METABOLIC RATES OF RESTING SALTICID AND THOMISID SPIDERS

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ABSTRACT. Rates of metabolism of jumping and crab spiders were evaluated to determine if life-style characteristics are associated with rates of energy expenditure in these 'sit-and-wait' predators. Resting rates of oxygen consumption were measured under standardized conditions in nine species of salticid and three species of thomisid spiders. These rates and those previously reported ranged from 50–70% of that expected for their size in these families. They are similar to those of other families of spiders with similar modes of prey capture, life span, and distribution. No significant differences in this measure were detected between the two families.

Rates of energy expenditure in spiders exhibit much variation, and it has been my goal to document and account for this diversity (Anderson 1970; Anderson & Prestwich 1982; Anderson 1994). As in most organisms (Peters 1983), body size is the major source of variation in energy expenditure in spiders (Humphreys 1977; Greenstone & Bennett 1980; Anderson & Prestwich 1982). Nonetheless, considerable variation in this measure remains after adjustment for size. Most spiders have low rates of metabolism ($\sim$ 50% of expected for their size) compared to other ectothermic poikilotherms. This feature is considered an adaptation to an unpredictable food supply (Anderson 1970; Greenstone & Bennett 1980) in these predators. This interpretation is consistent with the observation that those species with very low metabolic rates, i.e., less than 50% of expected for their size, live much longer than one year, often colonize marginal habitats, and are restricted in distribution to lower latitudes (Anderson & Prestwich 1982; Anderson 1994). Conversely, the high rates of metabolism ($\sim$ 100% of expected) found in orb-weavers and comb-footed spiders are associated with high reproductive rates, rapid growth, high population densities, and widespread distribution (Anderson 1994).

The proposed associations between energetics and biology were made by measurement of rates of respiratory gas exchange in resting spiders. Since spiders are inactive most of the time, this measurement represents a significant fraction of their total energy requirement (Andrews & Pough 1985). Interpretation of such comparisons is complicated because any given trait may reflect selection associated with environmental constraints as well as phylogenetic affiliations (Huey 1987; Wang & Abe 1994). Huey (1987) recommends that studies of closely related species most effectively resolves such ambiguities. Conversely, Andrews & Pough (1985) suggested that associations between energy metabolism and ecology of a species could be evaluated from data obtained on species with similar ecological characteristics but who differ phylogenetically.

I selected species in the families Salticidae and Thomisidae as a compromise between these two recommendations. There is little information available relating to energetics in these important taxa. Both families constitute a large and important component of the spider fauna. They contain 4,000 and 2,000 described species, respectively, out of a total 34,000 spiders in this order and are cosmopolitan in distribution (Coddington & Levi 1991). Obviously they differ in phylogeny as they are separated at the familial level. The two families are, however, closely related (Coddington & Levi 1991). They differ greatly in morphology but are similar in certain particulars: both are diurnally active and do not use a web to capture prey. Jumping spiders have a better sense of vision and often pursue prey over some distance. Larger spe-

cies are stationary: from their vantage point they visually scan the environment for prey (Enders 1975; Richman & Jackson 1992). Smaller jumping spiders spend much of their time moving and then stopping to look for prey (Enders 1975). In contrast, crab spiders are relatively stationary and ambush prey coming in close proximity. As such, thomisids reside at locations where prey commonly occur, i.e., flowers, tree trunks, stems of vegetation, and in litter (Dondale & Redner 1978; Morse 1983). Most exhibit cryptic coloration (Gertsch 1979).

My aim here is to measure resting rates of metabolism and use these data to assess the validity of the relationship between life-style characteristics and energetics. I predict the rates of both jumping spiders and crab spiders will be *ca.* 50–60% expected for their size. I base this prediction on the notion that they share certain characteristics with other spiders whose rates of metabolism have been reported (Anderson 1970; Greenstone & Bennett 1980). Their life-style characteristics are more similar to wolf-spiders (Lycosidae) than they are to orb-weaving spiders (Araneidae) and comb-footed spiders (Theridiidae). Comparisons between the salticids and thomisids might also be instructive. Enders (1976a, b) has shown that thomisids have larger clutch sizes and percent growth increases during molting than salticids. This suggests that thomisids would have a higher rate of metabolism. Conversely, the greater activity of salticids presumes a relative larger muscle mass which in turn might be associated with a higher rate of metabolism even at rest. Comparison of data on energetics from species in these two families might provide answers to these questions.

METHODS

Animals.—Species selection was based on availablity and ability to identify specimens. The three thomisid spiders obtained were *Misumenoides formosipes* (Walckenaer 1837), *Misumenops celer* (Hentz 1847) and *Xysticus funestus* (Keyserling 1880). The salticids studied were *Eris marginata* Peckham 1886, *Marpissa bina* Hentz 1846, *Metaphidippus galathea* (Walckenaer 1837), *Phidippus audax* (Hentz 1845), *P. clarus* Keyserling 1885, *P. pulcherrimus* Keyserling 1885, *Sarinda hentzi* Banks 1913, *Thiodina sylvana* (Hentz 1885)

and *Zygoballus rufipes* (Peckham & Peckham 1885).

All spiders were collected from locations around Gainesville, Florida. They were kept individually in plastic containers under ambient photoperids at room temperatures ranging from 22–24 °C. Specimens were fed weekly on a variety of prey as recommended by Greenstone (1979) and Uetz et al., (1992). These included adult fruit-flies and different life stages of crickets and mealworms. Some spiders were deposited as voucher specimens in the collections of the Division of Plant Industry of the Florida Department of Agriculture and Consumer Services at Gainesville when the study ended. The remainder were released at sites where collected.

Rates of metabolism.—Rates of metabolism were measured at 20 °C and 100% relative humidity to make comparisons with published data. Although 20 °C may seem unrealistic for this area, it is the average yearly temperature in northern Florida (Bradley 1972). This temperature is approached during evening hours even in summer. The rates of metabolism of both salticids and thomisids were measured overnight when these animals are normally inactive and about one week after their last meal (Anderson 1970).

Rates of oxygen consumption ($\dot{V}O_2$) were used as measures of metabolic rate. Disposable syringes of 30 or 60 cm^3 capacity, depending upon animal size, were used as 'closed system' metabolic chambers (Vleck 1987). The syringes were fitted with three-way valves which allowed sealing their contents from the atmosphere during measurement and gas sampling to determine O_2 composition. A small piece of moistened filter paper was added to each syringe to hold relative humidity at 100% during incubation. Spiders were weighed and placed individually within syringes. The syringes were ventilated with room air prior to adding spiders. The syringes were closed to the atmosphere and placed in a darkened incubator kept at 20 °C. Three empty syringes served as controls for each set of measurements. The length of incubation was controlled such that the O_2 did not decrease more than 0.5% to preclude the effects of abnormal gas concentrations on respiration. Previous tests indicated the syringes do not leak (Anderson et al. 1989) under the conditions and times used here. The O_2 frac-

Table 1.—Relationship between oxygen consumption and live body mass at 20 °C. Dimensions for $\dot{V}O_2$ and M are μLO_2/hr and mg, respectively. The regressions are based on log transformed data and are all significant at $P = 0.004$ or less.

Family Species	n	Range in body mass (mg)	$\dot{V}O_2 = aM^b$ a	$\dot{V}O_2 = aM^b$ b	Reduced major axis slope	r^2	SEE
Thomisidae							
Misumenoides formosipes	42	11–154	0.62	0.70	0.90	0.60	0.132
Misumenops celer	63	4.0–76	0.52	0.71	0.98	0.53	0.138
Xysticus funestus	61	4.8–55	0.29	0.88	0.98	0.82	0.113
Salticidae							
Eris marginata	36	3.9–43	0.44	0.78	1.10	0.48	0.199
Metaphidippus galathea	24	2.6–14	0.63	0.48	0.84	0.29	0.129
Phidippus audax	41	3.9–338	0.50	0.81	0.83	0.93	0.121
Phidippus pulcherrimus	131	12–196	0.34	0.85	0.99	0.73	0.116
Thiodina sylvana	15	24–110	0.30	0.91	1.06	0.71	0.127

tion of a minimal 20 cm³ sample from a syringe was determined at the end of incubation using an Ametek S-3A O_2 Analyzer (see Anderson et al. 1989 for details). Rates of metabolism (in μL O_2/hr) were calculated using the equation modified from Vleck (1987):

$$\dot{V}O_2 = \frac{V(F_{IO2} - F_{EO2})}{(1 - F_{EO2}) \cdot t}$$

Here V is the initial volume of dry, CO_2-free air in the syringe at STP; F_{IO2} and F_{EO2} are O_2 fractions within the syringe at the beginning and end of incubation, respectively; and t is the length of incubation in hours.
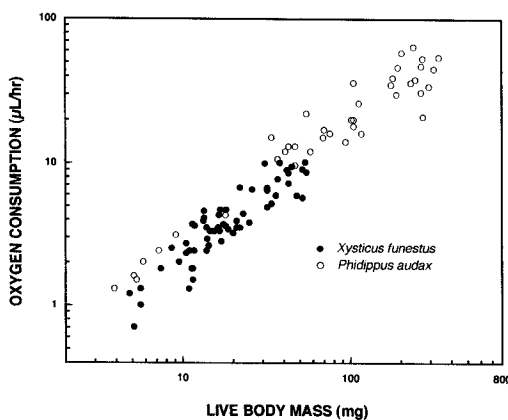
Analysis and comparison of rates of me-

Figure 1.—Relationship between oxygen consumption and live body size in *Xysticus funestus* and *Phidippus audax*.

tabolism.—Where possible, i.e., species with large range in body size, I analyzed the data to describe the relationship between metabolism and body size to provide a reference for making comparisons between spiders of different mass (Packard & Boardman 1987; Anderson 1994). I did evaluate whether the untransformed data provided a better fit than log transformed data. The latter provided a better fit in six of the eight species. Since the fit was only nominally better using the untransformed data I used log transformed data to calculate a and b in the allometric equation

$$\dot{V}O_2 = aM^b$$

Here a is a coefficient of proportionality (it provides an estimate of the rate of metabolism for a spider of one unit mass), b is the scaling exponent, and M is body mass. Given the conceptual and statistical problems associated with allometric relationships, I followed the suggestions of Smith (1984) and LaBarbera (1986) and reported the range in body mass, standard errors of estimates (SEE), coefficients of determination (r^2), and reduced major axes slope (RMA) for each regression. I used a P value of ≤ 0.05 as the signficance level for statistical decisions.

RESULTS

The parameters describing the relationship between rates of metabolism $\dot{V}O_2$ and body size are reported in Table 1 for those species whose data sets were appropriate for regres-

Table 2.—Oxygen consumption of some adult salticid spiders at 20 °C. Reported values are means ± SD.

Species	n	Live body mass (mg)	$\dot{V}O_2$ (μL O_2/hr)
Marpissa bina	3	168 ± 51	26 ± 2.6
Phidippus clarus	7	260 ± 74	46 ± 22
Sarinda hentzi	2	4.6 ± 1.8	2.0 ± 0.8
Zygoballus rufipes	2	3.0 ± 0.3	0.6 ± 0.1

sion analysis. The variation in proportionality coefficient (a) is inversely correlated to scaling exponent (b) illustrating the mathematical interdependence of these variables (Gould 1966; Anderson 1994). Figure 1 depicts the relationship between $\dot{V}O_2$ and body size during ontogeny in a thomisid, *Xysticus funestus*, and a salticid, *Phidippus audax*. The representation is typical of this relationship within a spider species in showing that much variation exists at any one body size (see also Anderson 1994) even though the figure represents logarithmically transformed data. Rates of metabolism for adult salticids whose weight ranges and sample size precluded regression analysis are reported in Table 2.

DISCUSSION

I compared rates of metabolism of thomisids (Table 3) and salticids (Table 4) with an empirical standard (Hemmingsen 1960) to assess the validity of my prediction that these spiders should have rates of energy expenditure of about 50% expected for their size. These comparisons are made on the basis of adult-sized females of each species. Selection pressures associated with energetic constraints are different for the two sexes. Males are relatively short-lived and the energy used in gamete production is small. The high energy demands associated with courtship behavior of males is important, but only in a proximal sense. Females must obtain energy at rates necessary to maintain their larger body size over a longer life span as well as for the higher energetic cost of gamete production. I used proportionality coefficients (a) and scaling exponents (b) to estimate $\dot{V}O_2$ for the largest individual for each species listed in Table 1 or the average $\dot{V}O_2$ of the adult spiders listed in Table 2 as the basis for comparison. The comparison also includes data from published studies normalized to 20 °C using a Q_{10} of 2.0. The comparisons agree with predictions. The observed rates of metabolism of the crab-spiders averaged 53% (SD ±8) of expected for their size while those of the jumping spiders averaged 67% (SD ±18) of expected. This agreement supports the view that energy metabolism is related to a species' natural history. There are at least two other families, the Clubionidae and Gnaphosidae, whose members share certain characteristics with thomisids and salticids. The similarity in length of life-cycle, relative rates of reproduction, and method of prey capture suggest their rates of metabolism would be similar. Published values (Greenstone & Bennett 1980) for specimens in these families are *ca.* 30–40% but are based on only two specimens. More work is necessary to validate this prediction.

Table 3.—Comparative rates of metabolism of adult crab spiders. Expected values were calculated using Hemmingsen's (1960) equation: $\dot{V}O_2 = 0.82\ M^{0.75}$. Data for '*Misumenops species*' are from Greenstone & Bennett (1980).

Species	Adult live mass (mg)	Observed $\dot{V}O_2$ (μL O_2/hr)	Expected $\dot{V}O_2$ (μL O_2/hr)	OBS / EXP
Misumenoides formosipes	154	21	36	0.58
Misumenops celer	76	11	21	0.52
Misumenops species	34	5.0	12	0.42
Xysticus funestus	55	9.9	17	0.58

Table 4.—Comparative rates of metabolism of adult jumping spiders. Expected values were calculated using Hemmingsen's (1960) equation: $\dot{V}O_2 = 0.82\ M^{0.75}$. Data for *M. bivittatus, M. vitis,* and *P. johnsoni* are from Greenstone & Bennett (1980). Those for *P. otiosus* and *P. regius* are from Anderson (1970).

Species	Adult live mass (mg)	Observed $\dot{V}O_2$ (μL O_2/hr)	Expected $\dot{V}O_2$ (μL O_2/hr)	OBS / EXP
Eris marginata	43	8.3	14	0.59
Marpissa bina	168	26	38	0.68
Menemerus bivittatus	28	8.8	10	0.88
Metaphidippus galathea	14	2.2	5.9	0.37
Metaphidippus vitis	5.7	2.3	3.0	0.77
Phidippus audax	338	56	65	0.86
Phidippus clarus	260	46	53	0.87
Phidippus johnsoni	173	20	39	0.51
Phidippus otiosus	337	48	65	0.74
Phidippus pulcherrimus	196	30	43	0.70
Phidippus regius	568	54	95	0.57
Sarinda hentzi	4.6	2.0	2.6	0.77
Thiodina sylvana	110	22	28	0.79
Zygoballus rufipes	3.0	0.6	1.9	0.32

Comparisons between thomisids and salticids are equivocal. Although rates of metabolism of the salticid species appear higher than those of thomisids of comparable size (Fig. 2), the difference is not significant. I used analysis of covariance (Packard & Boardman 1987) to compare rates of metabolism of adults (Tables 3, 4) using both species ($P \sim 0.21$) and genus ($P \sim 0.27$) as independent statistical units. I am aware of the argument that lower taxonomic units are probably not statistically independent as the trait
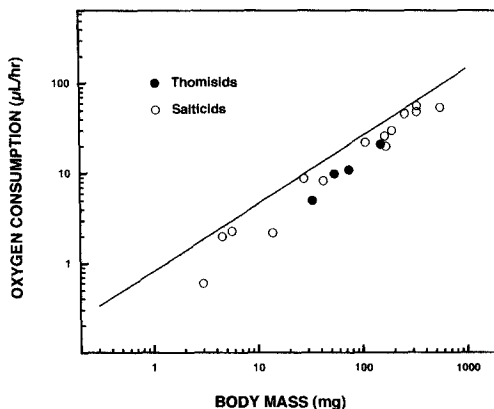

Figure 2.—Relationship between oxygen consumption and live body size in adult salticid and thomisid species. Solid line represents Hemmingsen's (1960) equation for this relationship in ectothermic poikilotherms.

in question has not evolved independently (Harvey & Pagel 1991). The small number of species, especially thomisids, precluded meaningful application of the method (program supplied and described by Purvis 1991) of 'Independent Contrasts' to partition out the effect of phylogeny. The question therefore is not resolved. Nonetheless the question has been posed and its answer awaits futher data. The possibility exists that these low rates of metabolism are plesiomorphic in spiders (Coddington & Levi 1991) and probably in other predatory arachnid groups. The depression of rates of metabolism in 'sit-and-wait' predators reaches its ultimate in ticks. Lighton & Fielden (1995) reported rates only 12% of expected in these animals when compared to other arthropods including spiders.

The many reported differences between members of these two morphologically distinct families have a smaller energetic impact than does the association with the low rates of metabolism associated with the sit-and-wait foraging pattern common to both families. This association between foraging pattern and energetics has also been found in other ectothermic predators such as snakes (Cruz-Neto & Abe 1994) thus supporting this notion.

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