FORAGING STRATEGY AND METABOLIC RATE IN SPIDERS

Matthew H. Greenstone and Albert F. Bennett

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 inferences on the relationship between heart rates, which they mis-
Table 1. Masses and resting metabolic rates of spiders studied. Metabolic rates determined at 22°C and corrected to STPD conditions.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Mass (mg)</th>
<th>$V_O_2$ (μL O₂/hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plectreuridae (Plectreurids)</td>
<td>Plectreurys tristis</td>
<td>340.4</td>
<td>20.9</td>
</tr>
<tr>
<td></td>
<td>Plectreurys tran</td>
<td>81.0</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>Plectreurys sp.</td>
<td>64.7</td>
<td>4.6</td>
</tr>
<tr>
<td>Theridiidae (Cobweb weavers)</td>
<td>Slatoda madalisk</td>
<td>243.3</td>
<td>12.4</td>
</tr>
<tr>
<td></td>
<td>Linyphiidae (Sheetweb weavers)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Frontinella piramidella</td>
<td>4.6</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Frontinella pyramidalis</td>
<td>4.8</td>
<td>3.3</td>
</tr>
<tr>
<td></td>
<td>Frontinella sp.</td>
<td>7.6</td>
<td>6.4</td>
</tr>
<tr>
<td>Araneidae (Orb weavers)</td>
<td>Cyclosa cincta</td>
<td>105.5</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>Cyclosa cincta</td>
<td>105.5</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>Neoscona oaxacensis</td>
<td>140.5</td>
<td>23.4</td>
</tr>
<tr>
<td></td>
<td>Agelena aurantia</td>
<td>258.0</td>
<td>59.3</td>
</tr>
<tr>
<td></td>
<td>Argiope aurantia</td>
<td>858.0</td>
<td>153.1</td>
</tr>
<tr>
<td></td>
<td>Argiope aurantia</td>
<td>858.0</td>
<td>153.1</td>
</tr>
<tr>
<td>Agelenidae (Funnel web weavers)</td>
<td>Agelenopsis aperta</td>
<td>632.5</td>
<td>123.5</td>
</tr>
<tr>
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<td>Agelenopsis aperta</td>
<td>715.0</td>
<td>169.3</td>
</tr>
<tr>
<td></td>
<td>Agelenopsis aperta</td>
<td>320.8</td>
<td>63.2</td>
</tr>
<tr>
<td>Lycosidae (Wolf spiders)</td>
<td>Schizocosa pacifica</td>
<td>512.1</td>
<td>84.4</td>
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<tr>
<td>Oxyopidae (Lynx spiders)</td>
<td>Pecodiapis viridans</td>
<td>161.6</td>
<td>13.1</td>
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<td>Pecodiapis viridans</td>
<td>133.2</td>
<td>38.3</td>
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<td>Pecodiapis thomasei</td>
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<td>Graphosidae (Graphosoridae)</td>
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<td>Clubionidae (Sac spiders)</td>
<td>Liochranea sp.</td>
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<td>14.6</td>
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<td>Thomisidae (Claw spiders)</td>
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<td>Misumenoides sp.</td>
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<td>4.8</td>
</tr>
<tr>
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<td>Misumenoides sp.</td>
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<td>5.3</td>
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<td></td>
<td>Misumenoides sp.</td>
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<td>6.6</td>
</tr>
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<td>Salticidae (Jumping spiders)</td>
<td>Metatanta atrina</td>
<td>42.3</td>
<td>6.4</td>
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<td></td>
<td>Menemerus zubalensis</td>
<td>27.9</td>
<td>10.1</td>
</tr>
<tr>
<td></td>
<td>Phidippus johnsoni</td>
<td>173.0</td>
<td>22.9</td>
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</table>

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...

the gamut in foraging style from web spinners (Agelenidae, Araneidae, Linyphiidae, Loxoscelidae, Therididae) 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 superfamilly Scytodiformes, 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°C) 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°C 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_{24,24} = 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_{8,9} = 1.065, P > .5) but highly significant differences in elevation (F_{8,9} = 49.68, P << .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 found to be rejected with P << .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 depen-
dence of resting metabolic rates in spiders can be
obtained: log microlitres O_2 per hour = -0.133 +
2.710 (log mass in milligrams) (n = 47, r^2 = 0.91, P <
0.001). This regression is substantially below that cal-
culated for other poikilothermic animals: the meta-
abolic rate of a 100-mg spider is only 74% of predicted
values for other poikilothermic organisms (Hemming-
sen 1960). This result is not only that of Anderson
(1970), who first pointed out the low energetic de-
mands 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 (An-
derson 1970: Fig. 4).

Discussion
Our data do not support the contention that loxos-
celid 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 Gassa-
man 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 less active than other spiders. On the con-
trary, experienced collectors would agree with
Gerbach’s (1958) authoritative description of Loxos-
celis as “quite active” animals. The misconception
is probably due to their well-known ability to survive
much longer periods of starvation than do other spi-
ders. Rather than low resting metabolic rates, this
probability 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, Miyashita 1969,
Nak-
amura 1972, Anderson 1974). The lack of a connection be-
 tween foraging strategy and resting metabolic rate is
underscored by the one significant difference which
was found, that between the loxoscelids and the theri-
diids. Members of these two families are very similar
in habit and habitat. Like the loxoscelids, the theri-
diids are sedentary, web-building, sit-and-wait pred-
ators, and the species studied here are all charac-
teristic 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 ani-
mals. Other aspects of their metabolic efficiency in-
clude very low resting metabolic rates for embryonic
spiders (Anderson 1978), and the ability to depress
metabolic rates below resting rates during transient
periods of starvation (Itô 1964, Miyashita 1969, Nak-
amura 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 spi-
ders than for other animals of their size and trophic
position (Greenstone 1978). This may have profound
implications for the role of spiders in terrestrial com-
munities. It may account for a general lack of num-
erical 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 environ-
mental 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 envi-
ronment for other populations with which they inter-
act, principally as invertebrates and as prey of arthro-
podivorous vertebrates. Consistency of residence,
coupled with, with phenotypic densities (Dondale 1970),
would make spiders the most important group of in-
sects in some desert habitats.

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

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Ecology, Vol. 61, No. 5

— 1974. Responses to starvation in the spider Ly- 


Greenstone, M. H. 1974. The numerical response to prey availability of Pardosa ramulosa (McCook) (Araneae: Ly-


Hemmingsen, A. M. 1960. Effects of locomotory activity, temper-

ature, and hunger on the respiratory rate of Lycosa T- 
signata Boes. et Str. (Araneae: Lycosidae). Applied Ento-


Insulin Laboratorium, C. Hamburgers Bogtrykkeri, Copen-

hagen, Denmark.


gical energetics of arthropods. Utah State University Press, Logan, Utah, USA.

McHab, B. K. 1969. The thermoregistics of temperature regu-


— 1973. The rate of metabolic of the spiny rat. Proc-

edings symposium on flight on the ecological factors that influence the basal rate of metabolism in ro-


Swan, L. W. 1961. The ecology of the high Himalaya. Scien-

tific American 205:68–78.

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