FORAGING STRATEGY AND METABOLIC RATE IN SPIDERS[1]

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Predators are by definition at least two trophic levels removed from primary production. Because of low efficiencies of secondary productivity (Slobodkin 1961) and fluctuations in prey availability, they may be expected to experience food shortages of varying duration and intensity. Many predators have the ability to gorge and to store surplus energy as lipid or glycogen when prey are plentiful and to lower respiratory rates temporarily when prey are scarce. These traits have been interpreted as adaptations to unpredictable food availability (Bustard 1967, Martof 1969, Greenstone 1978).

One exclusively predaceous group, the spiders, demonstrates a more unusual energetic adaptation, exhibiting resting metabolic rates about half those measured for other poikilothermic animals of equal mass (Anderson 1970). This already low metabolic level makes even more remarkable the suggestion of Carrel and Heathcote (1976) that spiders of two families, Loxoscelidae and Scytotidae, have substantially lower mass-specific resting metabolic rates than do other members of the order Araneae. Members of these two families are sit-and-wait predators, the scytotids snaring passing insects by squirting them with a gluey secretion, and the loxoscelids employing irregular sticky webs. Their lower metabolic rate was supposedly related to their foraging styles as "primitive hunters and weavers," reflecting a low-energy foraging strategy. However, Carrel and Heathcote (1976) did not directly measure metabolic rates of these animals. Rather, they based their inference on the relationship between heart rates, which they mea-

TABLE 1. Masses and resting metabolic rates of spiders studied. Metabolic rates determined at 22°C and corrected to STPD) conditions.

Family	Species	Mass (mg)	$\dot{V}O_2$ ($\mu LO_2/h$)
Theraphosidae (Tarantulas)	*Aphonopelma eutylenum*	15 030	270.5
	Aphonopelma eutylenum	8 680	642.5
Loxoscelidae (Brown spiders)	*Loxosceles laeta*	97.2	10.6
	Loxosceles laeta	96.1	15.2
	Loxosceles laeta	111.2	20.4
	Loxosceles laeta	76.2	7.3
	Loxosceles laeta	197.9	27.5
	Loxosceles laeta	291.7	26.0
	Loxosceles laeta	327.9	48.1
	Loxosceles laeta	165.5	23.7
	Loxosceles laeta	183.9	33.5
	Loxosceles deserta	79.0	9.1
	Loxosceles deserta	63.2	5.9
Plectreuridae (Plectreurids)	*Plectreurys tristis*	340.4	20.9
	Plectreurys tristis	81.0	8.7
	Plectreurys sp.	64.7	4.9
Theridiidae (Cobweb weavers)	*Steatoda medialis*	24.3	12.4
	Latrodectus mactans	350.5	104.7
	Latrodectus mactans	48.2	57.7
	Latrodectus mactans	169.0	87.9
Linyphiidae (Sheetweb weavers)	*Frontinella pyramitela*	4.6	1.8
	Frontinella pyramitela	4.8	3.3
	Frontinella pyramitela	7.6	6.4
Araneidae (Orb weavers)	*Cyclosa conica*	10.5	5.8
	Cyclosa conica	10.8	5.5
	Neoscona oaxacensis	140.6	23.4
	Neoscona oaxacensis	193.1	31.6
	Argiope aurantia	258.0	59.3
	Argiope aurantia	858.0	153.1
	Argiope aurantia	853.0	175.2
Agelenidae (Funnel web weavers)	*Agelenopsis aperta*	632.5	143.5
	Agelenopsis aperta	715.0	169.9
	Agelenopsis aperta	320.8	53.2
Lycosidae (Wolf spiders)	*Schizocosa pacifica*	512.1	84.4
Oxyopidae (Lynx spiders)	*Peucetia viridans*	161.6	13.1
	Peucetia viridans	133.2	38.3
	Peucetia longipalpis	257.4	40.6
Gnaphosidae (Gnaphosids)	*Zelotes rusticus*	52.5	6.3
Clubionidae (Sac spiders)	*Liocranoides* sp.	145.5	14.6
Thomisidae (Crab spiders)	*Misumenoides formosipes*	48.7	17.2
	Misumenops sp.	27.9	4.8
	Misumenops sp.	36.0	5.3
	Misumenops sp.	30.0	6.8
	Misumenops sp.	42.3	6.4
Salticidae (Jumping spiders)	*Metaphiddipus vitis*	5.7	2.6
	Menemerus bivittatus	27.9	10.1
	Phiddipus johnsoni	173.0	22.9

sured, and published respirometry data which did not include the two families of interest. Their primary observations are that resting heart rates in loxoscelids and scytotids are substantially lower than those of other spiders. No measurements of metabolic rate have been reported previously for these groups. The object of this project was to test their hypothesis directly by measuring resting metabolic rates in lox-oscelids and comparing them with those of other spiders.

Materials and Methods

Forty-seven animals, comprising 21 species in 13 families, were collected in central and southern California during the spring and summer of 1978 (Table 1). They ranged in mass from 4.6 mg to 15 g and ran
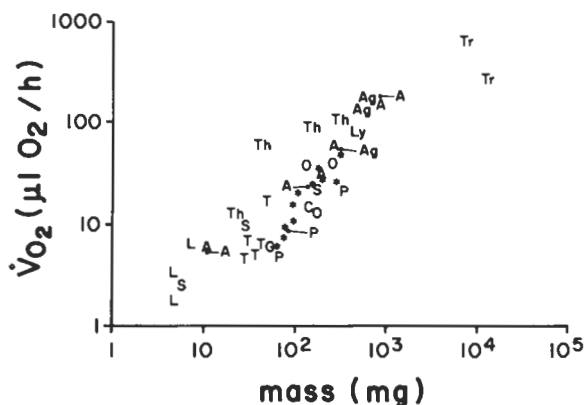
FIG. 1. Oxygen consumption (V_{O_2}) as a function of body mass in spiders at 22°C (47 individuals, 20 species, 13 families). Familial designations: A = Araneidae, Ag = Agelenidae, C = Clubionidae, G = Gnaphosidae, L = Linyphiidae, Ly = Lycosidae, O = Oxyopidae, P = Plectreuridae, S = Salticidae, T = Thomisidae, Th = Theridiidae, Tr = Theraphosidae, * = Loxoscelidae.

the gamut in foraging style from web spinners (Agelenidae, Araneidae, Linyphiidae, Loxoscelidae, Theridiidae) to active pursuers (Lycosidae, Oxyopidae, Salticidae), with intermediate styles represented by the remaining families. We were unable to find any scytotids in our area and assume that the loxoscelids are representative of the superfamily Scytodoidea, to which both families belong. In accordance with established procedure (Anderson 1970; Carrel and Heathcote 1976), we used only females in our analyses. Of the 36 nonloxoscelid individuals, 33 were adult females and 3 were penultimate females; the 11 loxoscelids represented two species and comprised 6 adult and 5 penultimate females.

The protocols for maintenance and metabolic rate determinations were similar to those of Anderson (1970) and Carrel and Heathcote (1976). Animals were maintained individually in containers for 3 wk in July and August at 20°C (±1°) on a 16 h light–8 h dark photoperiod. For the first 2 wk, the spiders were fed appropriate prey in sufficient quantity to maintain constant body mass. They were then fasted for 1 wk before experimentation. Water was available to all animals except the loxoscelids and theridiids, since these are known to be xeric-adapted and the loxoscelids, at least, will languish under prolonged conditions of high humidity (M. H. Greenstone, *personal observation*). The spiders remained healthy, many producing egg cases during the acclimation period.

Rates of oxygen consumption were determined manometrically at 22 ± 1° in Warburg-type flasks of a Gilson microrespirometer and water bath, except

for *Argiope* and *Aphonopelma*. The manometric flasks contained water to establish saturated humidity conditions and 5% KOH to absorb carbon dioxide. All animals known to be diurnally active (salticids, oxyopids, thomisids, and agelenids) were measured at 2200–2400 local time since Anderson (1970) has shown that diurnal spiders achieve their lowest resting metabolic rates at night; all others were measured during the day (1100–1500 local time). Animals were equilibrated in their flasks for 1 h and oxygen consumption was measured continuously for 2 h; the lowest observed 30-min interval was utilized as resting oxygen consumption. All reported gas volumes are corrected to standard temperature and pressure dry (STPD) conditions. Oxygen consumption in *Argiope* was determined from the decrement in oxygen content measured with an Applied Electrochemistry oxygen analyzer in a closed metabolic chamber fashioned from a glass syringe. Oxygen consumption of *Aphonopelma* was determined with the oxygen analyzer with open flow oxygen analysis as described by Depocas and Hart (1957).

Results

Rates of resting energy utilization measured as oxygen consumption are given in Table 1 and Fig. 1. Before comparing the loxoscelid mass-metabolism regression with that for all other spiders, the two data sets were tested for homogeneity of variances (Sokal and Rohlf 1969). The variances are significantly different ($F_{34,9} = 5.65$, $P < .01$). It is obvious from inspection of Fig. 1 that the larger variance of the nonloxoscelid set is due to the inclusion of data from 12 families, as opposed to just one for the loxoscelids. The data were therefore broken down into families and a comparison made of the regressions for all families represented by at least three data points (this eliminated only the Theraphosidae, Lycosidae, Gnaphosidae and Clubionidae). Among the nine regressions there are no significant differences in slope ($F_{8,24} = 1.065$, $P > .5$) but highly significant differences in elevation ($F_{8,32} = 49.68$, $P \ll .001$). In order to test Carrel and Heathcote's (1976) hypothesis that loxoscelids have lower resting metabolic rates than other spiders, we compared the elevation of the loxoscelid regression with that of each of the other families by Scheffé's (1959) method of simultaneous confidence intervals. Since the hypothesis of equality of elevations was soundly rejected with $P \ll .001$, the smallest confidence interval employed for the detection of differences should be .99. Using this interval only the theridiids differ in elevation from the loxoscelids, and even at the .90 level no new differences are detected.

If all of the data collected in the study are com-

bined, a general expression for the mass dependence of resting metabolic rates in spiders can be obtained: log microlitres O_2 per hour = $- 0.133 +$ 0.710 (log mass in milligrams) ($n = 47$, $r^2 = .91$, $P <$ .001). This regression is substantially below that calculated for other poikilothermic animals: the metabolic rate of a 100-mg spider is only 74% of predicted values for other poikilothermic organisms (Hemmingsen 1960). This result agrees with that of Anderson (1970), who first pointed out the low energetic demands of this group. It is interesting that the highest resting metabolic rate measured by Anderson also belonged to a theridiid, *Achaearanea tepidariorum*, although two other theridiid species did not appear to have excessively high resting metabolic rates (Anderson 1970: Fig. 4).

Discussion

Our data do not support the contention that loxoscelid spiders have unusually low metabolic rates. We are unable to discriminate the resting rate of energy utilization of these animals from those of other spiders of comparable mass which we measured, except for the theridiids. Metabolic rates certainly are not one-fifth those of other spiders, as the differential in their heart rates would otherwise suggest (Carrel and Heathcote 1976). Our results underscore the dangers of making inferences about metabolic rates from measurements of rates of other processes. Heart rate in particular is known to be an unreliable predictor of metabolic rate in other groups (Johnson and Gessaman 1973).

We consequently find no support for the assertion that "primitive hunting and weaving" spiders have a low metabolic rate linked to a low-energy foraging strategy. Carrel and Heathcote's (1976) suggestion that *Loxosceles* possess such a foraging strategy was apparently based on the misconception that they are much less active than other spiders. On the contrary, experienced collectors would agree with Gertsch's (1958) authoritative description of *Loxosceles* as "quite active" animals. The misconception is probably due to their well-known ability to survive much longer periods of starvation than do other spiders. Rather than low resting metabolic rates, this probably indicates an extreme development of the ability, already known from some other spiders, to depress metabolic rates below resting rates during prolonged periods of starvation (Itô 1964, Nakamura 1972, Anderson 1974). The lack of a connection between foraging strategy and resting metabolic rate is underscored by the one significant difference which was found, that between the loxoscelids and the theridiids. Members of these two families are very similar in habit and habitat. Like the loxoscelids, the theridiids are sedentary, web-building, sit-and-wait pred-

ators, and the species studied here are all characteristic of desert habitats.

Our results confirm Anderson's (1970) conclusion that spiders as a group have lower resting metabolic rates than the majority of other poikilothermic animals. Other aspects of their metabolic efficiency include very low resting metabolic rates for embryonic spiders (Anderson 1978), and the ability to depress metabolic rates below resting levels during transient periods of starvation (Itô 1964, Miyashita 1969, Nakamura 1972, Anderson 1974, Humphreys 1977). This metabolic versatility is part of a suite of physiological, anatomical, and behavioral adaptations which have the net effect of making energy less limiting for spiders than for other animals of their size and trophic position (Greenstone 1978). This may have profound implications for the role of spiders in terrestrial communities. It may account for a general lack of numerical responses to insect prey availability, at least in temperate zone spiders (Greenstone 1978). Freedom from energetic constraints also may permit feeding behavior that optimizes acquisition of nutrients, rather than one that merely maximizes energy intake (Greenstone 1979). The ability to tolerate low food availability may also buffer spiders against environmental fluctuations and make it unnecessary for them to emigrate from momentarily unproductive habitats (M. H. Greenstone, *personal observation*). Spiders therefore may be a more consistent part of the environment for other populations with which they interact, principally as insectivores and as prey of arthropodivorous vertebrates. Consistency of residence, coupled with phenomenal densities (Dondale 1970), would make spiders the most important group of insectivores in some terrestrial habitats.

Studies of other groups suggest that reduced metabolic rates are not necessarily an adaptation to reduced mean food availability as a consequence of a predatory existence. Rather, they may be found sporadically throughout the animal kingdom in animals with an unpredictable food supply (McNab 1969, 1973, 1974). In the case of spiders this may have contributed to their ubiquity in terrestrial habitats, making it possible for them to exist in environments which are closed to some other groups of insectivores (Swan 1961). We do not, however, find any interfamilial differences among spiders in resting rates of energy utilization which are reflective of different modes of prey capture or foraging strategy.

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