females, although the adaptive significance of these changes remained unclear. For adult males collected in August, depression of standard metabolism at 20°C was tentatively correlated with natural starvation resulting from high locomotor activity and inadequate nutrition.

Respiratory quotient (RQ) did not change with starvation for females but did increase significantly for freshly collected mature males following laboratory feeding. Measured RQs indicated a predominant utilization of lipid as a substrate in respiration.

Oxygen consumption at 25°C under 10% and 80% relative humidity (rh) did not differ significantly for either freshly collected or laboratory-starved adult males. For severely desiccated scorpions, metabolic rates were extremely high and variable at 10% rh, but decreased substantially following exposure to 80% rh.

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INTRODUCTION

General.

The respiratory physiology of a large and successful group of terrestrial arthropods, the arachnids, is becoming better understood. Information on the respiratory metabolism of spiders has been presented by Phillipson (1962, 1963), Anderson (1970, 1974), Mouer and Ericksen (1972), Myrcha and Stejgwillo-Laudanska (1973), and Seymour and Vinegar (1973). Studies by Dresco-Derouet (1960, 1964, 1967), Hadley and Hill (1969), Anderson (1970), Hadley (1970a), Shorthouse (1971), Crawford and Wooten (1973), and Crawford and Riddle (1975), have dealt with scorpion respiratory physiology. Anderson (1970) has also studied the minor arachnid orders Solifugae and Amblypygi (the sun-spiders and amblypygids, respectively), while Ahearn (1970) has examined the respiration of whipscorpions (order Uropygi). The respiratory physiology of mites (order Acarina), and its relationship to water relations also has been examined (Kanungo, 1965; Arlian, 1975).

The subject organism of this dissertation, the vejovid scorpion _Paruroctonus aquilonalis_, occupies a desert-grassland habitat that displays wide and unpredictable variations in ambient temperature and available moisture in both daily and seasonal time spans. Activities of resident arthropods including scorpions are understandably attuned to physiologically optimal thermal and water conditions of the physical environment; therefore, activity is often restricted to night periods during warmer seasons. The extent to which environmental extremes can be avoided, either by behavioral or physiological means, clearly influences survival. An arachnid predator like _P. aquilonalis_, in

addition to avoiding the temperature and desiccation extremes within its physical environment by burrowing and nocturnality, also deals with a more or less unpredictable availability of prey. Conservation of stored energy reserves in the light of both variable temperature conditions and an unpredictable food supply suggests the existence of homeostatic means of controlling the loss of stored energy in respiration.

Desert scorpions have evolved morphological and behavioral mechanisms for dealing with temperature and desiccation extremes (Hadley, 1974; Cloudsley-Thompson, 1975). Previous studies on the respiratory physiology of scorpions have dealt with size and the general nature of respiration rate: temperature (R:T) relations; however, acclimation and acclimitization changes in metabolic rate have not been examined thoroughly. Nutritional and seasonal influences on R:T relations have received no experimental attention.

This dissertation summarizes the results of previous studies that have dealt with the respiratory responses of invertebrate poikilotherms to six potentially important factors, namely size, sex, temperature, nutrition, season, and water relations. In addition, it presents results of experiments designed to assess the influence of these factors on the respiratory metabolism of the scorpion, *Paruroctonus aquilonalis* (Stahnke).

Modes of metabolic adaptation to temperature change by poikilotherms.

Scholander *et al*. (1953) indicated that homeostasis of metabolic rate in poikilotherms can be achieved in three ways. First, it can be attained through a lateral translation of the organism's metabolic

rate: temperature (R:T) curve; which tends to maintain relatively constant rates of metabolism with long-term or seasonal changes in environmental temperature. Second, on a short-term or daily basis, reduced temperature dependence of respiration (lower respiratory temperature coefficient or Q_{10}) tends to render rapid temperature change less effective in changing metabolic rate than would be the case if a high temperature dependence (high Q_{10}) existed. Finally, homeostasis of metabolic rate is favored by the organism's selection of a more or less constant thermal environment.

Bullock (1955) considers that long-term or seasonal temperature compensation can be accomplished among poikilotherms by shifts in R:T curves which are often accompanied by changes in the elevation or slope of curves with acclimation. Common patterns of temperature adaptation of rate functions and underlying patterns of biochemical adaptation such as changes in enzyme kinetics and isozyme production are fully described by Prosser (1973).

Evidence exists for translation (Prosser, 1973) of R:T curves resulting from laboratory acclimation or seasonal acclimitization for a wide variety of invertebrate poikilotherms. In laboratory acclimation experiments with terrestrial gastropods (Segal, 1961; Roy, 1963; Rising and Armitage, 1969), lateral translation of R:T curves to the right (favoring lower metabolic rates at higher temperatures) following warm-acclimation are evident or at least suggested. However, in acclimation experiments with two species of land snails (Riddle, in press), R:T curves following warm-acclimation were elevated, though not significantly so, over those of cold-acclimated animals. Elevated R:T curves for

cold-acclimated intact specimens and isolated tissues of the sea urchin were clearly demonstrated by Percy (1974a). For terrestrial arthropods, similar, though less well-defined trends are shown in R:T curves for cold- and warm-acclimated isopods (Edney, 1964) and millipedes (Dwarakanath, 1971).

Clear seasonal changes in R:T relations have not been noted among all poikilotherms previously studied in this context. For sea urchins collected in summer, translation to the right of R:T curves for both intact animals (Percy, 1972) and excised tissues (Percy, 1974b) closely resemble those following warm-acclimation in the laboratory (Percy, 1974a). Similarly, winter R:T curves for a cestode parasite of fish were elevated relative to those of summer-collected worms, but only between 10°C and 30°C (Davies and Walkey, 1966). For three species of cirriped crustaceans, however, the only consistent changes in seasonal R:T relations were depressed midwinter curves relative to those obtained during warmer seasons (Barnes and Barnes, 1969). No evidence for seasonal acclimitization were found in R:T curves for shrimp (McFarland and Pickens, 1965), millipedes (Gromysz-Kalkowska, 1970) or for marine snails (Huebner, 1973). Only inconclusive evidence for seasonal acclimitization by translation of R:T curves was noted for litter-inhabiting montane centipedes (Riddle, 1976).

Seasonal acclimitization through changes in R:T relations does not appear common in insects (Keister and Buck, 1964). Scholander _et_ _al_. (1953) also concluded, based on studies of both arctic and tropical insects, that there is little or no seasonal acclimitization of respiration rate to temperature. While seasonal acclimitization may not

be common in adult insects in their active season, during adverse environmental conditions many insects undergo diapause. Keister and Buck (1964) have characterized diapause as a "long, experimentally useful period during which metabolic rate, on a unit basis, is extraordinarily low and (temperature) stable."

In addition to seasonal changes in R:T relations among some poikilotherms, seasonal changes in oxygen consumption measured at a single temperature have been found. Elevated spring respiration rates at 16°C in terrestrial isopods were tentatively related to reproductive activities (Phillipson and Watson, 1965). For overwintering desert millipedes, oxygen consumption at 20°C sharply declined during the inactive season spent underground, while it remained high during the short summer surface-active season (Wooten and Crawford, 1974). Evidence for a depression of oxygen-consumption rates among overwintering centipedes was also suggested in the results of Crawford _et al_. (1975).

The second potential avenue of homeostasis of metabolic rate cited by Scholander _et al_. (1953) was that of general temperature insensitivity of respiratory rate as indicated by low Q_{10} values. Low Q_{10} values have been found in several marine invertebrates by Newell and Northcraft (1967). Central to the significance of that study was that two distinct types of metabolism existed for these animals: a thermosensitive type displayed by actively moving or ventilating animals, and a resting type, which is largely insensitive to temperature change and which is characteristic of inactive animals. Patterns of active and resting metabolism in marine invertebrates have since been verified by Mangum and Sassmann (1969) and Coyer and Mangum (1973), but comparable temperature

insensitivity by low Q_{10} was not found. Other evidence for temperature insensitivity in intertidal invertebrates has come from the results of Newell and Pye (1970a, 1970b, 1971a) for intact animals, and from Percy and Aldrich (1971) for excised tissues. In contrast, temperature insensitivity of standard metabolism was not noted in other work with crabs and intertidal molluscs, in which both whole animals and excised tissues were examined (Davies and Tribe, 1969).

In insects, general temperature dependence was clearly established for standard metabolic rates of a fly (Tribe and Bowler, 1968). Those results were consistent with the results of Scholander _et al_. (1953), who found no case of adaptation of metabolism to temperature change by low Q_{10} among arctic and tropical poikilotherms, and who further suggested that metabolic adaptation to temperature, if it occurs, lies in lateral displacement of R:T curves.

Nutrition may influence the temperature sensitivity as well as the magnitude of respiration. In the barnacle _Balanus balanoides_, starved animals expressed low Q_{10} values, while fed animals showed higher Q_{10} values (Barnes _et al_., 1963). When this species was deprived of food, stored carbohydrates were utilized first, followed by lipid and protein. In subcellular preparations of tissues from the intertidal snail _Littorina littorea_, Newell and Pye (1971a, 1971b) correlated temperature dependence of oxygen consumption with the availability of metabolic substrates. A similar relationship was demonstrated in subcellular preparations from well fed and starved crabs (Marsden, 1973). A decrease in both the level and the slope of R:T curves for oxygen consumption following starvation of intact crabs has also been established (Marsden _et al_., 1973).

The influence of size on Q_{10} values for a variety of rate functions in poikilotherms has been discussed by Rao and Bullock (1954). In analyzing data from a number of sources, the authors found that Q_{10} usually increased with increasing size of the organism. This generalization was not without exception, however, and was based only on a few samples. Subsequent experiments by Mason (1971) with woodland snails supported that generalization. In contrast with the size and Q_{10} generalizations of Rao and Bullock (1954), Q_{10} values have also been shown to decrease with increasing live weight in several invertebrates (Akerlund, 1969; Barnes and Barnes, 1969). Results of Roberts (1957), Read (1962), Pamatmat (1969), and Huebner (1973), did not indicate either increasing or decreasing Q_{10} values with size in the invertebrate poikilotherms they studied.

Finally, homeostasis of metabolic rate can be influenced by the selection of a constant thermal environment. The extent to which extremes of temperature can be avoided by burrowing was demonstrated by Hadley (1970b) for the scorpion *Hadrurus arizonensis*. During a 24-hour period in summer, when soil-surface temperatures varied between 20°C and 66°C, vertical movements within a burrow were responsible for a scorpion's body temperature change of only 12°C (30°C to 42°C) during the same period. Avoidance of extremely low winter temperatures by vertical movements in burrows for the scorpion *Diplocentrus spitzeri* was suggested by Riddle and Pugach (1976).

Respiratory metabolism of arachnids.

1. Influence of mode of predation, temperature, size, and sex.

Anderson (1970) has interpreted the results of his studies on the

respiratory metabolism of spiders in terms of predation strategy and evolution. His results show much lower rates of oxygen consumption among arachnids generally than among other poikilotherms of comparable size, with members of primitive spider groups displaying lower rates than spiders in more advanced taxa. He proposed that low metabolic rates and consequently diminished energy expenditure were essential qualities for dealing with unpredictable availability of prey.

The capacity for compensation of metabolic rates following a single, acute temperature increase was found to vary between spiders displaying different predation strategies. This variability was demonstrated in two species: *Phidippus regis* (a "hunting" spider) and *Filistata hibernalis*, (a "sedentary" web-building spider). *Phidippus* expressed a metabolic rate roughly twice that of *Filistata* at 20°C. This higher rate was interpreted as highly adaptive and consistent with the active mode of predation of *Phidippus*. More important was the finding that the hunting species *P. regis* demonstrated considerable compensation after 3 days of exposure to 30°C following acclimation at 20°C. This new rate was comparable to that maintained by its sedentary counterpart *F. hibernalis* at 30°C following the same temperature change. Anderson (1970) proposed that high compensation ability is an inherent quality of spiders possessing relatively high metabolic rates and speculated that "minimal" rates, sufficient to keep spiders alive and responsive, are similar in both species. Noncompensating, "sedentary" spiders would be living close to their "minimal" rate at each temperature. This strategy is conducive to minimum energy expenditure, and is consistent with the sedentary mode of predation of *F. hibernalis*. Anderson suggests that

actively foraging spiders are afforded the "luxury" of relatively high metabolic rates in utilizing more dependable food sources.

The scorpions Centruoides sculpturatus and C. hentzi studied by Anderson (1970) displayed weight-specific metabolic rates at 20°C that were among the lowest of the wide variety of arachnids examined, and below those of most spiders of comparable weight. His graphically presented results showed that arachnids occupy a position well below the metabolic rate: weight relationship proposed by Hemmingsen (1960) for other poikilotherms.

In contrast to the examples cited above for some marine invertebrates, metabolic compensation for temperature through low Q_{10} values is not evident for most arachnids. Respiratory Q_{10} results for selected arachnids are summarized in Table 1. Those results should be interpreted with care because of the differing respirometry techniques employed and also because acclimation and feeding pretreatments varied. However, these results adequately demonstrate that for the arachnids examined, the potential for metabolic homeostasis by utilizing low Q_{10} is only of limited significance.

Two exceptions to the general trend of overall temperature dependence of metabolism are evident in Table 1. First, for the tarantula Aphonopelma, a trend of decreasing Q_{10} with increasing temperature is apparent. The very low Q_{10} at 30-40°C could be adaptive in conserving respiratory energy, and occurs at a range of temperatures to which those spiders were exposed during nighttime surface activity (23-31°C) or in burrows (30-35°C daily range). The second example of low Q_{10} values over sizable temperature ranges (23-29°C and 29-39°C) is evident in the

results for Lycosa carolinensis. It is significant that the temperature ranges at which low Q_{10}'s occurred for that spider changed seasonally, roughly corresponding to changes in environmental temperature.

Using weight: metabolism regression equations of Shorthouse (1971) for the scorpion Urodacus yashenkoi, the influence of live weight on Q_{10} can be estimated. Q_{10} values for U. yashenkoi presented in Table 2 can be directly compared with those of Table 1 and with results from P. aquilonalis that are reported in the present study.

Table 2 shows highly variable Q_{10} values over 5°C temperature changes for U. yashenkoi. Q_{10}'s from 20-30°C are comparatively low for 0.5 g scorpions when compared with those of 3.0 g animals. This trend of higher Q_{10}'s with increasing live weight is consistent with the size and Q_{10} generalization found by Rao and Bullock (1954) and Mason (1971). When a 25 to 35°C temperature change is considered, little influence of live weight on Q_{10} is evident.

Live weight has been shown to influence metabolic rate in both Lycosa carolinensis spiders (Mouer and Ericksen, 1972) and Urodacus yashenkoi scorpions (Shorthouse, 1971). In Lycosa carolinesis spiders oxygen consumption at 39°C was substantially influenced by live weight only for spiders weighing up to about 0.8 g. In that weight range, oxygen-consumption rates were about four times higher for spiders weighing 0.2 g than for those weighing 0.6 g. Linear regressions relating live weight to metabolic rate were not calculated for this small weight range due to small sample size, but a trend of higher rates among smaller spiders was apparent. For Urodacus yashenkoi scorpions, rates of oxygen consumption were measured for various-sized scorpions

at a variety of temperatures. When double logarithmic plots of weight: metabolism regressions were constructed (not shown), negative slopes were found indicating an inverse relationship between weight and metabolic rate. The position and slope of regression lines changed with the temperature at which oxygen consumption was measured, but indicated an overall inverse dependence of oxygen consumption with live weight.

Double logarithmic plots of weight: metabolism results for other poikilotherms indicated increasingly steep negative regression line slopes with increasing temperature for aquatic snails (Akerlund, 1969); and collembolans (Tilbrook and Block, 1972). In contrast, other studies with collembolans (Block and Tilbrook, 1975) and with crabs (Roberts, 1957) showed slopes which remained similar over a range of test temperatures.

Sex did influence metabolic rate in previous studies with scorpions. Examples of higher metabolic rates for male scorpions can be found in the results of Dresco-Derouet (1964) and Hadley and Hill (1969). For both studies, higher metabolic rates may have been attributed at least in part to the smaller size of male scorpions.

Dresco-Derouet (1964) found that gravid female scorpions often displayed higher rates than males, suggesting an elevation of metabolic rates due to the embryonic development of young. Increasing metabolic rate at 5°C during winter among female scorpions was also tentatively correlated with embryonic development (Crawford and Riddle, 1975).

2. Influence of thermal acclimation.

Compensation of metabolic rates of spiders following an acute temperature increase from 20 to 30°C has been discussed above in terms

of predation strategy (Anderson, 1970). For actively foraging spiders, temperature increase was associated with an initial "overshoot" in metabolic rate followed by a marked decrease in rate within a few days at the higher temperature. No compensation was noted for similarly exposed "sedentary" spiders. Metabolic rates of spiders of these two predation types were also measured at 20°C following feeding and maintenance at 20°C for 3 weeks. Oxygen consumption was then measured following a temperature decrease to 10°C. Metabolic rates for all spiders at 10°C remained low and did not show any significant increase during the following 8 days of measurements. Although this lack of compensation did not suggest metabolic homeostasis, it was considered adaptive by Anderson. Its adaptive significance was based on the assumption that the activity of the spider's potential prey would be inhibited at 10°C. If this occurred, it would be adaptive for spiders facing a "cold-inhibited" food supply to maintain low rates at 10°C rather than to increase them as part of a compensatory change in metabolic rate.

As part of other acclimation experiments, Anderson (1970) found that for three of the four spider species examined, appreciably higher rates at 30°C were observed for specimens previously acclimated to 10 or 20°C than for those acclimated to 30°C. The species showing no change in metabolic rate was Filistata hibernalis, which had also demonstrated no compensation in metabolic rate over time following either an increase or decrease in temperature from 20°C.

Mouer and Ericksen (1972) also demonstrated compensation following an acute temperature increase from 29 to 39°C with Lycosa carolinensis

spiders. Oxygen-consumption levels measured daily at 39°C following temperature increase dropped significantly after 8 days. Compensation was not evident following a small temperature increase (39 to 41°C); rather, oxygen consumption increased only slightly during the 2 days following temperature increase.

In contrast to the compensatory changes in metabolic rate of spiders following an acute temperature increase (Anderson, 1970; Mouer and Ericksen, 1972), results of Crawford and Riddle (1975) with *Diplocentrus spitzeri* scorpions indicated non-compensatory changes in metabolic rate following an acute temperature change. In their experiments, scorpions collected in January were maintained at 5°C (the estimated habitat temperature) for 2 days following collection. Oxygen consumption was then measured at 22°C immediately following exposure at that temperature, and after 3 and 10 days of continuous exposure to 22°C. For both males and females, oxygen consumption at 22°C was substantially higher on the tenth day than on the first. For females, the mean rate after 10 days was similar to that of females at 22°C in June. For males, however, rates on the tenth day were still far below those displayed in June.

The acclimation results cited above for *D. spitzeri* are significant insofar as they imply that the capacity for compensatory changes in metabolism (favoring lower metabolic rates for some time following exposure to a higher temperature), if it does exist, may be seasonally limited. Secondly, the results of that study show a lack of compensation ability for *D. spitzeri* scorpions which is consistent with the trend described for "sedentary" spiders (Anderson, 1970), and by inference expected of other "sedentary" arachnid predators. Finally, the work of

Crawford and Riddle (1975) suggests that seasonal trends in metabolism may be present in scorpions. High midsummer metabolic rates for male scorpions were not developed simply by acclimating winter scorpions to a "summer" temperature of 22°C; rather, elevated summer metabolic rates appeared to be a seasonal phenomenon, possibly associated with a metabolism attuned to mate-searching activity (Williams, 1966).

Thermal acclimation properties of scorpions were investigated by Dresco-Derouet (1967). In contrast with studies of compensatory adaptation following an acute temperature increase or decrease, she examined the influence of long- and short-term exposure to relatively high and low temperatures on oxygen consumption at an intermediate temperature. Her results indicated that scorpions acclimated 4 days at 3-5°C displayed significantly higher rates at 16°C or 21°C than those acclimated at 26-27°C. When 2-3 week acclimation periods at those temperatures were imposed, no differences in rates were found.

The only previous study with arachnids directed at examining possible changes in R:T relations following acclimation was conducted by Seymour and Vinegar (1973) on the tarantula *Aphonopelma*. Their results clearly demonstrated that 2-week acclimation at 10°C or 30°C did not modify R:T curves over a range of temperatures from 10 to 40°C.

3. Influence of season.

Mouer and Ericksen (1972) have provided information on the seasonal respiratory metabolism of the desert wolf spider, *Lycosa carolinensis* from Arizona. R:T curves were constructed for oxygen-consumption rates from 29°C to 47°C for spiders collected in June, and from 23°C to 47°C for January-collected spiders. June and January R:T curves were

essentially of the same slope, but the June curve was translated to the right relative to the January curve. This translation favors seasonal homeostasis of metabolism, because it provides lower rates among warm-adapted (June) spiders, than among cool-adapted (January) animals at the same temperature.

The respiratory physiology of the scorpion Diplocentrus spitzeri was investigated by Crawford and Riddle (1975) as part of a study of overwintering physiology and cold hardiness. Adult females collected in December, 1972 and January and February, 1973 had different metabolic rates at 5°C. Rates increased steadily from December (about 25 $\mu l\ g^{-1}\ hr^{-1}$) through January (about 41 $\mu l\ g^{-1}\ hr^{-1}$) to February (about 60 $\mu l\ g^{-1}\ hr^{-1}$). December and February rates differed significantly ($P<0.01$). February, 1972 and February, 1973 levels (both measured at 5°C) did not differ, suggesting constancy of oxygen consumption during the same month of the year. Except for changes noted during the winter, females showed roughly comparable metabolic rates while estimated habitat temperatures ranged among 12°C (April), 20°C (October), 22°C (June), and 25°C (August), suggesting possible seasonal acclimitization. Seasonal respiration for adult male D. spitzeri was more variable. In contrast to winter rates of females, males showed more constant, though higher rates. During June and August, however, rates of males were greatly elevated over those of females.

In the case of a spider Pisura mirabilis, respiratory rates at 20°C were found to decline sharply in November, and to remain low throughout the winter, suggesting a reduced metabolic activity characteristic of diapause (Dondale and Legendre, 1971).

4. Influence of starvation.

Starvation has been discussed with regard to temperature dependence of metabolism for certain marine invertebrates. Starvation is also of potential importance in influencing the magnitude and temperature relations of respiration in terrestrial organisms. It is of special potential significance to arachnids for which food may not be continually available, and in particular to arachnids that are temperate-region predators and for which prey availability is also seasonally restricted. The influence of starvation on standard oxygen-consumption rates at 20°C of spiders has been reported in studies by Anderson (1974) and Myrcha and Stejgwillo-Laudanska (1972). In the former study oxygen-consumption rates decreased 30 to 40% after 20 days of starvation without any evident impairment of normal activities. In the latter study, metabolic rates decreased initially and then increased during prolonged starvation.

Starvation effects on R:T relations have not been previously investigated for arachnids, but have been studied in terrestrial isopods (Newell *et al.*, 1974) and centipedes (Riddle, 1976). In the former study, R:T curves for isopods starved 1 to 3 days were similar to those constructed from "standard" or "resting" rates of metabolism over a range of temperatures. In the latter study, starved centipedes showed both a decrease in the level of oxygen consumption at most temperatures and a decrease in the slope of R:T curves.

5. Influence of water relations and humidity.

Although active ventilation movements have not been observed for scorpions, the passive mode of gas exchange across the respiratory

surfaces of the book lungs (Zoond, 1930), is associated with some water loss. Studies by Hadley (1970a) and Crawford and Wooten (1973) have quantified the contribution of respiratory water loss to total water loss for two species of scorpions.

While those studies have tested the influence of respiration on water loss, little information exists on the influence of water-balance status and relative humidity on respiratory rates of desert invertebrates. For desert snails, exposure to low humidity during dormancy was associated with a depression of metabolic rates at 25°C (Riddle, 1975). Desert ants have the opposite pattern, with low relative humidity (rh) being associated with higher metabolic rates (Kay and Whitford, 1975). Hadley (1970a) observed significantly lower rates of oxygen consumption at 30°C among normally hydrated *Hadrurus arizonensis* scorpions at 0% rh that at 50-60% rh. Rates for previously desiccated scorpions were extremely high and variable, but did not differ significantly from those found for normally hydrated animals at 0% rh.

Summary.

The previous information presented for arachnids and other invertebrate poikilotherms has outlined trends of metabolic adaptation that may also be applicable to *Paruroctonus aquilonalis*. Major trends and their possible adaptive significance to *P. aquilonalis* are summarized below.

1. *Metabolic adaptation for temperature change (R:T relations, Q_{10})*.

Evidence for changes in R:T relations in marine and non-arthropod terrestrial invertebrates is substantial, while it is generally lacking for terrestrial arthropods. Seasonal R:T changes for desert spiders

suggest that seasonal and/or acclimation changes may also be present in _P. aquilonalis_. It should be noted that examples of seasonal compensatory R:T changes favoring homeostasis of metabolic rate have come both from animals which remain more or less active throughout the year and from those that do not. Compensatory R:T changes may not be adaptive to _P. aquilonalis_, which is completely inactive underground from October to March. Rather, non-compensatory R:T changes favoring lower metabolic rates and therefore improved energy conservation during the non-feeding, inactive season might better serve this scorpion. Short-term metabolic adaptation by maintaining a low Q_{10} appears an unlikely mode of adaptation for _P. aquilonalis_ because it seems rare among arachnids and poikilotherms in general. Metabolic compensation for temperature change by selection of a more or less constant thermal environment by appropriate daily vertical movements in burrows is probably utilized by _P. aquilonalis_ and other poikilotherms, and may be the only way scorpions deal with short-term changes in environmental temperature.

2. _Other factors (Size, sex, and nutrition)_.

The large body of information concerning the effect of size on metabolic rate leads to the prediction that smaller _P. aquilonalis_ scorpions should display higher metabolic rates than larger specimens. Since previous information on the influence of temperature on size: metabolism relations varied widely among the invertebrates discussed, the way in which temperature might influence weight: metabolism relations for _P. aquilonalis_ is difficult to predict.

Previous literature on scorpions indicates patterns of elevated metabolic rates for males during summer and possibly for females during winter. Both these metabolic changes are very likely to be displayed by *P. aquilonalis* as well, and might be related to seasonal reproductive activities.

The two major metabolic effects of starvation among the variety of invertebrates discussed are (i) a depression of standard metabolic rates and (ii) a lowering of the slope of R:T curves. Since *P. aquilonalis* depends on a limited and often inconsistent supply of food, both of these changes would be adaptive in decreasing respiratory energy expenditure.

MATERIALS AND METHODS

Collection and maintenance of animals.

Mature and immature Paruroctonus aquilonalis scorpions were collected from the soil surface during evenings in 1974 and 1975 near Albuquerque, New Mexico, at two collection sites. The first and most heavily utilized site (designated the "Rio Bravo" site) was located about 1.5 km east of Interstate Highway 25 in Tijeras Arroyo, and about 2.5 km SE of the intersection of Broadway and Prosperity Ave. SE. A dirt road originating opposite Prosperity Ave. provided access to the collection area. The second area (the "West Mesa" site) provided the remaining specimens used in humidity-metabolism experiments in 1975 (described below). This site was a desert-grassland area on the West Mesa of Albuquerque. It was located in an area about 100 m east of Atrisco Rd. NW. Access to the area was by a dirt road turning east off Atrisco Rd., roughly 200 m south of the entrance to Petroglyph State Park.

In order to secure scorpions during the winter of 1974-1975, burrows associated with surface-active scorpions were marked in August and September, 1974. Burrow markers were fluorescent-painted wood tongue depressors which indicated the size group (mature or immature) and sex of the scorpion presumed to occupy a particular burrow. Marked burrows were then carefully excavated in November, 1974 and January, 1975.

Scorpions were collected by grasping them by the metasoma ("tail") with forceps, and placing them in individual plastic bags ("Baggies").

They were then returned to the laboratory for immediate respirometry or used later in other experiments outlined below.

In the laboratory, scorpions were examined for any physical damage and sexed. Sex determination was made by utilizing the sexual dimorphism of the pectines located on the ventral prosoma. Male *P. aquilonalis* generally have longer pectines than females. Also, the internal angle formed by the posteriorly-directed pectines is less acute in males than in females. Among mature scorpions, males have broader, more massive chelae than females. By using these characteristics, larger scorpions could be sexed at a glance in the field. For the smallest immatures, however, closer examination was necessary. By examining and comparing individuals of a large group of immatures and selecting the most sexually dimorphic, confident identification of sex was assured.

For experiments necessitating laboratory maintenance of scorpions for prolonged periods, animals were maintained in constant darkness at roughly 100% rh in controlled temperature cabinets (Lab-Line, Ambi-Low Model 3550). Cabinet temperatures were maintained at 24±1°C. As part of desiccation and humidity experiments, animals were kept in a water-loss device described below within a walk-in insectary at 26±1°C under a simulated ambient photoperiod.

Experimental procedures.

1. Respirometry.

A Gilson differential respirometer (Model GME 14) equipped with 19, 18-ml, 2-sidearm flasks was used in all experiments. Carbon dioxide absorbant, "Ascarite" (A. H. Thomas Co.) was placed in one sidearm of

each flask and separated from a scorpion in the flask by insertion of a small piece of cotton in the mouth of the sidearm. The other sidearm contained cotton to prevent animals from entering. For all experiments, except those dealing with the effects of humidity on metabolism, a relative humidity (rh) of approximately 80% was maintained in flasks by adding distilled water and a strip of filter paper to the centerwell. Cobalt thiocyanate humidity indicator paper (The Tintometer, Ltd., London) was used to test flask humidities.

Metabolic rates were expressed as microliters (μl) of oxygen consumed per gram animal live weight per hour. Volumes of oxygen consumed were corrected to "standard" conditions of temperature (0°C) and pressure (760 mm Hg) of dry air (STPD). Correction of volumes of oxygen used under 80% rh to dry air equivalents involved the use of published values of the partial pressure of water vapor in mm Hg for each test temperature used. Corrections for the vapor pressure of water were not felt necessary for respirometry conducted at 10% rh in the humidity experiments outlined below. Live weight was used in all calculations of oxygen consumption except for 1975 humidity- and desiccation-metabolism experiments. At the end of those experiments scorpions were killed by freezing at -10°C and dried to constant weight at 60°C. Oxygen consumption was expressed on a dry weight basis.

In order to determine metabolic rate: temperature (R:T) relations as part of seasonal-metabolism, starvation, and acclimation experiments, oxygen consumption was measured at a variety of temperatures. Scorpions were weighed to within 0.1 mg, placed in flasks, and thermally equilibrated on the respirometer at 5°C for 2 hours. Oxygen consumption

was then measured for 3 hours at each of a series of increasing temperatures: 5, 14, 19, 24, 29, and 36°C. A 1-hour equilibration period was provided between each test temperature as the temperature of the water bath was raised.

For all R:T and humidity-metabolism experiments, groups of 19 scorpions were used in respirometry. In 1975, during respirometry with other invertebrate species, it was found that slight fluctuations in gas volumes occurred in animal-free flasks as the result of slight changes in room temperature. In order to measure these volume changes, four "blank" flasks, similarly prepared but lacking animals were prepared. The average volume change occurring in these flasks during measurement periods was used to adjust volume changes due to respiration. As a consequence of this procedure, groups of only 15 scorpions were used in 1975 humidity-metabolism and standard metabolism/RQ studies.

2. Weight:metabolism studies.

In order to determine the influence of live weight on metabolic rate, oxygen consumption of both males and females representing a variety of live weights was measured at 5, 14, 19, 24, 29, and 36°C as in R:T experiments. To minimize the possible effects of season, scorpions were collected over the following brief periods in 1974 when animals were abundant: 28 May to 8 June (females) and 28 May to 11 July (males). The longer period of male collection was necessary due to the late seasonal appearance of mature males at the soil surface.

Live weight and oxygen consumption were recorded at each test temperature for each scorpion. For these data, linear regression equations in the form $\log Y = a + b \log X$ were calculated in which

"Y" represented oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$) "a" the intercept of the regression, "b" the slope, and "X" the live weight in mg. Log_{10} transformations of weight and oxygen consumption correlates were selected since linear regressions using this transformation gave higher correlation coefficients (r) than did regressions based on untransformed data. Sample sizes (N) used in the regressions were 45-52 for females, and 71-76 for males, depending on temperature. Sample sizes varied because individual manometer readings occasionally became erratic, and the data were discarded as unreliable. Using the regression equations established, oxygen consumption for any test temperature could be estimated for a scorpion of a selected live weight by entering values of live weight (X) into the appropriate regression equation.

3. Seasonal metabolism experiments.

Possible seasonal changes in R:T relations of adult scorpions were examined in 1974 and 1975. R:T curves of males were constructed for specimens collected 11 July 1974, about two weeks following their first appearance at the soil surface, and were compared with those displayed by males collected 6 September 1974. R:T curves of females were constructed for animals taken at six collection times from June 1974 to June 1975. Part of the R:T data for adult males and females collected 28 May to 11 July 1974 were also used in weight: metabolism estimates.

All collections were of surface-active specimens except for those made 17 November 1974. On that date scorpions were taken during the day from among 42 previously marked and excavated burrows. For

that group respirometry procedure was modified to measure respiration at 5, 10, 15, 20, and 25°C, rather than at the six temperatures previously used. This procedure was adopted to provide a realistic range of test temperatures for R:T determinations of winter animals. Those metabolism determinations were to be compared with subsequent results from scorpions collected in January, 1975. Unfortunately, similar excavations of about 40 burrows on 2 January 1975 produced only 3 animals, not enough to justify respirometry.

4. Starvation experiments.

The possible effect of prolonged starvation on R:T relations was investigated for adult females collected 12 September 1974. Metabolic rates were measured immediately following collection, and the data were used additionally for seasonal R:T relations of females. Following respirometry, scorpions were starved on moist soil in darkness at 24°C for about 3 weeks until 3 October, when oxygen consumption was measured again. Animals were then starved an additional 3 weeks until 24 October 1974, when metabolic rates were measured once more. Animals were then fed mealworms (*Tenebrio molitor*) periodically in screen-top plastic containers for about 1 month when oxygen consumption was measured a final time. Scorpions were denied food 3 days prior to respirometry.

5. Acclimation experiments.

Experiments were designed in 1975 to test the possible influence of prior thermal acclimation on the R:T relations of mature and immature scorpions of both sexes. Scorpions were collected on the evenings of 7 and 8 June (mature females), 14 through 16 June (mature females and

all immatures), and 15 and 16 July (adult males). They were then weighed and placed on moist soil without food under constant darkness at either 10°C or 24°C. Eight groups containing 19 scorpions were established so that comparisons could be made between the metabolic rates of 10°C- and 24°C-acclimated scorpions of two size groups (mature and immature) of both sexes. In order to compare oxygen-consumption rates of 10°C- and 24°C-acclimated animals, mean weight differences between acclimation groups were minimized as much as possible. Groups of immature animals of both sexes were approximately of the same live weight. However, live weight differences between adult males and females were large, making valid intersexual comparisons of oxygen consumption difficult. The duration of acclimation at 10°C and 24°C, respectively, and the mean live weights in grams (in parentheses) of groups were as follows: (i) immature females: 18 days (0.1725), 15 days (0.1805); (ii) mature females: 15 days (0.4603), 13 days (0.4629); (iii) immature males: 20 days (0.1778), 17 days (0.1789); and (iv) mature males: 16 days (0.2896), 17 days (0.2837).

All scorpions acclimated in the laboratory were denied food during temperature exposure to a given acclimation temperature. Scorpions were not fed during experiments because feeding tended to be inconsistant in adults at room temperature and was expected to be depressed at 10°C. Another consideration was the lack of appropriate food items for immature scorpions.

6. Standard metabolism/RQ experiments.

According to Prosser (1973) oxygen-consumption rates for animals displaying different degrees of (locomotor) activity represent "standard"

or "rest" metabolism when activity is extrapolated to zero value. In addition to being in a quiescent state, animals showing standard rates should also be in a post-absorptive digestive state. Due to these considerations the R:T procedures outlined above do not provide an adequate measure of "standard" metabolism at any of the test temperatures presented. These procedures did not permit scorpions to become completely quiescent in flasks at a single temperature, but rather involved exposing them to a series of acute temperature changes. In addition, for R:T experiments performed on freshly collected animals, post-absorptive digestive states could not be presumed. For these reasons, oxygen-consumption levels of scorpions in R:T experiments probably fell between "standard" and "active" levels and could best be called "routine" or "excited" metabolic rates (Newell et al., 1973). Therefore, the procedures used to determine standard rates of metabolism differed from those used in R:T experiments in that the former: (i) allowed ample time for animals to become as quiescent as possible in respirometer flasks, and (ii) imposed only minimal disturbances due to temperature change and to handling prior to respirometry.

Determinations of standard metabolism at 20°C were preceded in each case by estimates of respiratory quotient (RQ). RQs provided a qualitative index of the type of respiratory substrate (fat, carbohydrate or protein) being consumed in respiration. RQ is defined as the volume of carbon dioxide (CO_2) evolved by an organism divided by the volume of oxygen consumed in respiration during the same period. For oxidative metabolism of pure carbohydrate an RQ of 1.0 is expected, for fat it is about 0.7, and for protein it approximates 0.8 (Florey, 1966).

In order to determine both RQ and standard metabolic rates, scorpions were placed in respirometer flasks lacking CO_2 absorbant but otherwise prepared as above. Flasks were placed in the water bath of the respirometer at 20°C and allowed to equilibrate for 2.5 hours. Following this period, the volume change occurring in flasks was measured for each animal for 1 hour and recorded. Ascarite absorbant was then added to sidearms in the water bath without removing flasks from manometers, and flasks were allowed to re-equilibrate for 2.5 hours. At that time volumes of oxygen consumed were recorded for 1 hour. Volume changes occurring in flasks without absorbant represented the net difference between oxygen consumed and CO_2 produced. Volume changes after addition of absorbant represented oxygen consumption. The difference between the two volume changes provided estimates of the CO_2 evolved. RQ was obtained by dividing those estimates by values of oxygen consumed.

The method outlined above is based on the "direct method" described by Umbriet _et al_. (1964). Its use assumes that oxygen consumption of animals is not appreciably influenced by the accumulation of CO_2 in flasks during experiments. In order to test this assumption, a high concentration of CO_2 within flasks was established using Pardee's solution (Umbriet _et al_., 1964). Pardee's solution provides a constant 1% CO_2 concentration within reaction vessels and absorbs CO_2 when levels above 1% are reached.

To test the influence of a 1% CO_2 level on scorpions, 19 adults previously used as part of starvation experiments (mean weight = 0.4189 g) were placed in flasks containing Pardee's solution in the centerwells.

Oxygen consumption was measured at 20°C and found to increase during the first hours of the experiment from about 10 µl g^{-1} hr^{-1} to about 30 µl g^{-1} hr^{-1}, at which point it remained relatively constant for the next six hours. Mean rates for the fifth through the tenth hours under 1% CO_2 were 30.50, 29.97, 30.50, 30.25, 28.25, and 29.50 µl g^{-1} hr^{-1} respectively (grand mean = 29.95 µl g^{-1} hr^{-1}). Since the test animals had been starved for 15 days prior to testing, their rates were compared with those the same animals had displayed after a previous starvation period of 22 days. An estimate of the mean metabolic rate at 20°C from R:T curves of starvation experiments was about 30-31 µl g^{-1} hr^{-1}. Since rates displayed at 1% CO_2 compared favorably with the last cited results, the RQ procedure described above was felt to be adequate. Subsequent estimates of standard metabolism in 1975 at 20°C for adult females of a comparable mean weight (0.4002 g) and starvation duration (18 days) gave 27.95 µl g^{-1} hr^{-1} which was also comparable to those recorded in 1% CO_2.

To estimate standard metabolic rates, oxygen consumption was measured hourly at 20°C following RQ estimates until stable rates were found. After 5 hours this point was reached. The final (6th hour) mean rate was felt to adequately represent standard metabolism and was used for statistical comparisons.

Standard metabolism/RQ experiments were designed to test for possible influences of (i) season, (ii) <u>ad lib</u> feeding, and (iii) starvation on oxygen consumption at 20°C. Seasonal standard metabolism/RQ experiments were performed on samples of field-collected males. These animals were collected on 28 June, 14 July, 28 July, 7 August, and

15 September 1975, and were kept overnight in plastic bags in darkness at 24°C. In each case, respirometry was begun the following morning at 0900 to 1030 hours. Feeding experiments utilized males collected on 28 June 1975, kept for 15 days in darkness in plastic containers at 24°C, and fed mealworms ad lib up to 3 days prior to testing. Finally, starvation experiments utilized adult females collected on 12 October 1975 and starved under the same conditions for 18 days prior to respirometry.

7. Desiccation and humidity experiments.

Two separate experiments were designed to assess the influence of high and low relative humidity (rh) levels on oxygen consumption at 25°C. The first experiment was performed on a single group of freshly collected mature females collected on 6 September 1974. A second group of experiments in 1975 tested the possible influence of prior desiccation and starvation in modifying the effect of humidity on metabolic rates of mature males. As part of each humidity-metabolism experiment, both 80%- and 10%-rh levels were established in respirometer flasks. By adding about 0.4 ml of distilled water and a strip of filter paper to the centerwell an 80% rh was obtained. When no water was added a 10% rh level was established. Humidity levels were tested with cobalt thiocyanate humidity indicator paper. Established minimum precision of this indicator was ±5% rh for levels above 65% rh, and ±10% rh for lower levels (Solomon, 1957). Respiration rates at 25°C were measured at 10% rh hourly for 5 hours in 1974 experiments and 6 hours in 1975 experiments. Water was then added to the centerwell

to provide 80% rh, the flasks equilibrated, and measurements made hourly for 5 or 6 hours.

Experiments in 1974 were designed to determine the influence of humidity on the metabolic rate of freshly collected scorpions. Adult females were collected at night and kept overnight at 24°C in darkness on moist soil prior to respirometry at 10% rh and 80% rh on the following day.

As part of 1975 starvation and desiccation experiments a water loss device similar to that used in previous experiments (Riddle, 1975) was used. This device consisted of a 1-gallon glass jar connected by tubing to a pressure-vacuum pump which circulated air at about 1 liter min^{-1}. Scorpions were placed inside the jar in individual 1-oz. glass cream containers stacked in vertical tiers, each tier being separated by window screening. This system was then connected by tubing to either a quart jar filled with granulated alumina desiccant (maintaining 0% rh in the circulating air), or to one containing a saturated solution of potassium dichromate ($K_2Cr_2O_7$). When air was bubbled through the potassium dichromate solution a 98% rh of circulating air was provided (Winston and Bates, 1968).

For 1975 experiments adult male scorpions were taken from the West Mesa collection site on 15 and 20 September 1975. Those collected on 15 September were desiccated and starved at 0% rh for 20 days and designated the "desiccated" group. Concurrent experiments examining blood osmolality following desiccation in *P. aquilonalis* showed that lethal levels of dehydration were approached after about 20 days of exposure in the desiccation device described (Riddle *et al.*,

in press). Scorpions collected on 20 September either were placed in an identical desiccation device at 98% rh and exposed for 20 days (the "starvation" group), or were kept overnight in darkness at 24°C on moist soil. Those kept overnight were used in respirometry the following morning and were designated the "freshly collected" group.

Scorpions were starved under 98% rh conditions in the water-loss device for the same period (20 days) that the desiccation group was exposed to dry air. This was done in order to separate the possible effects of desiccation and starvation. The effect of 20-day starvation alone could be determined by comparing oxygen consumption of the starvation group with those of freshly collected animals.

The groups of 15 scorpions used in the experiments outlined above were of similar mean live weight at collection: 0.2868 g, 0.2874 g and 0.2861 g, respectively. Following starvation under 98% rh scorpions lost an average of 8.25% of their live wieght. Those starved and desiccated at 0% rh lost an average of 18.28%. To minimize the influence of mean live weight variation between groups due to starvation and desiccation in calculations of metabolic rate, dry weights of animals were used. Mean dry weight for the freshly collected group was 0.0883 g, for those starved in moist air, 0.0832 g; and for desiccated scorpions, 0.0774 g. Assuming that an original dry weight of 0.0883 g (that of the freshly collected group) had characterized the dry weight of each group of scorpions prior to experiments, then starvation would have been responsible for about 5.78% dry weight loss, and starvation plus desiccation for a 12.34% dry weight loss. Dry weight differences between groups were substantial

but were clearly smaller than live weight differences.

8. Statistical methods.

Linear regression equations used in weight: metabolism experiments were tested for their fit using analysis of variance. This analysis was included as a part of an IBM 360 computer program STATPACK, used for linear regressions. The significance level of the F-value obtained following analysis of variance was determined using statistical tables (Rohlf and Sokal, 1969).

Individual mean rates of oxygen consumption and RQs were compared using t-tests. In those experiments in which the influence of the factor being examined could not be predicted to result in either higher or lower metabolic rates, means were compared to see if significant differences existed. In these cases "2-tail" tests were used to determine the level of significance of t-values. If sample t-values were greater than table values, the means were designated as "significantly different". Experiments designed to determine the influence of season, humidity, and sex were tested in this way.

For experiments in which one mean was expected to be either higher or lower than another, means were compared using a "1-tail test". These tests were applicable in starvation and feeding experiments. Starved animals were expected to display lower rates than either fed or freshly collected animals in both R:T and standard metabolism experiments. They were also applicable to acclimation experiments in which cold-acclimated animals were expected to show higher metabolic rates than warm-acclimated ones at all test temperatures.

RESULTS

Field observations.

Observations during evening collections at the Rio Bravo site in 1974 and 1975 indicated that immatures of both sexes as well as mature females first became active at the surface in mid- to late March, and remained active until mid-October. At the Rio Bravo site mature males were not observed on the soil surface until late June in 1974 and 1975. They were first seen in large numbers on 30 June 1974, while during the previous two evenings only a few adult males were seen. Mature females and immatures of both sexes were also common at this time, while gravid females had largely completed surface activity for the season. In 1975 a similar sharp rise in the numbers of mature males was noted on 28 June. Following their appearance they persisted at the surface for the remainder of the active season during both years.

Unlike immatures of either sex or mature females, mature males were commonly seen moving over the soil surface. This roving activity was most intense in late August. During this period mature males were very responsive to tactile stimulation, often displaying extreme defense posturing, which was characterized by an elevated body position, side-directed pedipalps with open chelae, and randomly directed and rapid striking behavior. During marking of burrows at the Rio Bravo site, mature males were seldom found near any burrow opening. Similar surface roving activity for mature male scropions has been noted for *Anuroctonus phaedactylus*, (Williams, 1966). Unlike mature males,

mature females at the Rio Bravo site could be found, remaining motionless, within about 15 cm from burrow openings throughout the active season.

In a separate study of possible seasonal changes in whole body lipid content of mature female P. aquilonalis, large specimens were dissected for developing embryos. In five collections of females from March through June 1975, embryos were not found until June, when one-third of the mature females examined were visibly gravid. A collection of mature females 25 June was of decidedly smaller mean weight (0.3696 g, n=20) than that of 1 June (0.5362 g, n=20), and contained no gravid individuals. Mean live weights of prior collections increased from late March (0.4469 g, n=20) until 1 June. These results suggested that gravid females no longer appeared at the surface during the evening in late June, but probably remained within burrows.

Shortly after birth, scorpions move to the back of the female parent for a short time, molt to the second instar and disperse (Stahnke, 1966; Williams, 1969). Female P. aquilonalis were not seen in the field carrying young. Second instar individuals were seen regularly throughout the active season at the Rio Bravo site.

Courtship "dances" were observed in the field on two occasions for P. aquilonalis: 23 August 1973 at near the West Mesa site and 30 August 1975 at the Rio Bravo site. It is not known if births occurring late in an active season were the result of matings earlier in the same season or during the previous season.

Morphometry studies conducted on large numbers of scorpions collected in 1973 from an area near the West Mesa collection site failed to firmly establish the numbers of instars characteristic of *P. aquilonalis*. The life span and timing of molting for this species is not known.

Size and metabolic rate.

Regression lines describing the influence of live weight on metabolic rate for male scorpions collected from 28 May through 11 July 1974 are presented in Fig. 1. Regression equations, sample sizes, and results of statistical treatments corresponding to those results are summarized in Appendix 1. Figure 2 presents weight: metabolism regressions under the same conditions for females collected from 28 May through 8 June 1974. Regression equations, sample sizes, and results of statistical treatments for those results are tabulated in Appendix 2.

In addition to determining the influence of live weight on metabolism at each test temperature, the influence of weight on R:T relations was also determined. In order to assess the effect of temperature change on metabolism of scorpions of different sizes, metabolic rates of a hypothetical "small" scorpion (30 mg live weight) and a "large" scorpion (300 mg) of each sex at each temperature were estimated using regression equations of Appendices 1 and 2. Those estimates and the respiratory temperature coefficients (Q_{10}) representing the magnitude of rate changes between test temperatures appear in Table 3 and 4. For both sexes, scorpions weighing 30 mg

displayed Q_{10} values which remained low for temperature changes occurring between 5°C and 19°C, while they showed high values for changes between 19°C and 29°C. For a 29°C to 36°C change, the Q_{10} values of 1.89 (males) and 1.49 (females) were intermediate between the extreme values found for temperature changes below 29°C. For 300 mg scorpions Q_{10} values remained more consistent over the entire temperature range than did those of 30 mg scorpions, differing most from those of smaller animals from 19°C to 29°C.

Sex and metabolic rate.

Rate: temperature relations for male and female scorpions used previously for weight: metabolism studies are presented in Figs. 3 and 4, respectively. A comparison of the curves for immature male and female scorpions indicate similar patterns of temperature dependence. For adult males and females, however, curves were distinctly different, with markedly elevated metabolic rates at lower temperatures for adult males. Higher metabolic rates were found among adult males than among immatures at 5, 14, and 19°C and resulted in the positive slopes of weight: metabolism regression lines shown in Fig. 1.

Thermal acclimation and metabolic rate.

Rate: temperature curves determined for mature and immature scorpions of both sexes following a period of thermal acclimation at 10°C or 24°C are presented in Figs. 5, 6, 7, and 8. T-test comparisons indicated that 10°C-acclimated immature male scorpions (Fig. 5) displayed higher means than did the 24°C-acclimated group at 19, 24,

29, and 36°C ($P<0.05$, $P<0.001$, $P<0.001$, and $P<0.05$, respectively). Adult males (Fig. 6) showed an essentially similar pattern, associating 10°C acclimation with higher rates at 14, 19, 24, 29, and 36°C ($P<0.01$ at 19°C, $P<0.001$ at other temperatures). Immature females (Fig. 7) acclimated at 10°C displayed significantly higher rates than did 24°C-acclimated scorpions at 19, 24, 29, and 36°C ($P<0.01$, $P<0.01$, $P<0.01$ and $P<0.001$, respectively). For adult females (Fig. 8) R:T curves for 10°C- and 24°C-acclimated animals differed less than they did for adult males. However, significantly higher metabolic rates were noted among 10°C-acclimated than for 24°C-acclimated animals at 24, 29, and 36°C (all $P<0.01$). With the exception of mature males acclimated at 10°C, overall slopes of R:T curves were essentially similar for all scorpions regardless of size, sex, or acclimation conditions. The percent increase or decrease in metabolic rates for 10°C-acclimated animals above or below rates shown by 24°C-acclimated animals at each test temperature is presented in Appendix 3.

The effects of starvation and feeding on metabolic rate.

The effect of starvation and subsequent laboratory feeding on R:T relations of adult female scorpions is shown in Fig. 9. Metabolic rates of scorpions following feeding were higher at 19, 24, 29, and 36°C ($P<0.001$ at all temperatures) than those of animals starved 55 days. Metabolic rates following feeding were also significantly higher than 22-day starvation levels at 19, 24, 29, and 36°C ($P<0.05$, $P<0.001$, $P<0.001$, and $P<0.001$, respectively).

The effects of starvation on the temperature coefficient (Q_{10}) of oxygen consumption between selected test temperatures are summarized

in Table 5. For temperature changes from 14°C to 19°C Q_{10} values decrease with more severe starvation and increase following refeeding. The mean Q_{10} from 14°C to 24°C determined for each group also indicates decreasing values following starvation and higher ones following refeeding. However, Q_{10} values for temperature changes below 14°C or above 24°C do not show this trend.

Metabolic rates following feeding were statistically similar to those found for freshly collected animals at 24, 29, and 36°C. At 5, 14, and 19°C, however, rates following feeding remained lower than those of freshly collected animals at 5°C ($P<0.05$), 14°C ($P<0.001$) and 19°C ($P<0.01$).

Season and metabolic rate.

R:T curves for adult males tested following collection on 11 July and 6 September 1974 (Fig. 10) were compared in order to assess possible seasonal changes. Males collected on 11 July displayed significantly different oxygen consumption rates at 5, 14, and 19°C ($P<0.05$, $P<0.001$, and $P<0.05$, respectively) than those shown by September males. The mean live weight of mature males collected on 11 July (0.3449 g) was slightly greater than that of 6 September animals (0.3104 g). Differences in R:T curves between July- and September-collected males cannot be accounted for on the basis of live weight differences between these groups, but rather may indicate actual seasonal changes in metabolism.

Seasonal metabolism was studied more completely for mature females. As groups of females were collected periodically from June 1974 to June 1975, their R:T relations were determined immediately following

collection (except for 17 November 1974 animals when different test temperatures were used). Rate: temperature curves for these groups are presented in Figs. 11, 12, 13, 14, 15, and 16.

Live weights of groups of females varied during the year, making direct comparisons of R:T curves for freshly collected scorpions difficult. Therefore, in addition to R:T curves found for freshly collected females, a second estimate (dashed lines in Figs. 11-16) estimated the oxygen consumption that would have been expected from a group of scorpions of the same mean live weight collected in the spring, 1974. These metabolism estimates were derived from entering the mean live weight (X) for groups of seasonally collected scorpions into the appropriate regression equation in Appendix 2 and estimating oxygen consumption (Y). In this way a "baseline" spring 1974 R:T curve could be compared with R:T curves for scorpions taken periodically during the summer and fall of 1974 and the spring of 1975.

Figures 11 through 16 indicate changing R:T relations of females taken from June 1974 to June 1975. Figure 11 shows a close agreement between the R:T curve for 8 June 1974 and that based on regression estimates. This agreement is largely because weight: metabolism regression equations (Appendix 2) were derived in part from data from 8 June females themselves. Figure 12 shows a large disparity between the R:T curve for freshly collected females and the estimate derived from the regression for comparably sized spring 1974 females. A similar disparity persists at the 17 November sampling (Fig. 13), although the different temperature regime (5, 10, 15, 20, and 25°C) employed invalidates strict comparisons. The regression-derived R:T

curve remains higher than that displayed by freshly collected scorpions on 15 April 1975 (Fig. 14) shortly after scorpions reappeared at the soil surface. Figure 15 shows an estimated R:T curve which also remained higher than that of animals collected 1 June 1975. At the last seasonal collection 25 June 1975 (Fig. 16), regression estimates of female metabolism in spring, 1974 again correspond closely with the observed curves from freshly collected animals.

Standard metabolism and respiratory quotient.

Results demonstrating the influence of season on standard metabolic rate at 20°C and respiratory quotient (RQ) for adult males are summarized in Table 6, and presented completely in Appendix 4. Those results show consistent standard metabolism levels through July followed by a sharp depression during August and a rapid return in September to levels similar to those found during June and July. Although mean live weights between sample collections varied, it is unlikely that the large differences noted could be accounted for on the basis of weight alone. "Routine" metabolic rates at 20°C estimated from R:T curves for adult males collected on 11 July and 6 September 1974 from R:T curves (Fig. 10) are about 85 and 50 $\mu l\ g^{-1}\ hr^{-1}$ respectively. The September 1974 estimate corresponds closely with the standard 20°C rates found 15 September 1975. In contrast, standard rates remained at about 50 $\mu l\ g^{-1}\ hr^{-1}$ from 28 June to 28 July 1975, well below the unusually high rate of about 85 $\mu l\ g^{-1}\ hr^{-1}$ estimated for 11 July 1974 males in Fig. 10.

The influence of feeding and starvation on standard 20°C metabolic rate for mature males and females is summarized in Table 7.

Those results indicate that metabolic rates were not significantly higher among males following ad lib feeding of freshly collected animals. For females, starvation lowered metabolic rates significantly. In contrast, RQ values were significantly increased by feeding (males), but remained unchanged with starvation (females). Complete results of starvation and feeding experiments are presented in Appendix 5.

Influence of humidity and desiccation on metabolic rate.

The influence of high and low relative humidity on metabolic rates was tested in two separate experiments with adult scorpions. Results of the first experiment with females collected on 6 September 1974 are illustrated in Fig. 17. Statistical comparisons between the final (5th hour) mean metabolic rate at 10% rh and each of the hourly means at 80% rh indicated no significant differences. Results of the second series of experiments performed in 1975 are presented in Fig. 18. For both field-collected male scorpions and those starved 20 days in moist air, no significant difference in rate was noted between the final (6th hour) means under 10% rh and those at 80% rh. At both 10% and 80% rh a comparison of final (6th hour) mean rates between starved and freshly collected scorpions indicated significant differences ($P<0.001$).

Desiccated scorpions (Fig. 18) tested at 10% rh showed extremely high and variable metabolic rates. At the final hour of exposure to 10% rh the mean rate was found to differ ($P<0.05$) from that of starved animals, but it did not differ from the final mean rate of field-collected animals. Since drinking of water from flask centerwells

occurred in 10 desiccated animals during 80% rh exposure, results for these scorpions and for those 5 which did not drink were examined separately. No significant difference was found between the final mean rate for desiccated, non-drinking scorpions (n=5) under 80% rh and the entire sample (n=15) of desiccated scorpions under 10% rh. Similarly, no statistical difference was found between the final mean rate of non-drinking scorpions at 80% rh and the final mean rate that the same 5 individuals displayed at 10% rh (not evident from Fig. 18, since means at 10% rh for the entire sample of 15 were presented).

DISCUSSION

The results presented above for P. aquilonalis present trends of physiological change. These trends are related to the size and sex of the scorpions themselves and to the external environment, both physical (temperature and water relations) and biotic (food supply). All of these factors are significant in the life of a scorpion because they modify the rate of energy utilization. The conservative use of metabolizable energy in respiration is an ecologically important aspect of the respiratory physiology of P. aquilonalis. Energy conservation provides the major viewpoint and framework within which the observed results can be interpreted.

Size and Sex.

Rates of oxygen consumption were not uniformly influenced by live weight over the ranges of test temperatures employed (Figs. 1 and 2). Metabolic rates of male and female scorpions were inversely dependent on live weight only at 29°C and 36°C, while at 24°C live weight was only slightly influential. For females (Figs. 2 and 4) at 5, 14, and 19°C, live weight had little influence, but for males (Fig. 1) positive slopes were noted. Had September-collected mature males been used for weight: metabolism regressions rather than July-collected mature specimens, regression lines similar to those of females might have been obtained.

As discussed previously, temperature has been found to modify weight: metabolism relations in a variety of invertebrate poikilotherms. The results observed with P. aquilonalis most strongly contrast with those of Urodacus yashenkoi scorpions (Shorthouse, 1971), for which

the inverse nature of weight: metabolism curves did not change appreciably over a range of temperatures.

The larger question posed by the weight: metabolism results for *P. aquilonalis* is one concerning the energetic consequences of size on scorpions. In terms of energetics, small size is not a potential disadvantage compared to large size at lower temperatures, while from 29°C and 36°C small size is clearly associated with comparatively high energy costs. In addition to elevated energy costs for small scorpions at those temperatures, more severe water loss would also be expected from small scorpions due to their higher surface:volume ratios. In terms of energetics and water balance, exposure to higher temperatures could be particularly disadvantageous to smaller scorpions.

Weight: metabolism relations based on respirometry performed on freshly collected scorpions of both sexes, (regression lines in Figs. 1 and 2) below 24°C probably depicted abnormally high rates. Evidence for this comes from the results presented in Fig. 9, which shows that rates for freshly collected females at those temperatures on September 6 remained higher than those of the same animals maintained and fed in the laboratory. The large disparity in R:T curves at those temperatures was probably associated with an elevation of metabolism due to excitement in transport and handling prior to respirometry, rather than to any acclimation effects. This is apparent because rates for the same animals following collection and after laboratory feeding coincided closely at 24°C and above. While it is likely that the positions of weight: metabolism regression lines below 24°C reflect higher metabolic rates than occur in nature, there is no evidence that

the slopes of these regression lines would have differed had scorpions been allowed to adapt briefly in the laboratory prior to respirometry.

Q_{10}.

As a consequence of changes in weight: metabolism relations with temperature, respiratory Q_{10} values changed with live weight in *P. aquilonalis*. Q_{10} values presented in Tables 3 and 4 were compared with those calculated from the weight: metabolism regression equations presented by Shorthouse (1971) for *Urodacus yashenkoi* (Table 2) over comparable temperature ranges. In *U. yashenkoi*, Q_{10} values indicated a trend of increasing Q_{10} with increasing live weight. In contrast, for "small" (30 mg) and "large" (300 mg) *P. aquilonalis* of both sexes over a comparable temperature range (19°C - 29°C), a strong trend of decreasing Q_{10} with increasing size was apparent. When Q_{10}'s measured from a temperature range of 25°C to 35°C are considered for *U. yashenkoi*, weight:Q_{10} trends become less evident, with Q_{10} values remaining fairly similar for small and large scorpions. Q_{10} values for *P. aquilonalis* calculated from the data in Tables 3 and 4 over a comparable temperature range (24°C - 36°C) continued to indicate a trend of decreasing Q_{10} with increasing size. "Small" and "large" scorpions respectively exhibited Q_{10}'s of 3.09 and 1.86 (males) and 2.62 and 1.84 (females).

The most significant adaptive advantage of low respiratory Q_{10} values to scorpions and other poikilotherms is in the metabolic homeostasis and consequent diminished energy expenditure that they provide following short-term temperature change. While there are potentially adaptive low Q_{10}'s for *P. aquilonalis* over temperature

ranges to which scorpions are likely to be exposed, relatively high Q_{10}'s, which clearly prevent metabolic homeostasis also occur, especially among smaller scorpions. This suggests that metabolic homeostasis by use of low Q_{10}'s is of only limited significance in P. aquilonalis.

Starvation.

Laboratory starvation experiments with P. aquilonalis have demonstrated two potentially adaptive patterns of physiological change. First, standard rates of metabolism measured at 20°C were significantly diminished by starvation (Table 7). Second, starvation modified R:T relations (Fig. 9), rendering metabolic rates of starved animals less sensitive to temperature change than those of well fed or freshly collected animals.

Depression of standard metabolic rates following starvation probably represents a most adaptive metabolic response for P. aquilonalis. For other invertebrates previously examined, patterns of both constancy and depression of standard metabolic rates with starvation have been found. In shrimp (Hagerman, 1970 cited in Marsden et al., 1973), marine snails (Stickle and Duerr, 1970), and in centipedes (Riddle, 1976) standard metabolic rates did not decrease with starvation. Among such animals standard metabolic rates can best be considered as relatively "fixed", and not subject to further depression by starvation. In contrast, millipedes (Gromysz-Kalkowska, 1970), crabs (Wallace, 1973), and spiders (Anderson, 1974) showed more "labile" standard metabolic rates that decreased following starvation. The "labile" response for spiders (Anderson, 1974) and for P. aquilonalis is particularly

adaptive for these predators, since it substantially reduces the rate of expenditure of stored energy during starvation periods.

Respiratory energy expended in locomotion involved in acquiring food is very modest in scorpions. Locomotion of adult female and immature scorpions is probably restricted to vertical movements during the day in burrows, to short-distance travel from the burrow opening to the surface in the early evening, and to a short return journey in the early morning; the remaining period of surface occupation is spent motionless awaiting prey. Thus, *P. aquilonalis* exemplifies a "sedentary" mode of predation that is essentially similar to that of web-building spiders (Anderson, 1970), and other vejovid scorpions (Hadley and Williams, 1968). Since *P. aquilonalis* scorpions expend relatively little energy in locomotor activities related to feeding, only "minimal" levels of metabolism, conducive to keeping scorpions responsive to potential prey, would be expected. Any energy expenditure above these "minimal" levels, while necessary perhaps during molting and/or reproduction, is potentially wasteful in feeding activity. It is significant that standard metabolic rates can be further depressed during starvation, providing reduced respiratory energy loss, without the impairment of normal predatory activity.

The adaptive significance of the observed depression of standard metabolism during starvation should depend largely on the degree to which scorpions are actually exposed to starvation in nature. It is possible that adult males collected at the soil surface on 28 June were among the first to appear in 1975, and may not have fed appreciably since surface activity ended the previous fall. Assuming

this was the case, reduced metabolic rates characteristic of starvation, as well as laboratory feeding resulting in elevated standard metabolic rates should have been expected. However, results indicated no elevation of metabolic rates following feeding (Table 7); rather, the post-feeding levels were similar to those freshly collected males until late July (Table 6).

The depression of standard metabolic rates at 20°C in August for mature males (Table 5) may have indicated natural starvation. Because surface locomotor activity was most intense in late August, relatively rapid use of energy in locomotion may have depleted food reserves and resulted in the low metabolic rates observed.

The modification of R:T curves (Fig. 9) represents the second physiological response of scorpions to starvation. In addition to lowered rates of metabolism at all test temperatures, R:T curves decreased in slope with increasing duration of starvation from 14°C to 24°C. Reduced Q_{10} values, (Table 5) indicated clearly that oxygen consumption was less influenced by temperature in starved scorpions than in well-fed ones. In fact, scorpions starved for 22 days improved their ability to regulate respiratory energy loss as temperature increased. Had scorpions with the same Q_{10} values as recently fed specimens been starved for 22 days exposed to 19, 24, and then 29°C (Table 5) their oxygen consumption rates would have been higher by 5.2%, 25.9%, and 36.7%, respectively, than the levels that were actually observed.

It is important to note that at 29° the larger percent reduction of metabolic rate with starvation shown above also represented a larger

absolute energy saving than at lower temperatures. This adaptation represents potentially substantial energy savings for a starving animal in nature, because reductions in Q_{10} occur over ranges of temperatures (14°C - 29°C) that are probably encountered in the habitat during the feeding season. This adaptation results in a lowered cost of utilizing relatively warm parts of the habitat that is lower for starving scorpions than for well fed scorpions.

Thermal acclimation.

Laboratory acclimation experiments (Figs. 5-8) indicated consistent patterns of change in R:T curves following exposure to 10°C and 24°C. These changes can best be described as "Pattern III" translations (Prosser, 1973) to the left in R:T curves with cold acclimation. Since comparable ad lib nutrition could not be provided each scorpion in acclimation experiments, the possible influence of starvation in modifying observed acclimation patterns must also be considered.

Starvation experiments for mature females (Fig. 9) indicated that metabolic rates of animals starved for 22 days were roughly half as high at 10°C as at 24°C. Therefore, utilization of respiratory energy reserves during starvation was about twice as rapid at 24°C than as at 10°C. If these differences in the rate of depletion of energy reflect differences in the severity of starvation, then the magnitude of depression in oxygen consumption tested following starvation should be twice as great for animals starved at 24°C as at 10°C.

In order to determine the possible influence of starvation on R:T relations following acclimation, the following assumptions were made: First, starvation at 10°C should result in one-half the depression of

metabolic rate at any temperature that occurs following starvation at 24°C. Second, the depression of metabolic rate for mature females acclimated at 24°C and starved for 14 days is roughly 64% as great as the depression due to starvation at 24°C for 22 days (14 days/22 days = 0.636). Third, the influence of starvation on R:T relations is comparable for mature females used in acclimation experiments at 24°C (collected on 6, 7 June 1975) and for similar specimens (collected 12 September 1974) starved at 24°C as part of starvation/feeding experiments.

If these three assumptions are accepted, then a reexamination of the results of acclimation experiments is possible. Appendix 6 gives an analysis of the results of starvation/feeding experiments (see also Fig. 9) which can be used to interpret the results of acclimation experiments. Appendix 6 first presents estimated oxygen-consumption rates at 24, 29, and 36°C for scorpions starved for 14 days (the average duration of exposure in acclimation experiments) rather than for 22 days. In addition, Appendix 6 shows the percentages by which metabolic rates should have increased after feeding in excess of rates estimated after 14 days of starvation. Using those percentages, observed 24°C-acclimation results were adjusted to estimate expected oxygen-consumption rates at 24, 29, and 36°C immediately prior to any acclimation and starvation (Appendix 7).

In order to assess the presumed effect of starvation on acclimation, two quantities were considered in Appendix 7: (i) the observed metabolic rates at 24, 29 and 36°C following 24°C-acclimation (which also reflected 14 days of starvation) and (ii), the estimated oxygen

consumption at those temperatures expected of scorpions prior to acclimation and starvation. If the presumed effects of starvation were influential and those of thermal acclimation were nil, then oxygen-consumption rates for 10°C-acclimated scorpions should have been about halfway between quantity (i) and (ii) above at 24, 29, and 36°C. Estimates were made in Appendix 7 of metabolic rates in 10°C-acclimated animals reflecting only the presumed effects of starvation and not acclimation, and these were compared with those actually observed for 10°C-acclimated scorpions. Results of those comparisons indicated that observed oxygen-consumption rates following 10°C acclimation were comparable to estimates which considered only the presumed effects of starvation. At 24°C roughly 55% of the increase of the 10°C-acclimated rates over 24°C-acclimated rates were accounted for by starvation. At 29°C, the entire difference between curves of 10°C and 24°C-acclimated scorpions can be accounted for by starvation. At 36°C, about 70% of the observed difference was attributable to starvation.

Based on these calculations it appears that differences in R:T curves for adult females acclimated to 10°C or to 24°C prior to respirometry are largely due to starvation rather than thermal acclimation. Results of acclimation in immatures of both sexes, and in mature males as well, indicated much larger acclimation differences than did results for mature females. It is probable that starvation effects accounted for at least part of the differences in R:T curves for immatures and mature males. Based on the assumed importance of starvation in explaining the observed acclimation results with mature females, and on the lack of information on the modifying effects

of starvation on acclimation of other experimental groups in this study, it is concluded that the results presented do not substantiate acclimatory changes in R:T relations for P. aquilonalis.

Season.

Possible seasonal adaptation of R:T relations of mature females (Fig. 11-16) is not necessarily a function of either seasonal changes in habitat temperature, or of embryonic development. Based on the results of Mouer and Ericksen (1973) with spiders, translation of R:T curves to the left with decreasing environmental temperatures might be expected for P. aquilonalis, which would tend to maintain similar metabolic rates during the year. In contrast to the expected results, R:T curves for P. aquilonalis were translated to the right in September (Fig. 12) relative to June 1974 estimates favoring the conservation of stored food energy prior to overwintering as environmental temperatures decline in the fall. However, this translation does not favor seasonal homeostasis in metabolic rate.

The adaptive significance of R:T curves for spring and summer 1975 (Fig. 14-16) is not understood. Had R:T curves changed in a direct way to increasing environmental temperatures, a more gradual return of curves toward the estimated June 1974 levels would have been expected. Rather than a gradual change, an abrupt return of slopes of R:T curves occurred between early and late June 1975.

Seasonal changes in R:T relations do not appear related to the reproductive state of female scorpions. Females used in 8 June 1974 respirometry were all visibly gravid. About one-third of the females used on 1 June 1975 were gravid, while none of those used on 25 June

1975 contained embryos. The close similarity shown in Fig. 16 between R:T curves for 25 June 1975 females (none gravid) and estimates based on fully gravid June 1974 scorpions suggests that embryonic development does not influence metabolic rate. This apparent lack of influence of embryonic development on metabolic rate contrasts with the results of Dresco-Derouet (1964), which showed cases of elevated metabolism for gravid scorpions. They also contrast with the results of Crawford and Riddle (1975), which tentatively associated elevated winter rates of oxygen consumption of scorpions with increasing embryonic development.

Water relations.

Scorpions are probably exposed daily to changes in atmospheric moisture during their active season due to movement from the burrow to the soil surface during the evening. The constancy noted in metabolic rates at 25°C of freshly collected and laboratory starved scorpions at 10% and 80% rh (Figs. 17 and 18) is adaptive in that it provides for comparable energy expenditure during periods when scorpions utilize both comparatively moist burrow habitats and drier surface feeding sites.

Severely desiccated scorpions (Fig. 18) displayed both elevated and highly variable levels of respiration under 10% rh conditions, which were partially reduced following exposure to 80% rh. Under natural conditions, comparably desiccated scorpions at 25°C and 10% rh would be expending roughly twice as much energy in respiration as normally hydrated scorpions. For these animals, movement to an 80% rh microhabitat would result in a reduction in metabolic rate by one-half, as well as in a reduction of additional water loss.

Concluding remarks.

The respiratory physiology *P. aquilonalis* scorpions can best be characterized as selectively responsive to external environmental factors. The respiratory metabolism of this species displays a simple dependence on temperature that is characteristic of the great majority of invertebrate poikilotherms. This temperature dependence is modified to a greater or lesser degree by short-term thermal acclimation and seasonal acclimitization, but is most strongly and predictably changed by starvation. Of all the metabolic responses displayed by *P. aquilonalis*, its response to starvation is of the greatest adaptive significance.

Scorpions are conspicious elements of desert faunas worldwide (Hadley, 1974). Burrowing, nocturnality, the development of a highly impermable cuticle, and excretory adaptations have all contributed to the success of scorpions in deserts. In addition to these features, metabolic adaptations, particularly in the form of relatively low metabolic rates and starvation metabolism, are of great adaptive significance.

CONCLUSIONS

1. Metabolic rate and body weight were inversely related in female and male P. aquilonalis scorpions above 24°C. No correlation between these parameters existed in females below 24°C; however, in males under the same conditions the relationship was positive due to seasonally elevated levels of oxygen consumption.
2. Trends of increasing respiratory temperature coefficients (Q_{10}) were found with decreasing live weight in both males and females at temperatures ranging from 14°C to 24°C.
3. Prolonged starvation of adult females lowered the slope of their metabolic rate: temperature (R:T) curves, and also depressed standard metabolic rates at 20°C. These changes were considered as highly adaptive means of conserving energy during starvation periods.
4. R:T curves of scorpions previously acclimated to either 10°C or to 24°C differed significantly at most test temperatures. However, these changes were probably complicated by starvation effects, so that evidence for thermal acclimation through changes in R:T curves was inconclusive.
5. Seasonal changes in R:T curves were found for mature females, although the adaptive significance of these changes was not clear. For adult males, depressions of standard metabolism at 20°C in August were correlated tentatively with starvation resulting from high locomotor activity coupled with inadequate nutrition.
6. Respiratory quotients (RQ) did not change with starvation for females but they did increase significantly for mature males

following laboratory feeding. Respiratory quotients (RQ) indicated a predominant utilization of lipid in respiration.

7. Oxygen consumption at 25°C under 10% and 80% relative humidity (rh) did not differ significantly either for freshly collected or laboratory-starved adult males. For severely desiccated scorpions, metabolic rates were extremely high and variable at 10% rh, but decreased substantially following exposure to 80% rh.

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FIGURES

FIGURE 1. Influence of live weight on oxygen-consumption rates at various temperatures for P. aquilonalis males. Regression equations and corresponding statistics appear in Appendix 1.

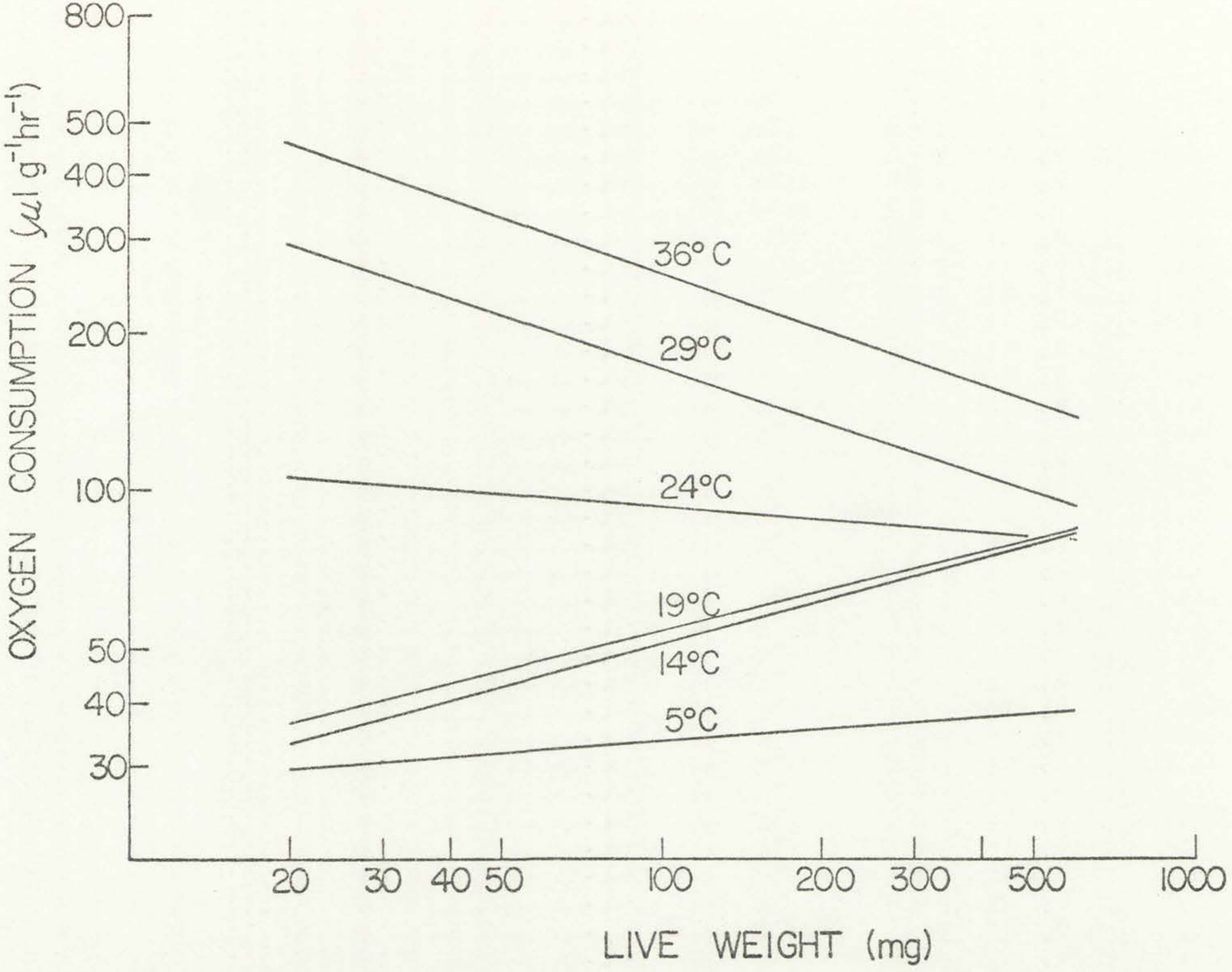

800
500
400
300
200
100
50
40
30
OXYGEN CONSUMPTION (μl g⁻¹hr⁻¹)
36° C
29°C
24°C
19°C
14°C
5°C
20
30
40
50
100
200
300
500
1000
LIVE WEIGHT (mg)

FIGURE 2. Influence of live weight on oxygen-consumption rates at various temperatures for P. aquilonalis females. Regression equations and corresponding statistics appear in Appendix 2.

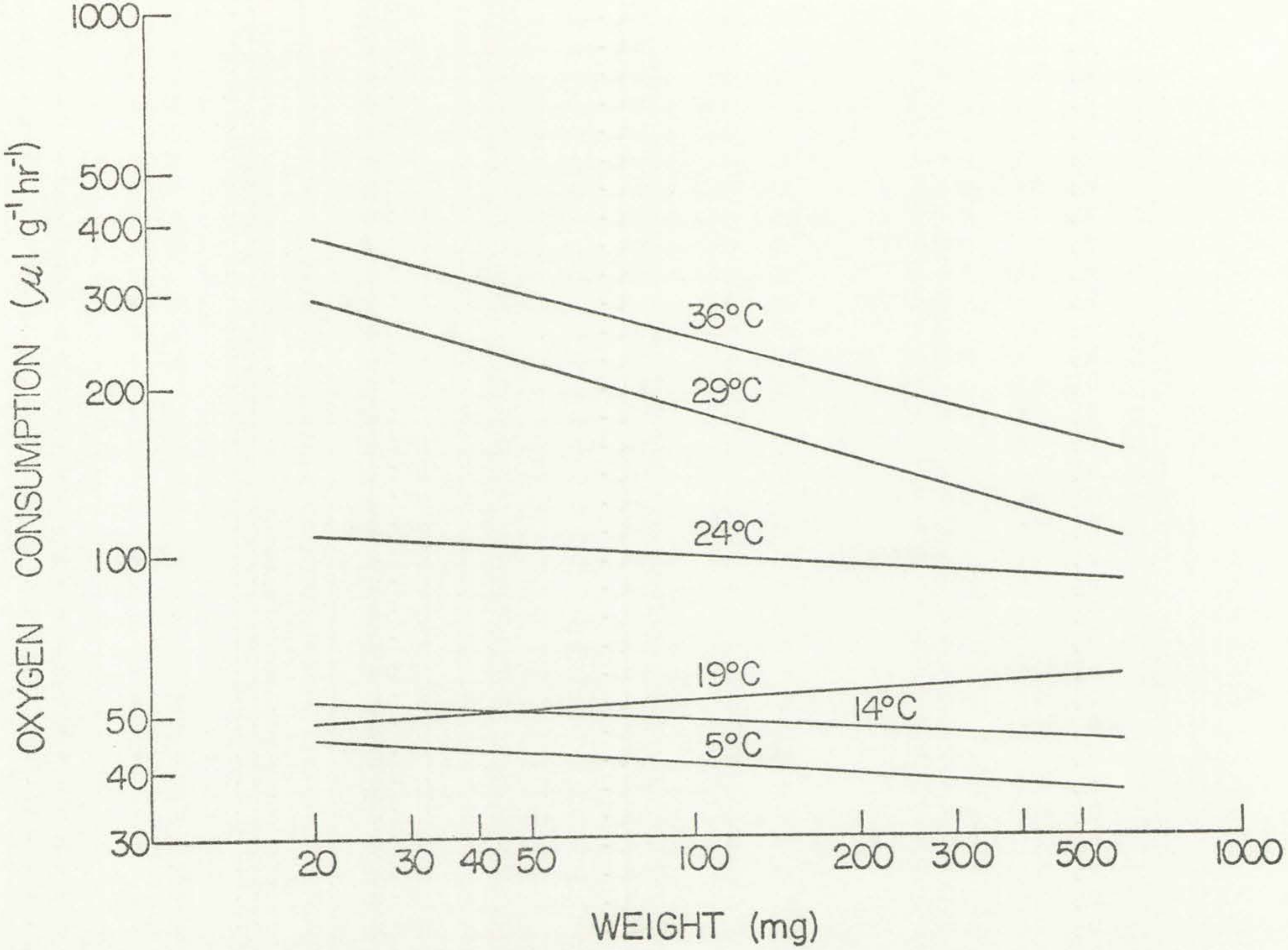

OXYGEN CONSUMPTION (μl g^{-1} hr^{-1})
1000
500
400
300
200
100
50
40
30
36°C
29°C
24°C
19°C
14°C
5°C
20
30
40
50
100
200
300
500
1000
WEIGHT (mg)

FIGURE 3. Metabolic rate: temperature curves for immature and adult *P. aquilonalis* males collected 28 May to 11 July 1974. Vertical lines represent standard errors, n=56 - 62 (immatures), n=14 (matures).

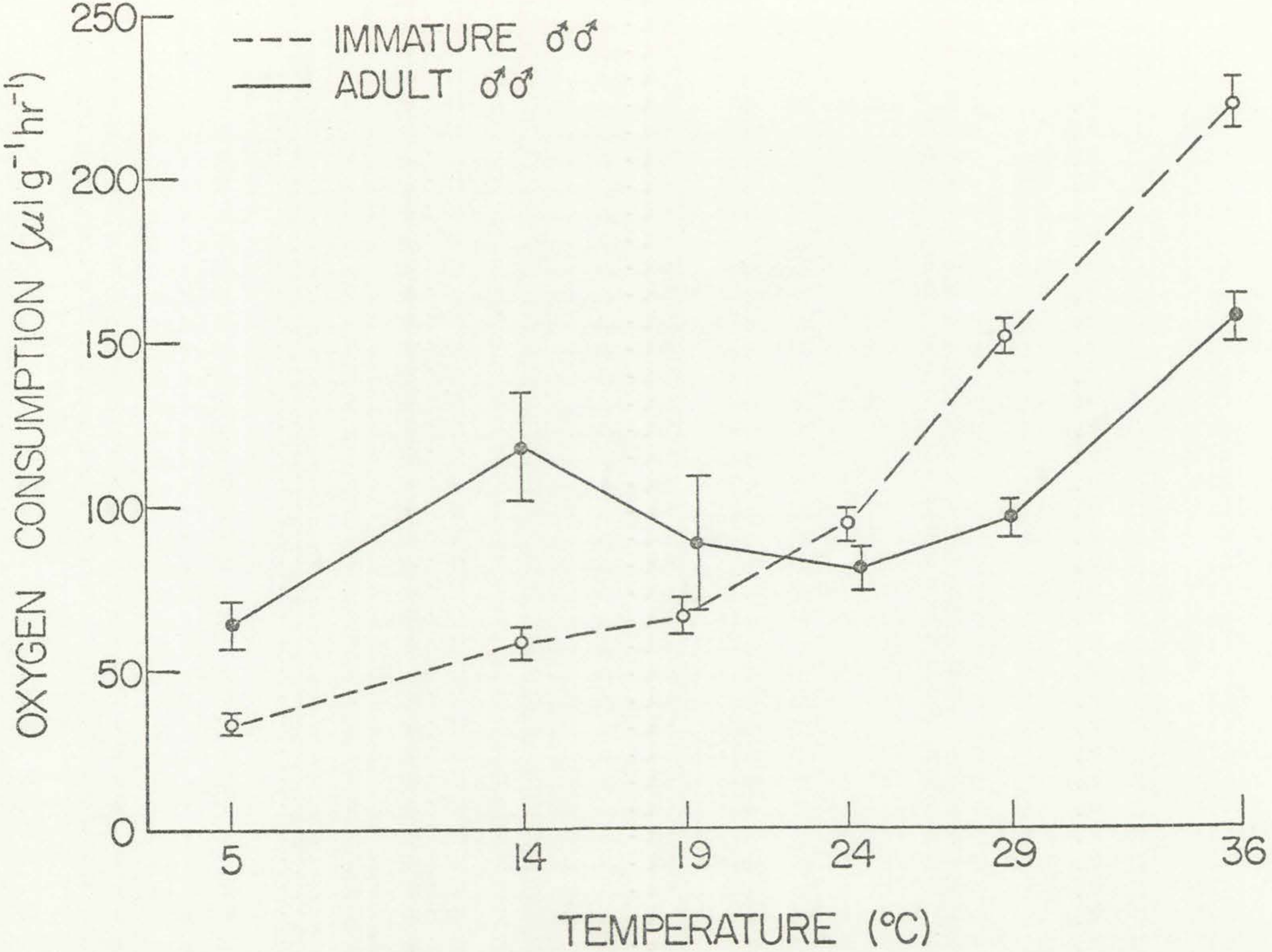

250
200
150
100
50
0
OXYGEN CONSUMPTION (μl g⁻¹ hr⁻¹)
--- IMMATURE ♂♂
— ADULT ♂♂
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 4. Metabolic rate: temperature curves for immature and adult _P. aquilonalis_ females collected 28 May to 8 June 1974. Vertical lines represent standard errors, n=29 - 33 (immatures), n=16 - 19 (matures).

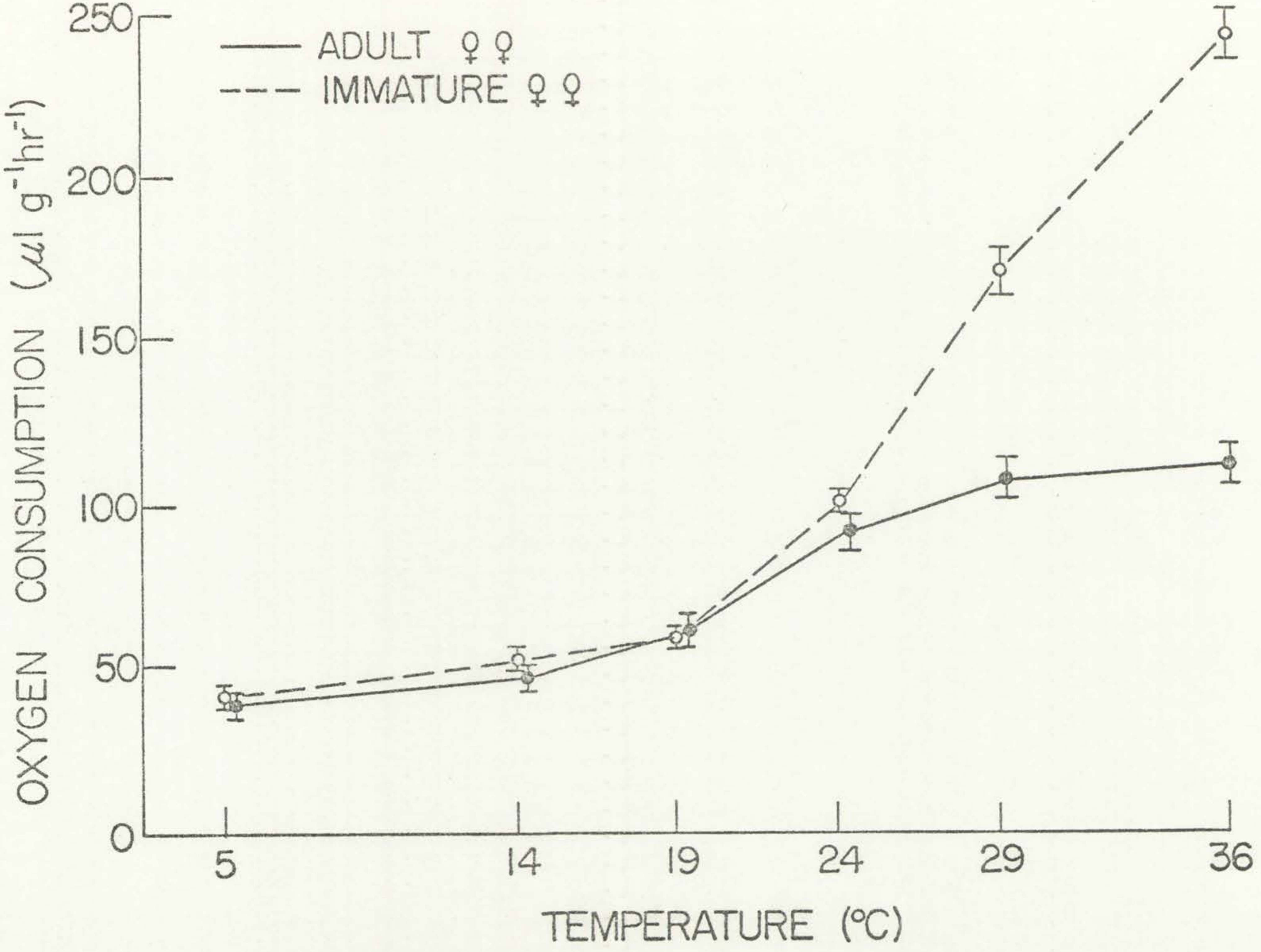

ADULT ♀♀
IMMATURE ♀♀
OXYGEN CONSUMPTION ($\mu l\ g^{-1}hr^{-1}$)
250
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 5. Metabolic rate: temperature curves for immature male P. aquilonalis previously acclimated to 10°C or 24°C. Vertical lines represent standard errors. Means are based on n=16 - 18 for 10°C-acclimated, and n=17 - 19 for the 24°C-acclimated group.

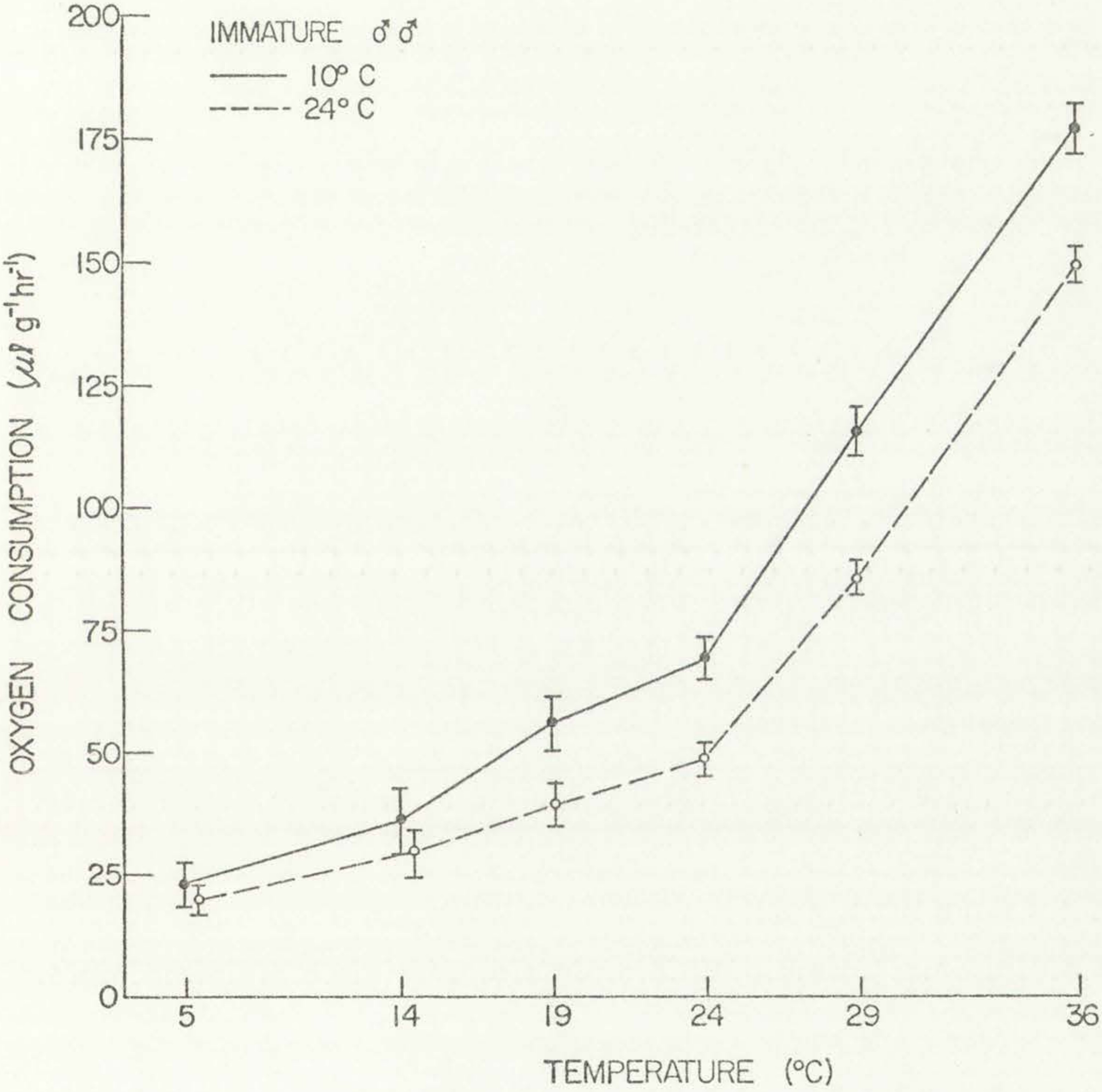
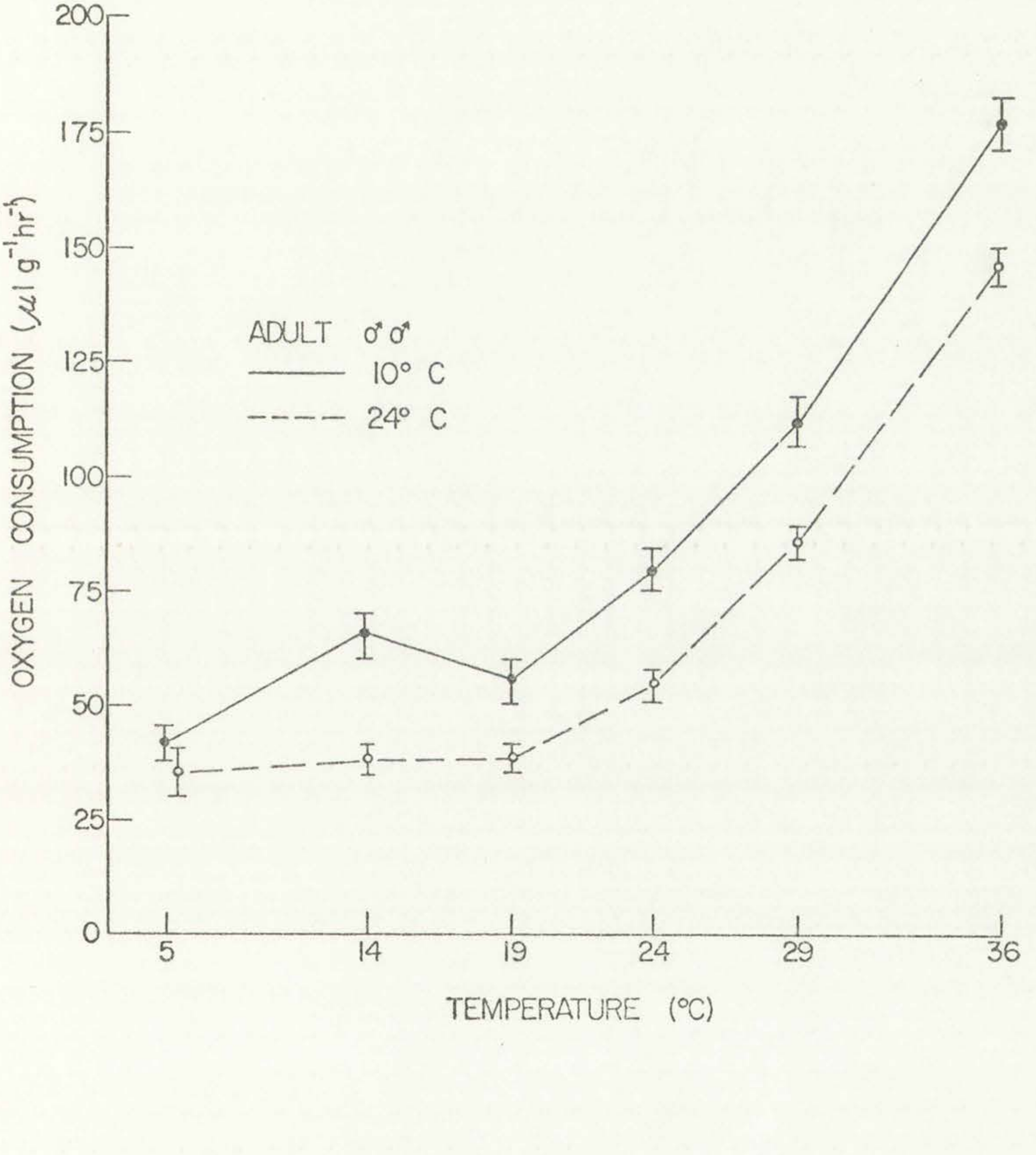
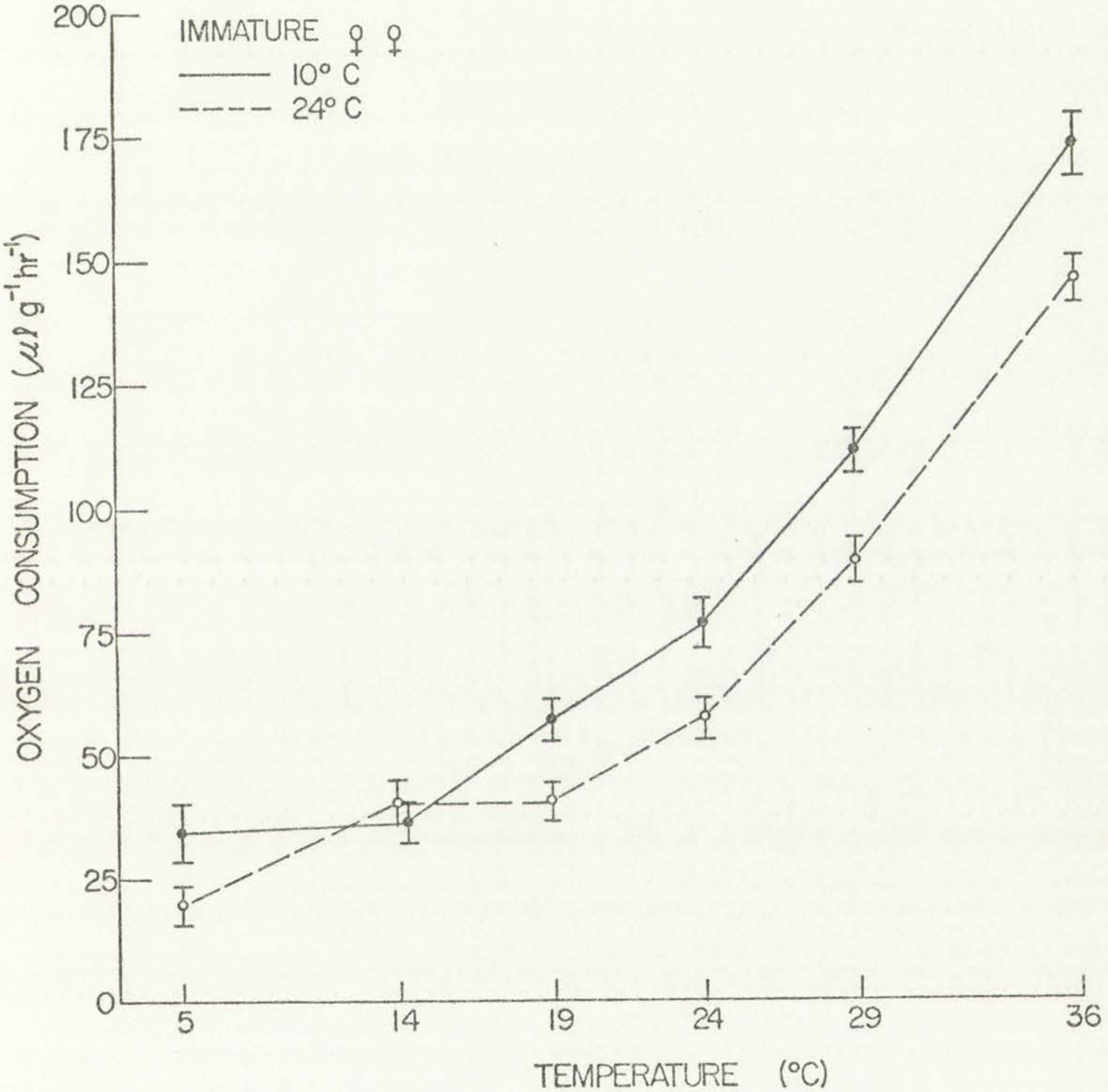

IMMATURE ♂♂
10° C
24° C
OXYGEN CONSUMPTION (μl g⁻¹hr⁻¹)
0
25
50
75
100
125
150
175
200
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 6. Metabolic rate: temperature curves for adult male *P. aquilonalis* previously acclimated to 10°C or 24°C. Vertical lines represent standard errors. Means are based on n=19 for 10°C-acclimated animals, and n=18 - 19 for the 24°C-acclimated group.



200
175
150
125
100
75
50
25
0
OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
ADULT ♂♂
10° C
24° C
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 7. Metabolic rate: temperature curves for immature female *P. aquilonalis* previously acclimated to 10°C or 24°C. Vertical lines represent standard errors. Means are based on n=16 - 18 for 10°C-acclimated animals, and n=17 - 19 for the 24°C-acclimated group.



IMMATURE ♀♀
10° C
24° C
OXYGEN CONSUMPTION ($\mu l\, g^{-1} hr^{-1}$)
200
175
150
125
100
75
50
25
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 8. Metabolic rate: temperature curves for adult female *P. aquilonalis* previously acclimated to 10°C or 24°C. Vertical lines represent standard errors. Means are based on n=18 - 19 for 10°C-acclimated animals, and n=19 for the 24°C-acclimated group.

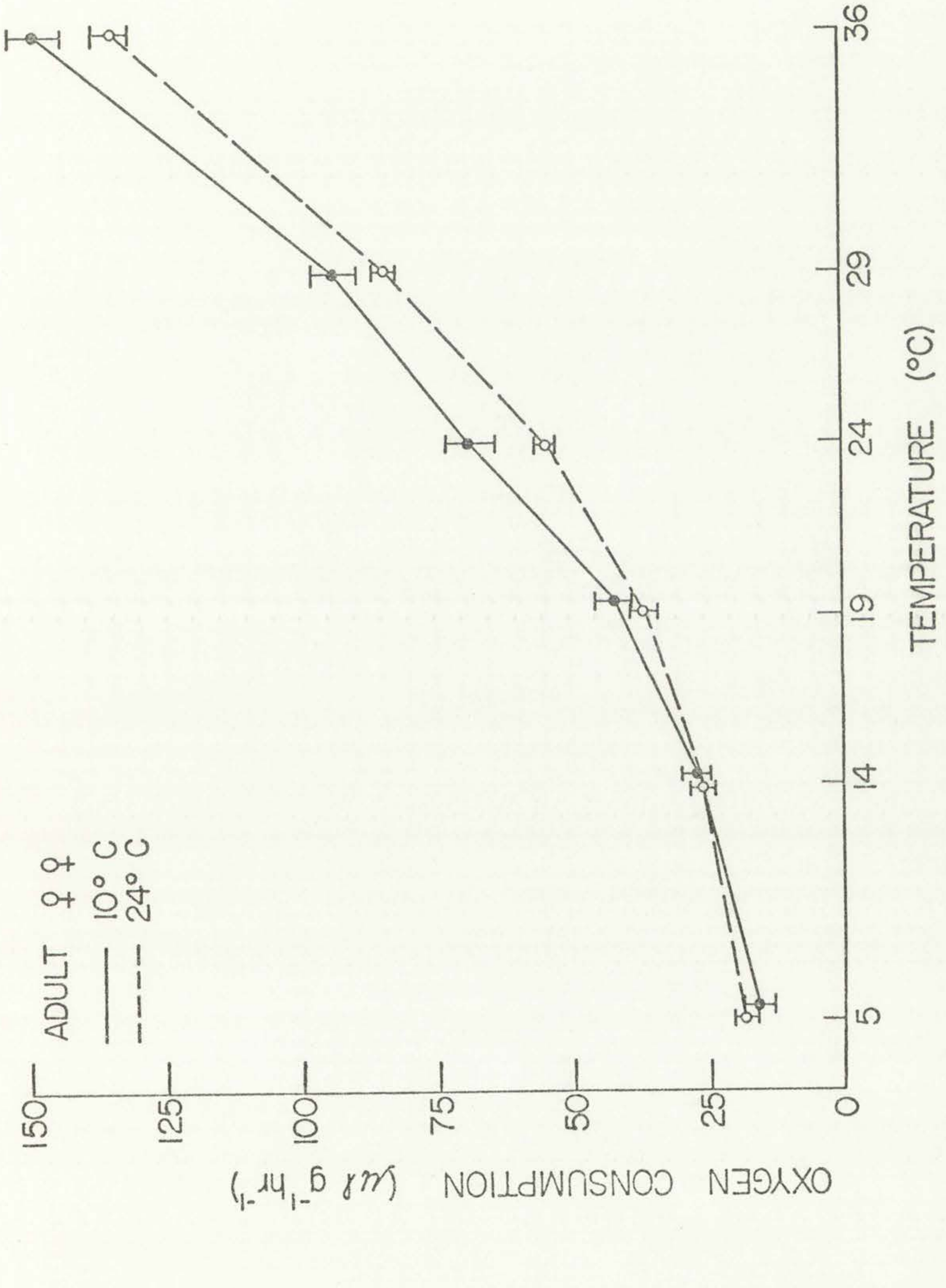

OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
0
25
50
75
100
125
150
5
14
19
24
29
36
TEMPERATURE (°C)
ADULT ♀♀
10° C
24° C

FIGURE 9. Metabolic rate: temperature curves for a group of adult female *P. aquilonalis* following collection and following starvation and laboratory feeding. Closed circles (●) represent means following collection 12 September 1974 (n=18 - 19); open circles (○) after 21 days starvation (n=12 - 19); open squares (□) after 55 days starvation (n=13 - 19) and open triangles (△) for scorpions 5 days after feeding (n=17 - 18). Vertical lines represent standard errors.

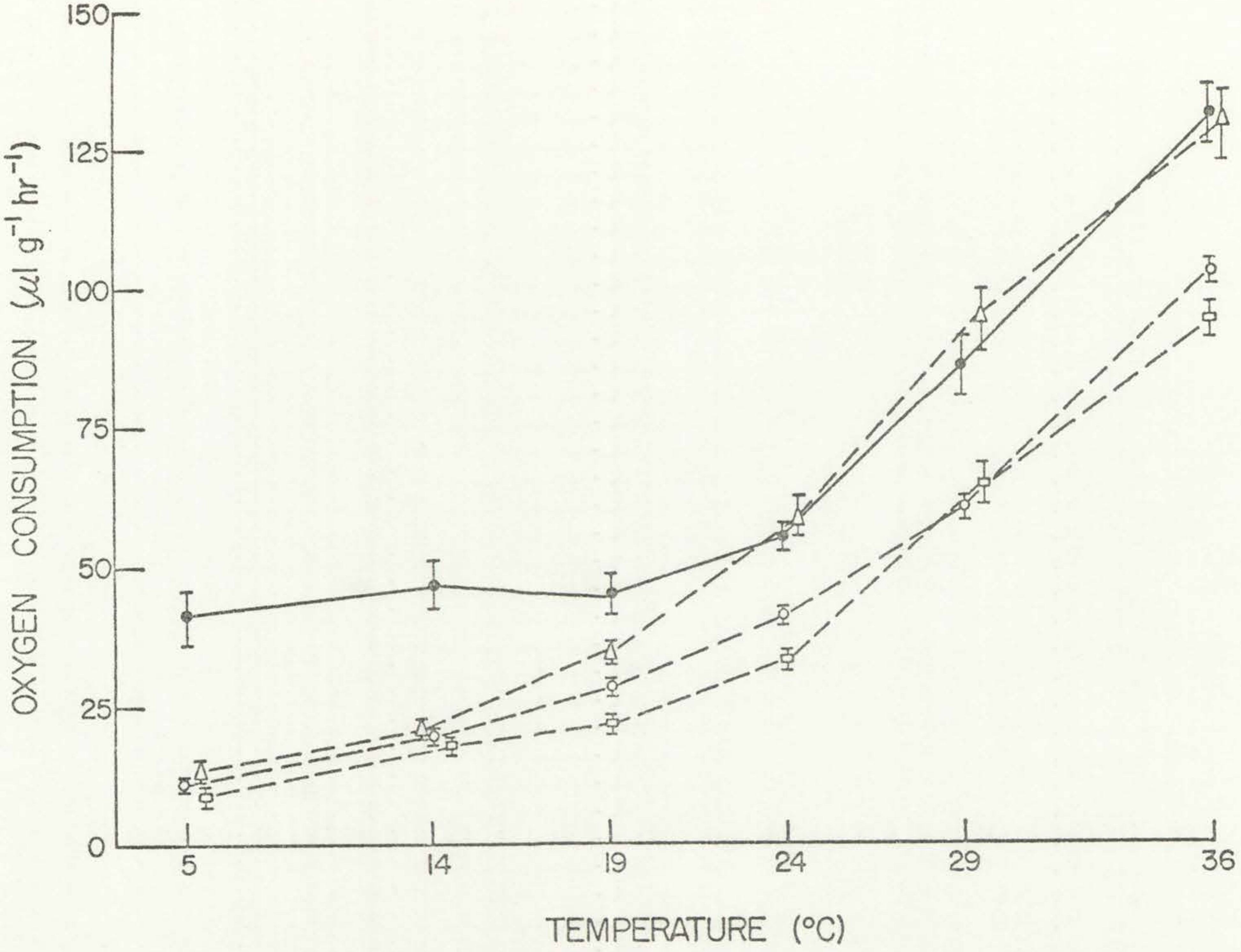

OXYGEN CONSUMPTION (µl g^{-1} hr^{-1})
150
125
100
75
50
25
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 10. Metabolic rate: temperature curves for adult male *P. aquilonalis* following collection on 11 July and 6 September 1974. Vertical lines represent standard errors. Means are based on n=14 for the 11 July group and n=18-19 for the 6 September group.

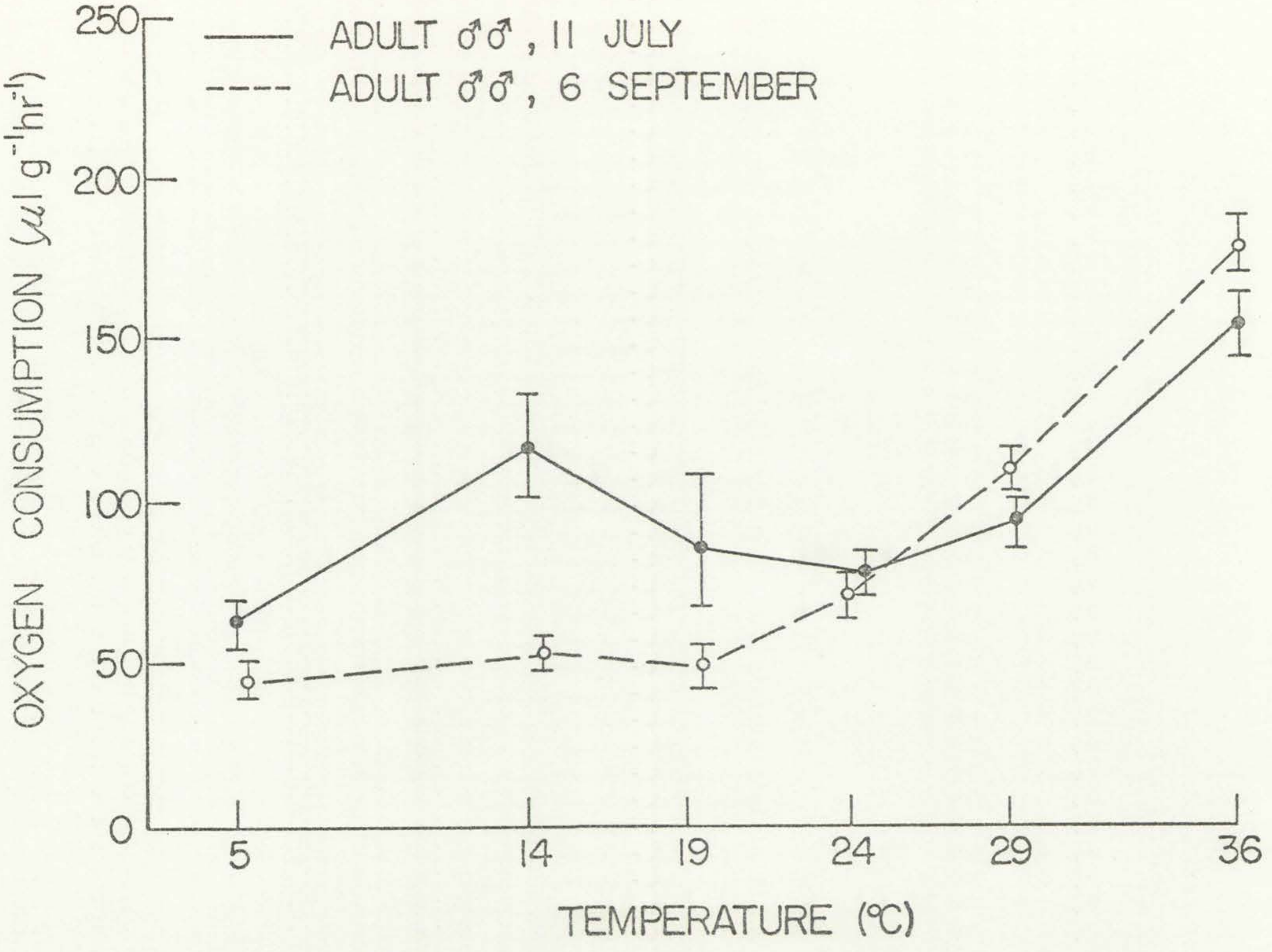

ADULT ♂♂, 11 JULY
ADULT ♂♂, 6 SEPTEMBER
OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
250
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 11. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection on 8 June 1974. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix 2).

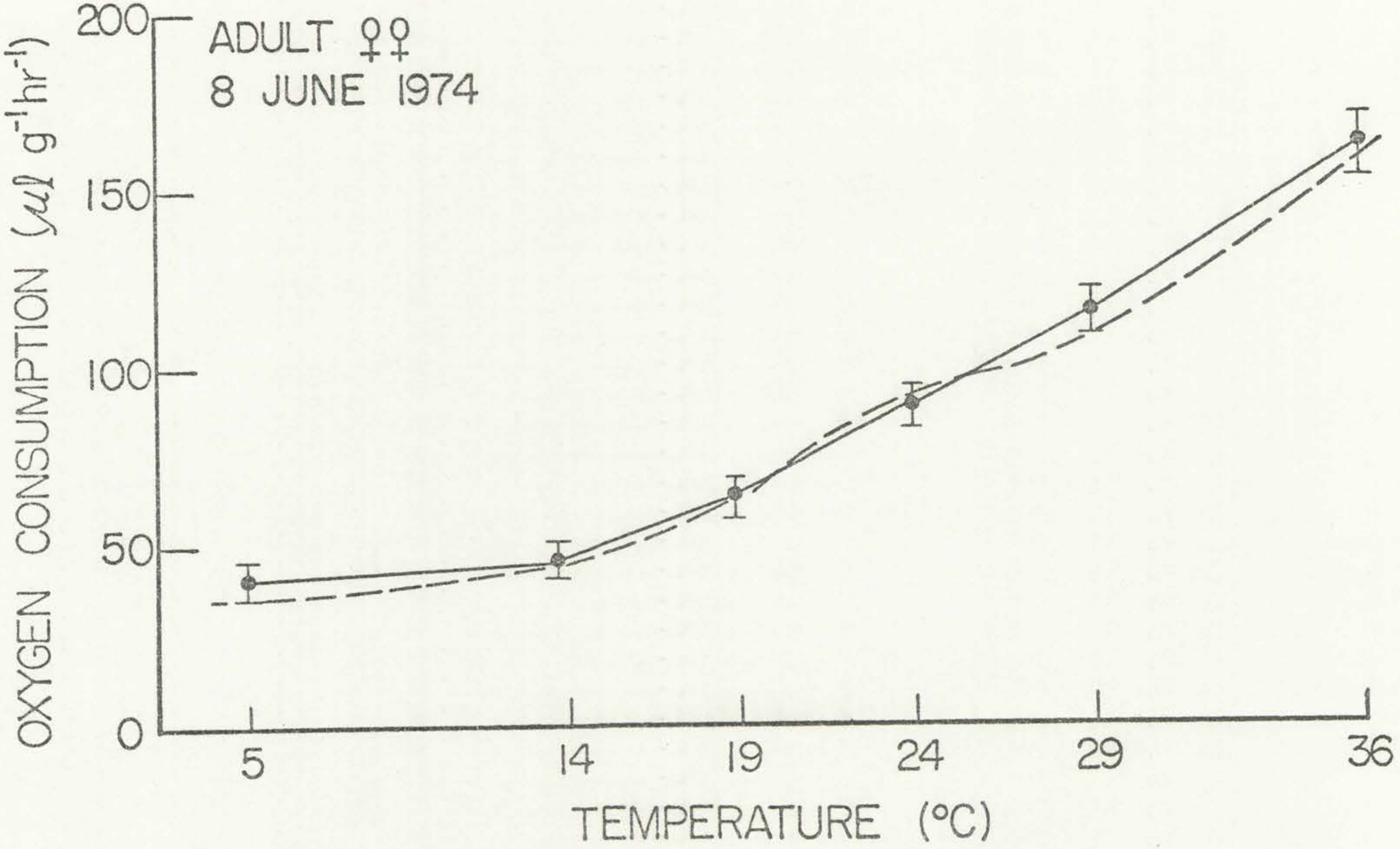

ADULT ♀♀
8 JUNE 1974
OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 12. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection on 12 September 1974. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix 2).

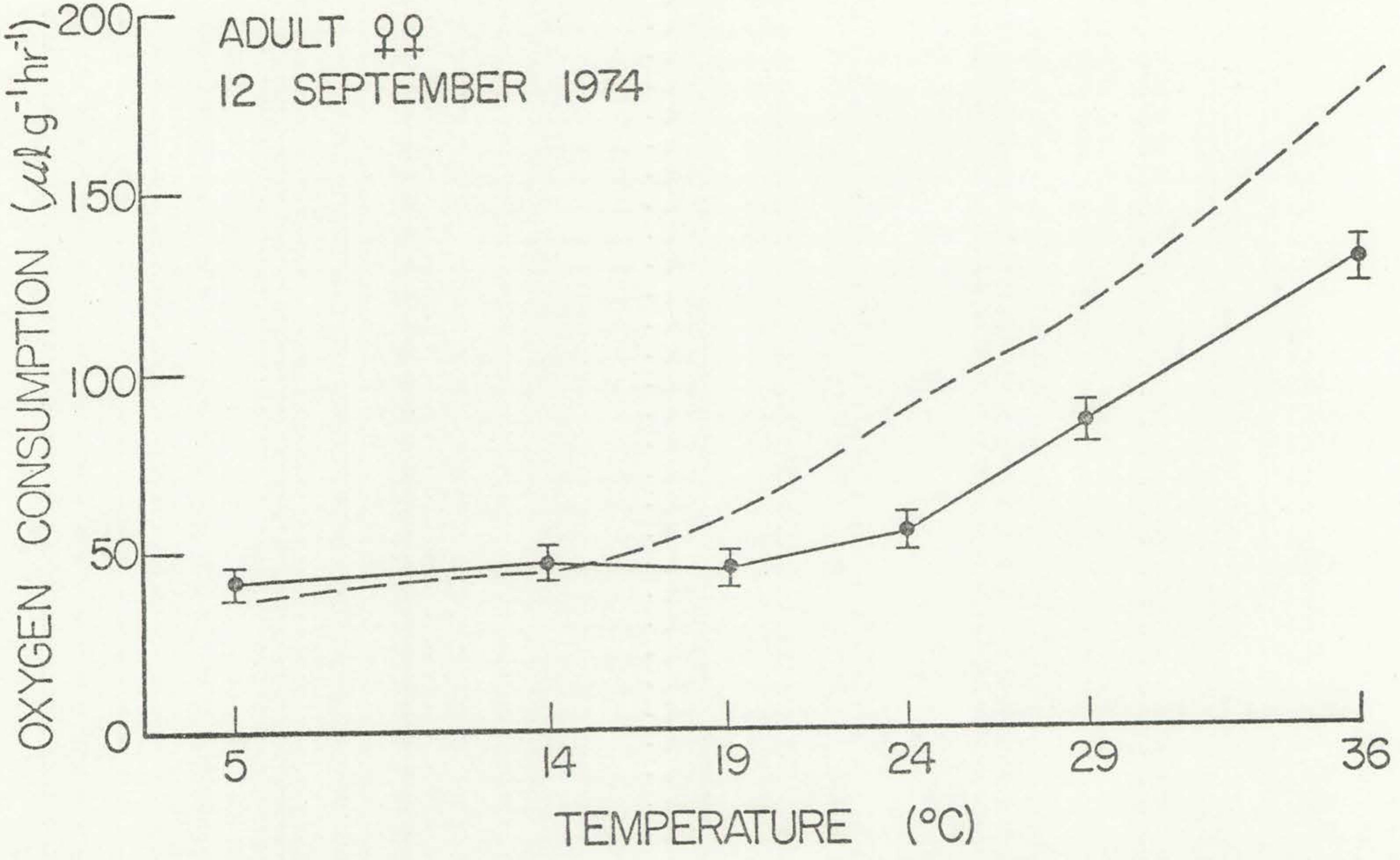
ADULT ♀♀
12 SEPTEMBER 1974
OXYGEN CONSUMPTION ($\mu l\,g^{-1}hr^{-1}$)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

Figure 13. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection 17 November 1974. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix2).

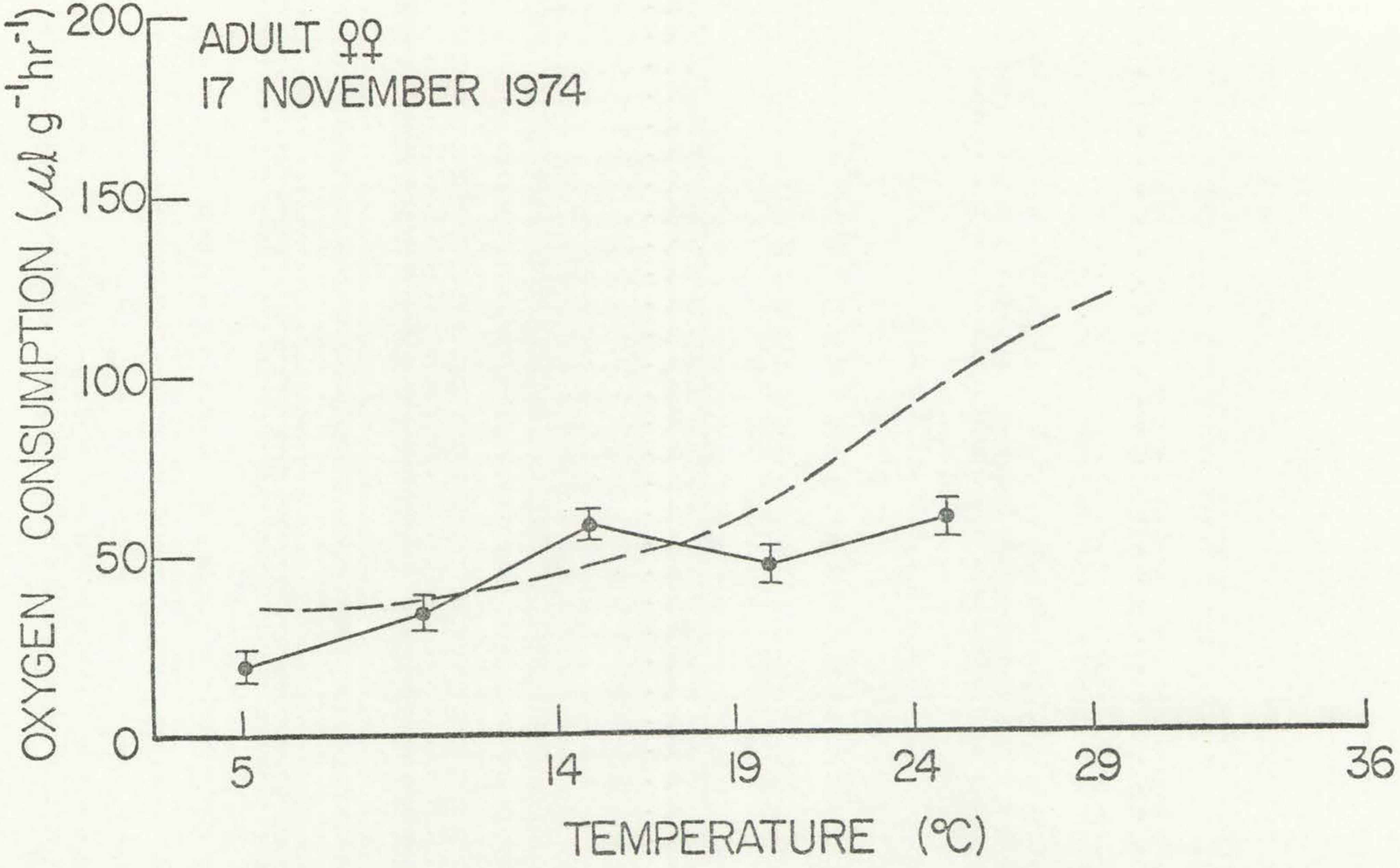

ADULT ♀♀
17 NOVEMBER 1974
OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 14. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection 15 April, 1975. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix 2).

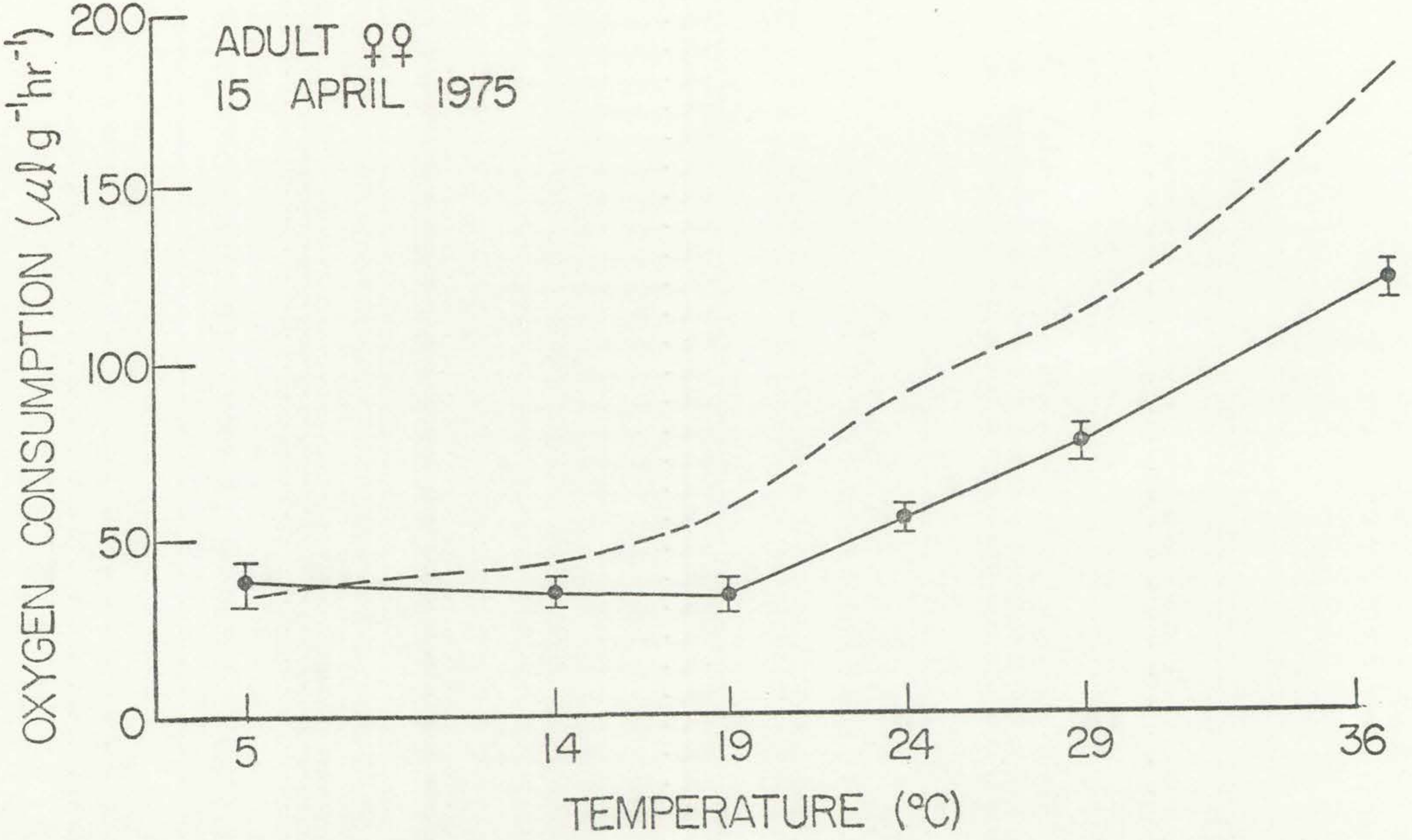

ADULT ♀♀
15 APRIL 1975
OXYGEN CONSUMPTION ($\mu l\ g^{-1} hr^{-1}$)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 15. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection 1 June 1975. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix 2).

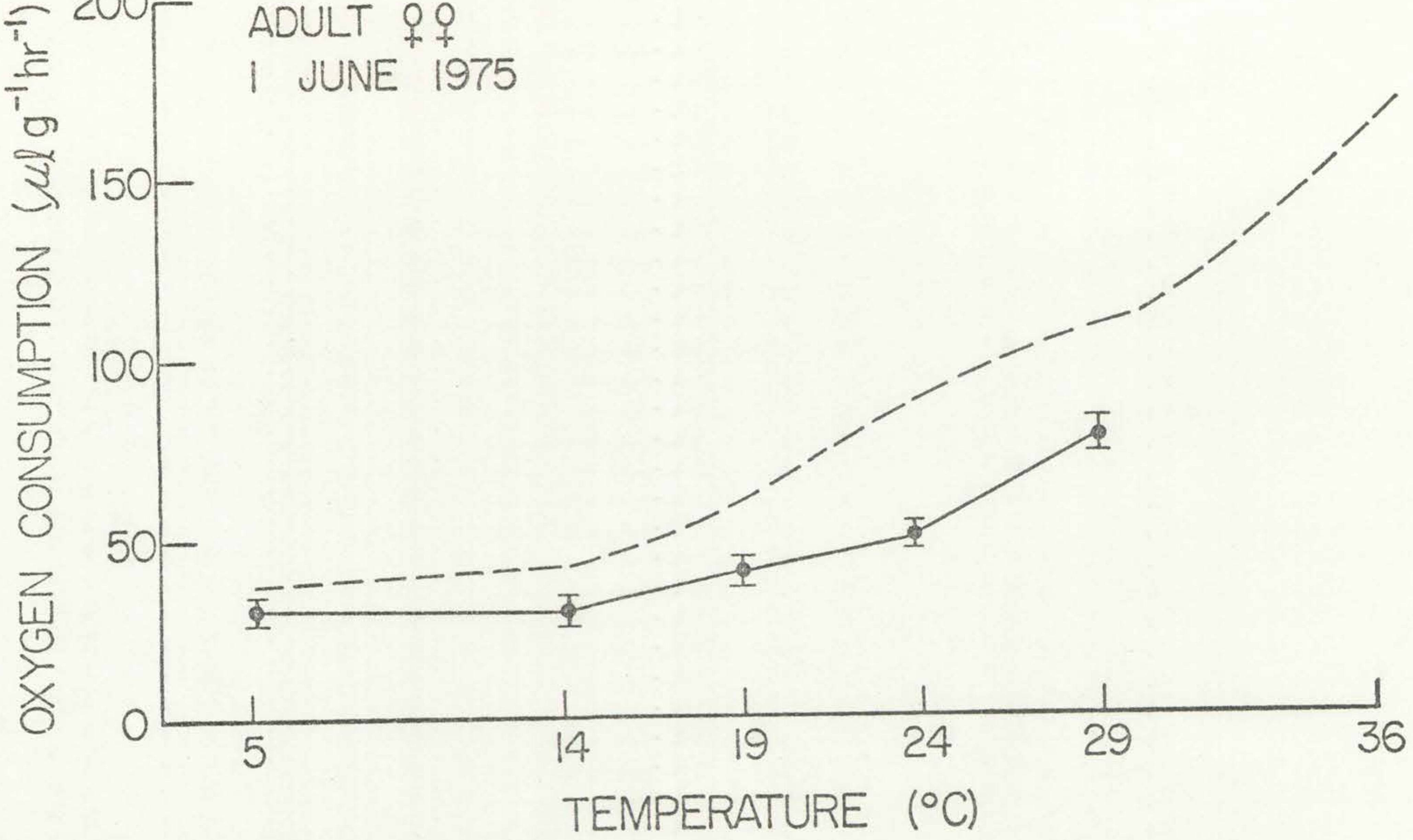

ADULT ♀♀
1 JUNE 1975
OXYGEN CONSUMPTION (µl g⁻¹hr⁻¹)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 16. Metabolic rate: temperature curves for adult female *P. aquilonalis* following collection 25 June 1975. Dashed-line curve represents spring 1974 R:T relations estimated from regression equations (Appendix 2).

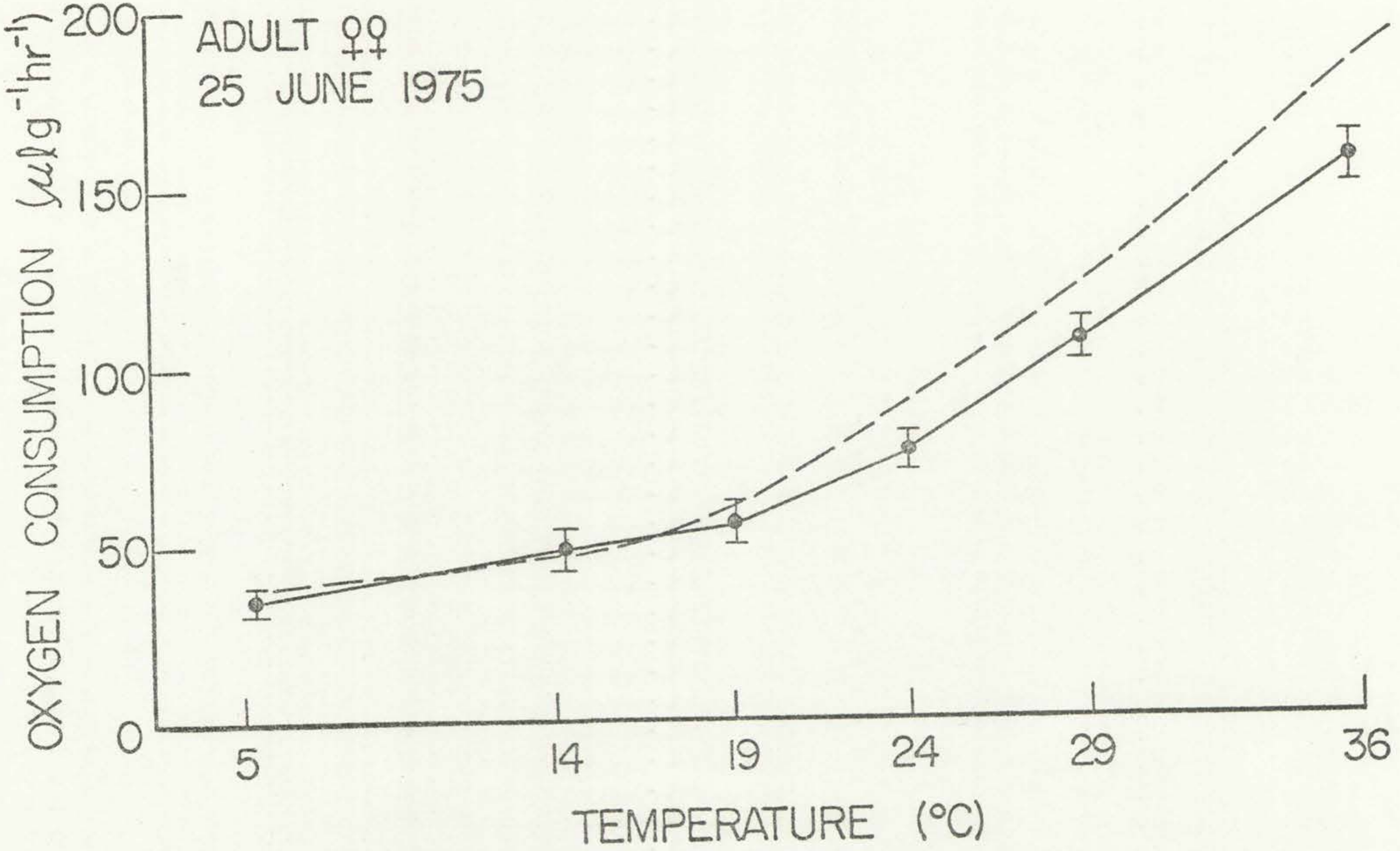

ADULT ♀♀
25 JUNE 1975
OXYGEN CONSUMPTION (μl g⁻¹ hr⁻¹)
200
150
100
50
0
5
14
19
24
29
36
TEMPERATURE (°C)

FIGURE 17. Influence of humidity on oxygen consumption at 25°C of freshly collected (6 September 1974) adult female P. aquilonalis. Vertical lines represent standard errors, n=18 - 19. Mean live weight = 0.3777 g.

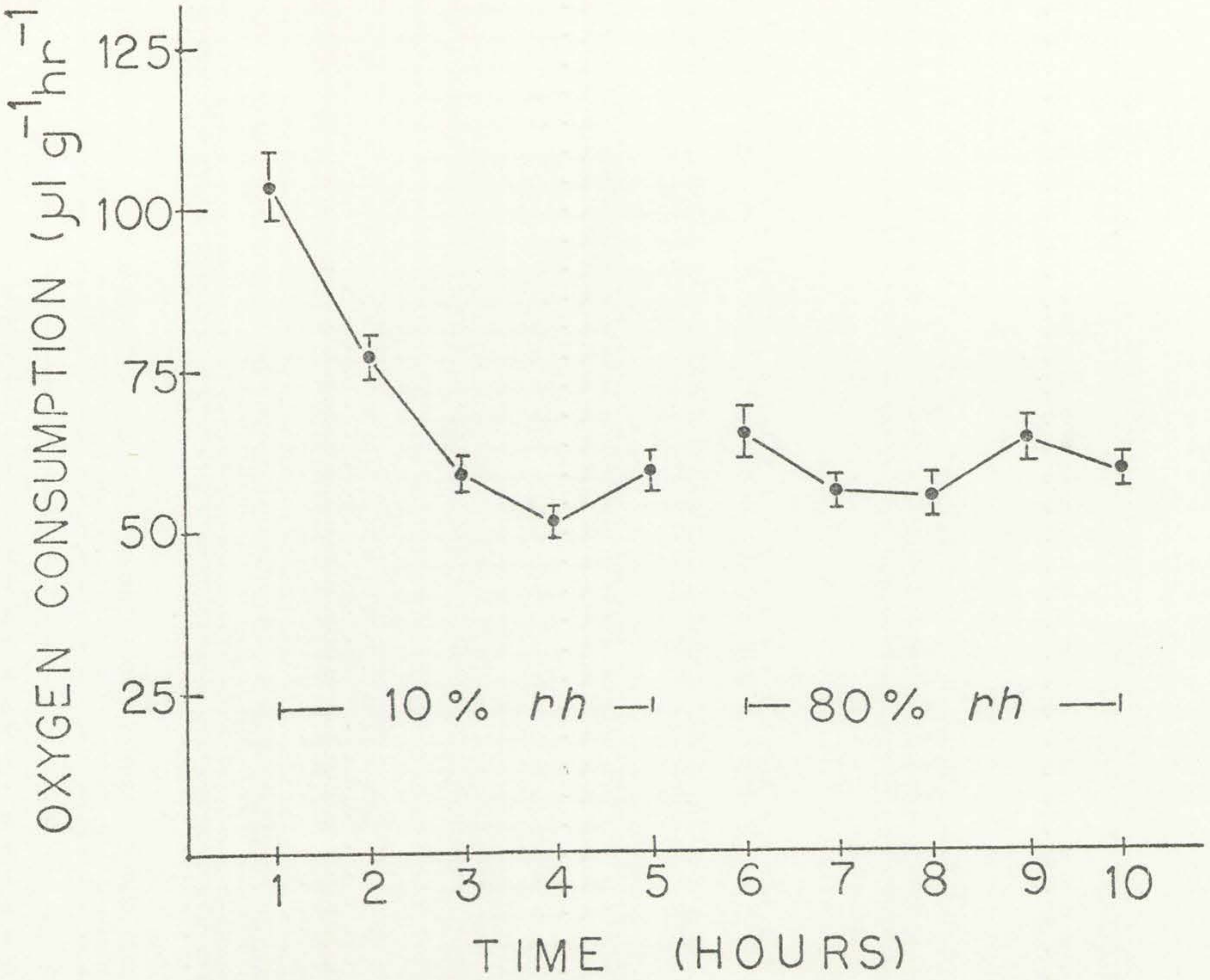
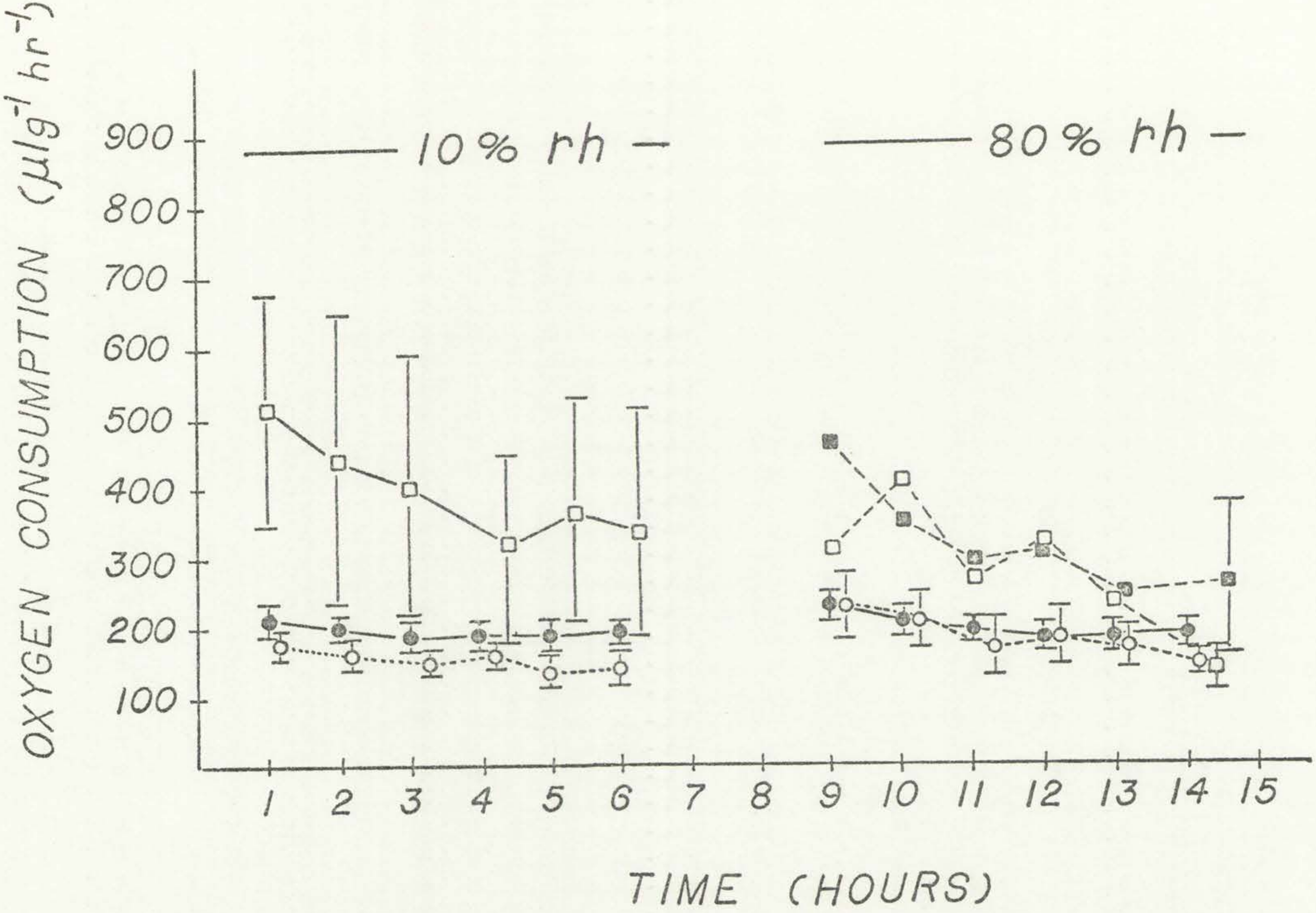

OXYGEN CONSUMPTION (μl g⁻¹hr⁻¹)
125
100
75
50
25
1
2
3
4
5
6
7
8
9
10
TIME (HOURS)
10% rh
80% rh

FIGURE 18. Influence of humidity on oxygen consumption of freshly collected, starved, and desiccated adult male *P. aquilonalis*. Closed circles (●) are means for freshly collected animals (n=14 - 15); open circles (○) for starved (n=14 - 15) and squares (□ and ■) for desiccated animals (n=15 at 10% rh). Under 80% rh open squares (□) are means for scorpions which did not drink water from flasks (n=5), while closed squares (■) represent means for those that did (n=10). Vertical lines represent 95% confidence limits.


OXYGEN CONSUMPTION ($\mu l g^{-1} hr^{-1}$)
900
800
700
600
500
400
300
200
100
10 % rh
80 % rh
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
TIME (HOURS)

TABLES

Table 1. Respiratory temperature coefficients (Q_{10}) for some selected arachnids

Order and species	Q_{10} and Temperature range (°C)			Reference
Araneae				
Aphonopelma sp.	3.35 (10-20)	1.93 (20-30)	1.11 (30-40)	Seymour and Vinegar, 1973
Lycosa carolinensis				
(January-collected)	1.21 (23-29)[1]	1.33 (23-33)	2.04 (33-45)	Mouer and Ericksen, 1972
(June-collected)		1.26 (29-39)	1.94 (39-45)	
Scorpionida				
Euscorpius italicus[2]	4.16 (5-15)	2.23 (10-20)	1.85 (15-25)	Dresco-Derouet, 1964
Nebo hierochonticus[2]	2.98 (5-15)	1.74 (15-25)	-	
Euscorpius flavicaudis[2]	2.46 (6-16)	2.24 (10-20)	2.40 (16-26)	Dresco-Derouet, 1967
Centruoides sculpturatus	2.18 (10-20)	1.96 (20-30)	2.24 (30-40)	Hadley and Hill, 1969
Hadrurus arizonensis[3]	2.2 (25-30)	1.5 (30-35)	1.9 (35-40)	Hadley, 1970a
Uropygi				
Mastigoproctus giganteus[3]	1.8 (25-30)	1.6 (30-35)	1.9 (35-40)	Ahearn, 1970

[1] Based on single temperature change from 23°C to 29°C. Other values for *L. carolinensis* based on 2°C temperature changes from 29°C to 45°C.

[2] Q_{10} values calculated from tabulated results.

[3] Q_{10} values estimated from R:T curves. Respirometry conducted at 0% rh.

Table 2. Influence of live weight on respiratory temperature coefficients (Q_{10}) for the scorpion <u>Urodacus yashenkoi</u>. Values calculated from weight:metabolism regression equations of Shorthouse (1971)

Temperature change (°C)	Estimated Q_{10} for "small" scorpions (0.5 g)		Estimated Q_{10} for "large" scorpions (3.0 g)	
	males	females	males	females
10 to 15	1.43	2.94	1.23	1.04
15 to 20	3.21	1.75	4.70	9.06
20 to 25	2.14	1.92	2.69	1.00
25 to 30	1.18	0.57	5.07	4.93
30 to 35	5.30	1.58	1.58	0.71
20 to 30[1]	1.59	1.45	3.56	2.19
25 to 35[2]	2.51	1.84	2.83	1.86

[1] Not for an acute change from 20 to 30°C; included exposure at 25°C.

[2] Not for an acute change from 25 to 35°C; included exposure at 30°C.

Table 3. Regression estimates of oxygen-consumption rates and temperature coefficients (Q_{10}) for *P. aquilonalis* males weighing 30 mg and 300 mg

	30 mg live weight		300 mg live weight	
Temperature (°C)	Estimated oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$)	Q_{10}	Estimated oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$)	Q_{10}
5	30.42		35.92	
		1.24		2.00
14	36.89		67.10	
		1.17		1.08
19	39.88		69.72	
		6.58		1.41
24	102.32		82.86	
		6.13		1.98
29	253.37		116.69	
		1.89		1.78
36	396.83		174.53	

Table 4. Regression estimates of oxygen-consumption rates and temperature coefficients (Q_{10}) for *P. aquilonalis* females weighing 30 mg and 300 mg

	30 mg live weight		300 mg live weight	
Temperature (°C)	Estimated oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$)	Q_{10}	Estimated oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$)	Q_{10}
5	44.68		37.66	
		1.21		1.23
14	53.11		45.40	
		0.59		1.67
19	40.88		58.66	
		7.40		2.52
24	111.24		93.14	
		5.79		1.99
29	267.58		131.55	
		1.49		1.74
36	353.76		194.12	

Table 5. Effect of starvation and feeding on the temperature coefficient (Q_{10}) of oxygen consumption for adult _P. aquilonalis_ females

Temperature change (°C)	Temperature coefficient (Q_{10})		
	22 days starvation	55 days starvation	After feeding
5 to 14	1.77	2.14	1.72
14 to 19	2.17	1.60	2.40
19 to 24	2.10	2.18	3.00
24 to 29	2.25	3.63	2.65
29 to 36	2.10	1.73	1.57
14 to 24[1]	2.13	1.87	2.68

[1] Q_{10} values in this row were calculated from 14°C and 24°C oxygen-consumption data.

Table 6. Results of t-test comparisons of final (6th hr) mean oxygen-consumption rates at 20°C and respiratory quotients (RQ) for adult _P. aquilonalis_ males collected June-September 1975

Collection date (mean live weight in grams)	Oxygen consumption[1] (μl g^{-1} hr^{-1})	RQ[1]
28 June (0.2675)	49.79 a	0.4712 a
14 July (0.2886)	52.27 a	0.6217 b c
28 July (0.3006)	50.40 a b	0.5789 a b
7 August (0.3221)	37.50 b c	0.6461 b c e
23 August (0.3573)	33.00 c	0.4591 a d
15 September (0.3328)	48.00 a	0.6719 e

[1] Means followed by at least a single common letter are not significantly different at $P<0.05$; others differ at $P<0.05$ to $P<0.001$. T-test comparisons tested for significant differences (2-tailed test).

Table 7. Influence of feeding and starvation on oxygen-consumption rates at 20°C and on respiratory quotients (RQ) of freshly-collected adult *P. aquilonalis* scorpions

Collection date or treatment	Oxygen consumption[1] (μl g^{-1} hr^{-1}±S.E.)(N)	P	Respiratory quotient[1] (R.Q.±S.E.)(N)	P
Feeding experiment:[2]				
28 June (♂♂)	50.33±2.38 (12)	ns	0.4779±0.0429 (12)	<0.05
Fed (♂♂)	50.90 ±.04 (12)		0.5910±0.0220 (12)	
Starvation experiment:[3]				
12 October (♀♀)	36.42±2.82 (14)	<0.05	0.6384±0.0301 (14)	ns
Starved (♀♀)	27.95±1.51 (14)		0.6495±0.0339 (14)	

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[1] Oxygen-consumption rates and RQ's were compared only for those animals which gained weight during feeding (mean weight gain = 23.5%).

[2] Scorpions collected 28 June and fed mealworms *ad lib* for 12 days at 24°C.

[3] Scorpions collected 12 October and starved 18 days at 24°C.

APPENDICES

Appendix 1. Regression equations and statistics for linear regressions relating live weight (X) in mg to oxygen consumption (Y) in $\mu l\ g^{-1}\ hr^{-1}$ for male *P. aquilonalis* in Figure 1

Temperature (°C)	Regression equation	N	Correlation Coefficient (r)	F-value[1]	P[2]
5	$\log Y = 1.37669 + 0.07211 \log X$	71	+0.062	0.258	ns
14	$\log Y = 1.18309 + 0.25983 \log X$	76	+0.250	4.943	<0.05
19	$\log Y = 1.24236 + 0.24262 \log X$	76	+0.264	5.449	<0.05
24	$\log Y = 2.14525 - 0.09160 \log X$	76	-0.116	1.107	ns
29	$\log Y = 2.90115 - 0.33673 \log X$	75	-0.535	29.204	<0.001
36	$\log Y = 3.12553 - 0.35673 \log X$	76	-0.623	45.856	<0.001

[1] F-values were derived from analysis of variance of the regression.

[2] Significance level of the F-value.

Appendix 2. Regression equations and statistics for linear regressions relating live weight (X) in mg to oxygen consumption (Y) in µl g^{-1} hr^{-1} for female P. *aquilonalis* in Figure 2

Temperature (°C)	Regression equation	N	Correlation Coefficient (r)	F-value[1]	P[2]
5	logY = 1.75983 - 0.07428 logX	45	-0.125	0.681	ns
14	logY = 1.82572 - 0.06809 logX	51	-0.093	0.430	ns
19	logY = 1.61148 + 0.06331 logX	52	+0.147	1.107	ns
24	logY = 2.16106 - 0.07711 logX	52	-0.250	3.347	ns
29	logY = 2.88292 - 0.30835 logX	52	-0.747	63.146	<0.001
36	logY = 2.93372 - 0.26065 logX	52	-0.708	50.610	<0.001

[1] F-values were derived from analysis of variance of the regression.

[2] Significance level of the F-level.

Appendix 3. Percent increase or decrease in mean oxygen-consumption rates of 10°C-acclimated specimens over 24°C-acclimated immature and mature male and female *P. aquilonalis* at various test temperatures

Temperature (°C)	Percent increase or decrease[1]			
	Immature scorpions		Mature scorpions	
	males	females	males	females
5	17.1	69.9	12.2	-12.6
14	23.1	-12.1	73.3	2.7
19	40.1	42.8	45.8	13.9
24	38.6	33.3	47.7	25.9
29	33.8	29.9	31.6	12.0
36	17.7	18.6	22.4	11.0

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[1] Percent decreases of 10°C-acclimated rate below 24°C-acclimated rate are indicated by "-".

Appendix 4. Seasonal oxygen-consumption rates measured hourly at 20°C and respiratory quotients (RQ) for adult *P. aquilonalis* males

Collection date (mean live wt., g)	Oxygen consumption $(\mu l\ g^{-1}\ hr^{-1})$ ±S.E.[1] (N)						RQ (N)
	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6	
28 June (0.2675)	61.35 4.62(15)	58.44 3.82(15)	56.01 2.83(15)	51.64 3.67(15)	49.51 3.05(15)	49.79 2.45(15)	0.4712 (14)
14 July (0.2886)	89.64 13.69(15)	66.58 6.52(15)	73.12 9.47(15)	53.35 3.64(15)	57.11 5.62(15)	52.27 4.90(15)	0.6217 (15)
28 July (0.3006)	60.47 6.91(15)	64.26 8.39(15)	61.73 7.37(14)	37.09 2.59(13)	51.17 4.48(15)	50.40 6.61(15)	0.5789 (15)
7 August (0.3221)	54.92 4.77(15)	48.66 3.81(15)	48.07 4.51(15)	55.06 4.09(15)	35.19 2.19(15)	37.50 1.76(15)	0.6461 (15)
23 August (0.3573)	44.91 4.50(14)	46.21 6.39(14)	35.75 2.06(14)	35.97 2.00(14)	35.76 2.88(14)	33.00 2.18(14)	0.4591 (14)
15 September (0.3328)	51.82 2.55(15)	48.38 2.17(15)	44.23 1.77(15)	48.56 1.69(15)	50.39 1.89(15)	48.00 1.84(15)	0.6719 (15)

[1] Standard errors

Appendix 5. Influence of starvation and feeding on oxygen consumption at 20°C and on respiratory quotient (RQ) of adult *P. aquilonalis*

Collection date and treatment (mean live wt.) (sex)	Oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$) ±S.E.[1] (N)						RQ (N)
	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6	
28 June[1] (0.2719) (♂♂)	61.90 ±4.61(12)	57.12 ±2.84(12)	55.84 ±2.94(12)	54.82 ±3.75(12)	51.47 ±3.11(12)	50.33 ±2.38(12)	0.4779 (12)
Fed[2] (0.3305) (♂♂)	57.15 ±6.54(12)	53.28 ±6.82(12)	51.02 ±5.96(12)	51.73 ±6.53(12)	55.60 ±7.69(12)	50.90 ±7.04(12)	0.5910 (12)
12 October[3] (0.4035) (♀♀)	39.71 ±3.17(14)	42.64 ±4.03(14)	37.62 ±3.44(14)	32.04 ±3.28(14)	43.02 ±4.87(13)	36.42 ±2.82(14)	0.6384 (14)
Starved[4] (0.4002) (♀♀)	40.69 ±3.07(14)	34.72 ±2.10(14)	29.98 ±1.80(14)	28.60 ±2.29(14)	26.61 ±1.39(14)	27.95 ±1.51(14)	0.6495 (14)

[1] Freshly collected scorpions

[2] 28 June-collected scorpions fed mealworms ad lib for 12 days at 24°C.

[3] Freshly collected scorpions

[4] Scorpions collected 12 October and starved 18 days at 24°C.

Appendix 6. Estimated oxygen-consumption rates after 14 days starvation at 24°C of mature <u>P. aquilonalis</u> females collected 12 September 1974 [1]

Test temperature (°C) and treatments	Oxygen consumption ($\mu l\ g^{-1}\ hr^{-1}$)	Percentage increase of post-feeding rates over estimated 14-day starvation rates[3]
24°C		
22-day starvation	40.71	23.3%
Post feeding	57.96	
Estimated 14-day starvation rates[2]	46.99	
29°C		
22-day starvation	61.02	29.0%
Post-feeding	94.44	
Estimated 14-day starvation rates[2]	73.18	
36°C		
22-day starvation	102.67	15.3%
Post-feeding	129.75	
Estimated 14-day starvation rates[2]	112.53	

[1] From data presented graphically in Figure 9.

[2] Oxygen-consumption estimates in this row are based on the assumption that 14-day starvation will represent 63.6% (14/22) of the total depression of rates attributable to 22-day starvation.

[3] Percentage amounts that post-feeding rates exceed estimated 14-day starvation rates.

Appendix 7. Estimated influence of starvation on oxygen consumption of mature *P. aquilonalis* females following acclimation at 10°C or 24°C

Test temperature (°C)	Oxygen consumption (μl g^{-1} hr^{-1})			
	Observed 24°C-acclimated rate (column 2)[1]	Estimated rate[2] prior to acclimation (unstarved) (column 3)	Estimated 10°C[3]-acclimated rate (considering starvation)	Observed 10°C-acclimated rate[1]
24	54.08	66.68	60.38	68.09
29	83.78	108.08	95.95	93.87
36	134.15	154.67	144.41	148.86

[1] From data graphically represented in Figure 8.

[2] Figures in this column represent rates from column 2 above plus an amount equal to the product of the "percentage increase of post feeding over 14-day starvation rates" (column 3, Appendix 6) multiplied by the rate in column 2 above.

[3] Figures in this column represent rates of column 2 above plus one-half the difference between the values in columns 2 and 3 above.

CURRICULUM VITAE

BORN: 3 November 1945, Madison, Wisconsin

ACADEMIC BACKGROUND:

B.S.	Zoology	1968	Utah State University
M.S.	Biology	1973	The University of New Mexico
Ph.D.	Biology	1977	The University of New Mexico

PUBLICATIONS:

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