# DECREASE IN RESPIRATORY RATE IN A WOLF SPIDER, PARDOSA ASTRIGERA (L. KOCH), UNDER STARVATION<sup>1</sup>

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### **INTRODUCTION**

Spiders, an important group of predators of arthropods in various environments, are often faced with starvation in nature (MIYASHITA, 1968a, b; ANDERSON, 1974; WISE, 1975). Hence their means of surviving under starvation is an important subject in studies of population dynamics and the evolution of spiders.

SAVORY (1928, cited in ANDERSON, 1974) was among the first to indicate that spiders could survive for a long time under starved conditions. ANDERSON (1974) reported that two spiders, *Lycosa lenta* HENTZ and *Filistata hibernalis* (HENTZ), could survive without food for surprisingly long periods, that is, 100-278 (208 on an average) days and 154-423 (276) days, respectively. Working on the development of spiders at different levels of food supply, TURNBULL (1962, 1965) and MIYASHITA (1968b) showed that spiders could survive and mature even under poor food conditions, but the duration of the instars was prolonged and they became smaller adults as compared with those reared under better conditions.

Further, IT6 (1964), working on a wolf spider, *Lycosa pseudoannulata* (BoEs. et *STR.),* found that the respiratory rate of adults notably decreased under starvation but when fed ample food for several days, it almost returned to the level prior to starvation. He suggested that this property should be adaptive for their predatory life. Since then similar results have been obtained in other spider species, e.g. *Pardosa astrigera (L.* KOCH) (MIYASHITA, 1969 b), *Lycosa lenta* HENTZ and *Filistata hibernalis* (HENTZ) (ANDERSON, 1974).

In the present paper, we report on the effects of starvation on the respiratory rate and survival period of a wolf spider, *Pardosa astrigera (L.* KOCH), and offer a contribution to the discussion on special feeding strategies in poikilotherm predators.

## MATERIALS AND METHODS

### Spiders

*Pardosa astrigera* (L. KOCH) is a common wandering spider living in grasslands in Japan (YAGINUMA, 1960). It overwinters in the immature stage and probably has two generations in a year because there are two separate peaks of adult numbers in

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spring and summer (MIYASHITA, 1969a). In the present paper, for convenience, adults emerging in spring and summer are called 'spring generation' and 'summer generation', respectively.

Nymphs were collected from the experimental fields of Nagoya University in 1979- 1980. They were reared to the final moult in the laboratory supplied with adults of *Drosophila melanogaster* MEIGEN, nymphs and adults of the planthoppers, *Laodelphax striatellus* FALLEN and *Niraparvala lugens* STAL. Only adult spiders were used for the experiments.

### Rearing

When spiders became adult, they were reared individually in test tubes  $(1.8 \text{ cm})$ in diameter, 18cm in length) with air-pervious silicone-plugs at the open ends and long strips of paper providing footholds for spiders under  $25^{\circ}$ C and  $16:8$  hr light:dark photoperiod. The adults were fed on adult leafhoppers, *Nephotettix cincticeps* UHLER, raised in the laboratory. Moist cotton was also supplied so that the spider could drink water.

Spiders were divided into four groups; 'well-fed', 'starved' and two 'limited food' groups. In the well-fed group, spiders were supplied with ample food, five to ten leafhoppers, every day or every second day. In the starved group, spiders were supplied initially with ample food like the well-fed group for ten to twenty days from the final moult and thereafter deprived of food but not water. In the limited food groups, each spider was supplied with one leafhopper every second day ('l/2-fed') or every third day ('l/3-fed'). Generations of spiders used for each group were as follows:

well-fed; spring and summer generations in 1979,

starved; summer generation in 1979,

1/2-fed; spring generation in 1980,

1/3-fed; spring generation in 1980.

Determination of respiratory rate

The respiratory rate was determined by measuring  $CO<sub>2</sub>$  expiration using a titration technique (IT6, 1964). The respiratory chamber was a plastic cylinder, 2.5cm in diameter and 15cm in length. After introduction of the spider the chamber was connected to a  $CO<sub>2</sub>$ -absorbent inlet tube containing soda lime. When the residual air in the chamber had been completely substituted by  $CO<sub>2</sub>$ -free air, the chamber was put into a room maintained at  $25^{\circ}$ C and  $16:8$  hr light:dark photoperiod for  $24$  hr. The chamber was then connected to an aparatus for  $CO<sub>2</sub>$  measurement and ventilated by  $CO<sub>2</sub>$ -free air for 20 min. The  $CO<sub>2</sub>$  expired by an experimental spider was absorbed by N/20 KOH solution (20 ml in volume) and excluded from the system of reaction through the following chemical reactions:

 $CO<sub>2</sub>+2KOH \rightarrow K<sub>2</sub>CO<sub>3</sub>+H<sub>2</sub>O$  $K_2CO_3 + BaCl_2 \rightarrow BaCO_3 + 2KCl.$ 

The remaining KOH was titrated by neutralization with N/50 HC1 solution. The amount of  $CO<sub>2</sub>$  was calculated from the difference between amounts of HCl solution required for neutralization for the experimental chamber and for an empty control chamber. The results are expressed as mg  $CO<sub>2</sub>$  expired/mg fresh body weight(f, w.)/hr.

Each spider was weighed before and after the measurement using the Chyo model  $C_3$ -100MD micro-balance (minimum accuracy; 0.01 mg), and the mean of two values was regarded as the fresh body weight at the time of measurement. No anesthetization was undertaken in any experiment.

#### RESULTS

#### Survival period

Starved spiders survived for a long time, 28.8 days (range 26-32 days) in males and 54. 4 days (range 35-74 days) in females, without any food (Table 1). Mean survival periods of starved spiders were 73.8% in males and 78.6% in females of the survival values of well-fed spiders. These values were calculated by the following equation:

Table 1. Mean lengths of survival periods and the standard deviations in days of *P. astrigera* under different food conditions.

		Well-fed	$1/2$ -fed	$1/3$ -fed	Starved
Spring generation	male			$64.0* \pm 21.6$ $93.8 \pm 22.2$ $61.6* \pm 32.2$	
		female $124.0* \pm 22.1$ 188.4 + 69.3 144.4* + 37.1			
Summer generation	male	$56.0 \pm 21.5$			$28.8* \pm 2.7* (45.8* \pm 7.8)^{b}$
	female	$81.0 \pm 29.0$			54, $4* \pm 18$ , $9^a(66, 2* \pm 19, 3)^b$

a Days from the commencement of starvation to death.

b Days from the final moult to death.

\* Significantly different between sexes at  $P<0.05$  by Mann-Whitney U-test.

N=5 for each group.

$$
\frac{Ls-P}{Lw-P}\times 100
$$

where  $\overline{L}$ s is mean longevity (i.e. the number of days from the final moult to death) of starved spiders,  $Lw$  is mean longevity of well-fed spiders and  $P$  is mean number of days in which the spiders of 'starved' group were supplied with ample food prior to starvation, that is, 17.0 days in males and 11.8 days in females. Therefore  $Ls-P$  means the survival period under no-food conditions, that is, 28.8 days in males and 54. 4 days in females.

Adult longevity of spiders was the shortest under starved conditions and the

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longest under 1/2-fed conditions, but the differences were not significant in either generation  $(P>0.05$ , Mann-Whitney U-test, CAMPBELL, 1974). There were significant differences between sexes in survival periods of well-fed and 1/3-fed spring generation and starved summer generation  $(P<0.05,$  Mann-Whitney U-test).

Respiratory rate in relation to body weight

The relationship of the respiratory rate of animals to body weight is often approximated by the following formula (EDWARDS, 1953):

 $R = aW^b$ 

or  $\log R = \log a + b \log W$ ,

where R, W, a and b are respiratory rate, body weight and two constants, respectively.

The relationship of respiratory rate per individual to fresh body weight in P.



Fig. 1. Relationship of respiratory rate per individual to fresh body weight in  $P$ . *astrigera* under well-fed conditions.  $\bullet$ : males of summer generation,  $\triangle$ : females of spring generation, Q: females of summer generation. The regression equation for summer generation (the broken line) is log  $R=-3.20+0.866$  log W with  $r^2=$ 0.753; that for the both generations (the solid line) is log  $R = -3.17+0.840$  log W with  $r^2 = 0.876$ .

*astrigera* was determined using the data on well-fed spiders (Fig. 1). In the well-fed group, five males and three females of the summer generation and two females of the spring generation were used for respiration measurements. As the points for the spring generation (Fig. 1, triangles) fell on the regression line calculated for the summer generation (Fig. 1, broken line), the regression was calculated from combined data on the two generations (Fig. 1, solid line) and was used thereafter. The index of determination was high ( $r^2=0.876$ ). Since the slope of the regression line, 0.840, approached unity, respiratory rate per unit body weight was assumed to be constant regardless of body weight. A regression of respiratory rate per unit fresh body weight to fresh body weight was calculated and expressed by the equation:

 $log R/W = -3.17 - 0.160 log W(r^2=0.204)$ .

The slope was not significantly different from zero  $(P>0.05)$ . In the present study, therefore, respiratory rate is expressed as  $CO<sub>2</sub>$  expiration in mg per unit fresh body weight per hr.

Changes in respiratory rates and body weights

Because there was no significant difference in the pattern of *respiratory* rate between the two generations, the mean respiratory rates and mean fresh body weights of well-fed spiders were calculated from data on all the individuals tested (i.e. results from spring and summer generations were pooled). Mean respiratory rates of well-fed males, although fluctuating, showed no tendency to increase or decrease with the aging of spiders except at the last stage of their life spans (after the 50th day), while that in well-fed females retained an almost constant level throughout the test period (Fig. 2). Mean respiratory rate in males was higher than that in females at every measurement time except on the 54th day; average for ten measurements were  $4.86 \times 10^{-4}$  mg CO<sub>2</sub>/mg f. w. /hr for males and 3.80 $\times 10^{-4}$ mg  $CO<sub>2</sub>/mg$  f. w. /hr for females.

Fresh body weight of spiders was represented as a percentage of the initial weight. Mean fresh body weight of well-fed spiders was maintained around a constant level except just after the final moult in females (Fig. 2).

In the starved group, measurements were, at first, conducted on every sixth day till the 30th day of starvation and thereafter on every tenth day (Fig. 3A, solid lines). Respiratory rates of males and females markedly decreased till the twelfth day of starvation but thereafter retained an almost constant level for each sex. Mean respiratory rates after the twelfth day were  $2.49\times10^{-4}$  mg  $CO<sub>2</sub>/mg$  f. w. /hr for males and  $2.76 \times 10^{-4}$  *mg*  $CO_2/mg$  *f.w./hr for females; these were 48.4% and 63.0% of the* initial values, respectively.

The measurements were then carried out on the zeroth, first, second, fourth, sixth and twelfth days of starvation  $(Fig. 3B)$ . It was shown by this procedure that the respiratory rates increased by 47% in males and 51% in females during the first two days of starvation but notably decreased from the third to the fourth day.



Fig. 2. Changes in mean respiratory rates and mean fresh body weights of *P. astrigera*  under well-fed conditions. Vertical lines represent the standard deviations of mean respiratory rates.  $\bullet$ : males,  $\bigcirc$ : females. N=5 for each sex.

Thereafter the rates gradually decreased.

Fresh body weights of starved spiders decreased almost linearly with time, **0.61%** in males and 0.79% in females per day of initial weights, throughout the starvation period.

One possible explanation of reduction in respiratory rate was that spiders were exhausted by starvation. In order to examine this possibility, spiders were supplied with ample food for five days after the starvation periods between six and thirty days. The respiratory rates and the body weights showed rapid recovery to the initial levels regardless of starvation time (Fig. 3A, broken lines), indicating that the reduction in respiratory rate was not due to spider exhaustion or senescence.

In the limited food (1/2-fed and 1/3-fed) groups, spiders consumed all the prey supplied except for several days just before death. When supplied with ample food,



Figs. 3A and B. Changes in mean respiratory rates and mean fresh body weights of P. *astrigera* under starvation *conditions. Broken* lines represent changes in those of spiders supplied with ample food for five days after the starvation periods. Symbols are the same as Fig. 2. N=5 for each point.

a spider of each sex consumed, on the average, 1.1 leafhoppers daily (TANAKA, unpublished). Accordingly consumption rates of  $1/2$ -fed and  $1/3$ -fed spiders were thought to be approximately a half and a third of that of well-fed spiders, respectively. Mean respiratory rates of 1/2-fed and 1/3-fed spiders, at an early stage of test period, *were much* the same as that of well-fed spiders and were associated with a small weight loss, but at a later stage the rates tended to decline and thereby weight losses were minimized (Fig. 4).

### Metabolic balance-sheet

In studing the energetics of living organisms, the calorie is especially useful for comparative purposes (PHILLIPSON, 1966). The  $CO<sub>2</sub>$  expiration rates in mol were divided by a given value of respiratory quotient  $(RQ)$  to convert it to the amount of  $O<sub>2</sub>$  absorbed, and then, the latter values were multiplied with the oxy-calorific coefficient (Oxykalorischer Koeffizient, IVLEV, 1934) to obtain calorific values. According to KLEIBER (1975), the RQ for the catabolism of carbohydrate and fat are 1.0 and 0. 71, respectively, and the RQ for protein is O. 83 assuming that all the nitrogen from catabolized protein is excreted as urea. In MACFADYEN's  $(1963)$  list the RQ is 0.82 for catabolism of dry plant matter and approximate human diet. According to HAGSTRUM (1970), who presented the only data on the RQ of spiders known to us, the mean RQ of a wolf spider, *Tarentula kochi* KEYSERLING, was 0.78.

IVLEV (1934) showed that the oxy-calorific coefficients (q) for carbohydrate, fat



Fig. 4. Changes in mean respiratory rates and mean fresh body weights of  $P$ . *astrigera* under 1/2-fed (A) and 1/3-fed conditions (B). Symbols are the same as Fig. 2. N=5 for each sex.

and protein were 3.529, 3.280 and 3.305 cal per  $1 \text{ mg } O_2$ , respectively. He suggested the use of a value of 3.38 cal per  $1 \text{ mg}$  O<sub>2</sub> for most animals. For the following calculations, we assume that the RQ is 0.82 and q is 3.38 cal/mg  $O_2$ . The mean respiratory rates of the well-fed adults of P. astrigera were  $4.86 \times 10^{-4}$  mg CO<sub>2</sub>/mg f. w. /hr for males and  $3.80 \times 10^{-4}$  mg  $\text{CO}_2/\text{mg}$  f. w. /hr for females (see p. 364). The metabolic rates per unit body weight per hr in calories were calculated to be 1.46 $\times$  $10^{-3}$  cal/mg f. w./hr for males and  $1.14 \times 10^{-3}$  cal/mg f. w./hr for females (Table 2). Metabolic rates of other spiders are also listed in Table 2.

Using the mean values of  $CO<sub>2</sub>$  expiration rates of starved *P. astrigera* during the period from the 12th to 24th day of starvation, when the respiratory rate of each sex was almost stabilized (see Fig. 3), the metabolic rates during starvation were estimated (column 2 of Table 3). Assuming that the body weight decreased linearly with time, mean values of energy consumed by a male and a female were calculated by multiplying the metabolic rate by the mean of the fresh body weights on the 12th day and the 24th day; the values being 4. 29 cal and 5.71 cal per individual, respectively, during the period mentioned above. Dry weight lost during the twelve days were 0.448mg for males and 0.790 mg for females. Thus we can assume that a starved spider may produce heat energy equivalent to 9. 58 cal in males and 7. 23 cal in females by catabolizing  $1 \text{ mg}$  dry body weight (the last column of Table 3). Energy equivalents per mg dry weight of prey animals for lycosid spiders were 5. 96 cal in the case of *Pardosalaura* KARSCH (NAKAMURA, 1972), 5.30-5.97 cal for *Shizocosa* sp. (MouLDER and REICHLE, 1972) and 5.68 cal for *Geolycosa godeffroyi*  (L. KOCH) (HUMPHREYS, 1977 a). It would appear that well-fed spiders catabolize substrates with 5 to 6 cal per mg dry weight on average. Values in Table 3 (9.58)

<b>Species</b>	Mean fresh weight (mg)	Temper- ature $(^{\circ}C)$	Metabolic rate $(10^{-3} \text{ cal/mg})$ f. w./hr	Author	
Lycosidae					
Pardosa astrigera (L. Kocn) (male)	20.07	25	1.46	present study	
Pardosa astrigera (L. Kocn) (female)	45.77	25	1.14	present study	
Pardosa astrigera (L. Kocn) (sub-adult)	ca.40	25	2.02	Мітаѕніта (1969 b)	
Pardosa lugubris (WALCKENAER)	ca. 100	20	1.25	EDGAR (1971)	
Pardosa laura KARSCH	ca.10	25	4.91	NAKAMURA (1972)	
Pardosa amentata (CLERCK)	55	15	0.581	FORD (1977 a)	
Lycosa pseudoannulata (Boes. et STR.)	ca. 100	29	1.44	Iτô $(1964)$	
Tarentula kochi KEYSERLING	ca. 100	25	$1.02 - 1.95$	HAGSTRUM (1970)	
Geolycosa godeffroyi (L. Koch)	ca. 1000	30	0.732a	HUMPHREYS (1977 b)	
Linyphiidae					
Lepthyphantes zimmermanni BERTKAU 4		15	1.15	FORD (1977 b)	
Argiopidae					
Araneus diadematus (CLERCK)	103	25	1.79	PEAKALL and WITT (1976)	
6 species (4 families)	25-970	20	$0.225 - 1.60$	ANDERSON (1970)	
21 species (13 families)	4.6-15030	22	$0.080 - 5.35$	GREENSTONE and <b>BENNETT</b> (1980)	

Table 2. Metabolic rates of spiders.

Metabolic rate of *G. godeffroyi* with 1000 mg fresh weight was calculated from the regression equation of oxygen consumption to the fresh weight.

Table 3. Energy and body weight loss of *P. astrigera* from the 12th to the 24th day of starvation.

	Respiratory rate (mg CO <sub>2</sub> / mg f.w./hr)	Metabolic rate (cal/mg f. w./hr	Fresh wt on the 12th day (mean $\pm$ SD) (mg)	Fresh wt loss $(\%)$	Mean fresh wt during $12-24th$ day(mg)	Energy loss (cal)	Drv wt loss <sup>a</sup> (mg)	Energy loss/ dry wt loss (cal/mg)
Male	$2.49 \times 10^{-4}$	$7.47 \times 10^{-4}$	$20.62 \pm 1.61$	6.48	19.95	4.29	0.448	9.58
Female	$2.76\times10^{-4}$	$8.28 \times 10^{-4}$	$25.05 \pm 4.07$	8.86	23.94	5.71	0.790	7.23

<sup>a</sup> Fresh body weight was converted into dry body weight using the following regression equation of dry weight  $(Y)$  to fresh weight $(X)$  in *P. astrigera* adults collected from the field of Nagoya University in September, 1979: log  $Y = -1.306 + 1.335$  log X  $(N=16, r^2=0.906)$ .

for males and 7. 23 for females) suggest that starved *P. astrigera* catabolize substrates with higher energy equivalents than well-fed spiders. According to MACFADYEN (1963), combustion of l mg dry matter produced the heat of 5.65 cal for carbohydrate, 9. 35 cal for fat, 4. 15 cal for plant protein and 3.90 cal for animal protein. Therefore it is suggested that the composition of substrates catabolized by *P. astrigera* under starvation is different from that under satiation; the proportion of

fat catabolism to the whole catabolism might be much larger under starvation conditions than normal (or satiation) conditions. In the calculation of the calorific values in Table 3, we conveniently used an RQ of 0.82 even for starved spiders. Since the increase in proportion of fat catabolism implies that the RQ approached 0.71 from 0.82, the figures in the second, the sixth and the last columns of Table 3 might be underestimated. However, such a bias in the RQ value does not deny but supports the possibility that the proportion of fat catabolism increased under starvation.

#### **DISCUSSION**

Males and females of a wolf spider, *Pardosa astrigera* (L. Koch), could survive for 28.8 $\pm$ 2.7 days and 54.4 $\pm$ 18.9 days, respectively, without any food. These values were  $73.8\%$  in males and  $78.6\%$  in females when compared with the survival periods of well-fed spiders, and we can conclude that *P. aslrigera* has a strong tolerance to starvation conditions. ANDERSON (1974) showed that some spiders could survive for a long time without food; mean survival periods of starved females of *Lycosa lenta*  HENTZ and *Filistata hibernalis* (HENTZ) were  $208 \pm 15$  days and  $276 \pm 28$  days, respectively; the former value being 68% of that of non-starved females. He also described that the survival periods of these two species were of the same order of magnitude as the starvation records cited by SAVORY (1928). KIKUYA (1980) reported that females of *Heptathela kimurai* (KlSrlIDA) survived for more than 72 days without food. These results suggest that spiders in general have a strong tolerance to starvation.

The strong tolerance to starvation in *P. astrigera* can be primarily attributed to the remarkable reduction in the respiratory rate under food shortage. It is suggested that reduction in respiratory rate is not due to spider exhaustion or senescence but to an intrinsic change in behaviour and/or metabolism. It was known that other spiders--adult females of *Lycosa pseudoannulata* (BoEs. et STR.) (IT6, 1964), subadults of *Pardosa astrigera* (L. KOCH) (MIYASHITA, 1969b) and adult females of *Lycosa lenta* HENTZ and *Filistata hibernalis* (HENTZ) (ANDERSON, 1974)--also reduced their respiratory rates under starvation. Thus it is possible that many spiders decrease the respiratory rate under starvation.

TANAKA and IT6 (1982) reported that a predaceous lady beetle, *Coccinella septempunctata bruckii* MULSANT, showed a similar changing pattern in respiratory rate under starvation. The respiratory rate increased on the first day of starvation but thereafter markedly decreased. Females of this beetle survived  $91.4 \pm 27.2$  days without food. On the other hand, a phytophagous lady beetle, *Henosepilachne vigintioctopunctata* FABRIClUS, did not decrease the respiratory rate under starvation and soon died  $(17.6 \pm 6.0$  days in males, and  $22.9 \pm 5.3$  days in females).

From such a changing pattern, a behavioural change of predators under starvation

may be predicted. When predators are starved, they will search for prey by active movement as reported in a web-building spider, *Achaearanea tepidariorum* (C.L. KOCH), (TURNBULL, 1964), larvae of an ant-lion, *Morter obsourus* RAMB., (GRIF-FITHS, 1980), and a mantis, *Paratenodera angustipennis* DE SAUSSURE (INOUE and MATSURA, 1975); in the latter species, *P. angustipennis,* the respiratory rate was the maximum on the fifth day of starvation, when its foraging activity became higher (MATSURA, 1981). But when predators have been starved for a long time, they change their behaviours from active searching to waiting. Thus decrease in respiratory rate of predators under starvation may be, in part, due to the decrease in activity. Such a strategy should be especially adaptive for sit-and-wait type predators as discussed by MATSURA (1981). Wandering spiders seem to be sit-and-wait type predators; according to FORD (1977a), a wolf spider, *Pardosa amenlata* (CLERCK), adopted a sit-and-wait strategy; its respiratory energy loss by active locomotion was only  $0.36$  to  $1.01\%$  of the total energy loss. Behavioural studies on foraging activity of spiders should be made under laboratory and field conditions.

It is suggested that spiders often encounter food shortage in nature. MIYASHITA (1968a) found that sub-adults of *P. astrigera* collected from the field showed as high a rate of feeding as those which had been reared in the laboratory at a low food level. Carapace widths of *P. astrigera* adults collected in the field were compared with those of adults which had been supplied with food during the immature stage at different intervals (every day, every second day and every fourth day) ; the former showed a similar distribution in carapace width as adults raised under every fourth day feeding (MIYASHITA, 1968b). ANDERSON (1974) evaluated the nutritional status of *Lycosa lenta* HENTZ and *Filistata hibernalis* (HENTZ) collected in fields by the ratio of abdominal width to carapace width. In both species, the ratios obtained for the field populations were equal to or less than those of the experimentally starved individuals. Wise (1975) conducted field experiments on supplementary food for a sheet-web weaver, *Linyphia marginata* C.L. KOCH. He showed that the addition of food to the webs improved the survival and fecundity of mature females but it did not improve the survival of immature spiders.

Prey usually have scattered distributions and their densities are not only low but also unpredictable. On the other hand, small herbivores generally live on their food-plant which often form large uniform aggregations. Even if the herbivores eat up one plant or one clump of plants, they can easily move to another. It has been stated that in terrestrial ecosystems only a small proportion of plant tissue is consumed by herbivores and most of that (according to PIANKA, 1974, nearly 90%) is directly transferred to decomposers, but secondary or higher consumers (carnivores) consume a large proportion of the trophic level which they use as food. Thus herbivores may only rarely be short of food, whereas predators may be faced with starvation quite frequently. This condition, in turn, leads predators to evolve a

strategy of energy metabolism to combat starvation periods. When starved, they normally search for prey by active movement, but when they cannot, in spite of their efforts, obtain food, they change their behaviour to stop movement and await recovery of their food resources, which results in a decrease in energy expenditure. The mobility of the prey enable the predators to adopt such a strategy; thus it is possible that many predators, at least poikilotherms which depend on mobile prey, adopt such a strategy.

It is suggested that starved spiders use a higher ratio of fat as the catabolic substrate than normally fed ones. There are many reports on main metabolic substrates of aquatic animals under starvation (for review, see GIESE, 1966; MARSDEN et al., 1973). But due to differences in the compositions of supposed substrates, this problem still remains unsolved. As to terrestrial animaIs despite earlier emphasis by IVLEV (1939), changes in metabolic pathways under starvation have been little studied so far. Changes in the RQ before and after the starvation of the phytophagous and predaceous poikilotherms should be investigated in future.

#### **SUMMARY**

Effects of starvation on the survival period and the respiratory rate in adults of a wolf spider, *Pardosa astrigera* (L. KocH), were investigated. The spiders used were divided into four groups: well-fed, starved and two limited food groups; in the latter two, each spider was supplied with one leafhopper every second or third day. Adult males and females of *P. astrigera* could survive for a long time;  $28.8 \pm 2.7$ days and 54.4 $\pm$ 18.9 days, respectively, without any food. The longevities shown here were 73.8% for males and 78.6% for females of those of well-fed spiders, indicating that *P. astrigera* adults have a strong tolerance to starvation. The respiratory rate of well-fed adults showed no tendency to increase or decrease with their aging; the mean respiratory rates were  $4.86 \times 10^{-4}$  mg CO<sub>2</sub>/mg f.w. (fresh body weight)/hr for males and  $3.80 \times 10^{-4}$  mg CO<sub>2</sub>/mg f.w./hr for females. The respiratory rates of starved spiders increased during the first two days of starvation but decreased markedly ifrom the third to the twelfth day, and thereafter retained an almost constant level for each sex. The mean respiratory rates after the twelfth day of starvation were 2.49 $\times$ 10<sup>-4</sup> mg CO<sub>2</sub>/mg f. w./hr for males and 2.76 $\times$ 10<sup>-4</sup> mg CO<sub>2</sub>/mg f.w./hr for females; these values were respectively 48.4% and 63. 0% of those prior to starvation. The fresh body weight of starved spiders decreased linearly with time but the rate was small. The respiratory rates of the limited food groups tended to decline with time and thereby their weight losses were minimized. The decrease in the respiratory rate under starvation was considered not to be due to spider exhaustion or senescence but due to an intrinsic change in behaviour and/or metabolism, because when the spiders were supplied with ample food for five days after starvation, the respiratory rate and the body weight rapidly recovered to near the levels

prior to starvation. It is suggested that starved spiders use a higher ratio of fat as catabolic substrate than normally fed or satiated ones. Feeding strategies of poikilotherm predators are discussed.

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#### ウヅキコモリグモの飢餓条件下における呼吸率の低下

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ウヅキコモリグモ成体の生存期間および呼吸率におよぼす飢餓の影響を明らかにするため、 飽食区・絶食 区・少量給餌区を設けて実験を行った。ウヅキコモリグモ成体は、絶食条件下で平均28.8±2.7日 (雄), 54.4±18.9日 (雌) 生存した。これらの値は、それぞれ飽食区の生存期間の73.8%, 78.6%に相当し、本種 が強い飢餓耐性を有することを示している。飽食させたクモの呼吸率は、齢が増すにつれて増加または減少 する傾向はなく, その平均値は 4.86×10<sup>-4</sup> mg CO<sub>2</sub>/mg f.w./hr (雄), 3.80×10<sup>-4</sup> mg CO<sub>2</sub>/mg f.w./hr (雌) であった。絶食させたクモの呼吸率は、絶食2日目までは増加したが、3日目から12日目までは大幅 に減少し、12日目以後はほぼ一定のレベルを維持した。絶食12日目以後の呼吸率の平均値は、2.49×10-4mg  $CO<sub>2</sub>/mgf. w./hr$  (雄),  $2.76 \times 10^{-4}$  mg  $CO<sub>2</sub>/mgf. w./hr$  (雌) であり, これらの値は, それぞれ絶食前の 値の48.4%, 63.0%であった。絶食させたクモの生体重は、時間とともに直線的に減少したが、減少率は小 さかった。少量給餌区のクモの呼吸率は、しだいに減少する傾向があり、一方、 生体重はほとんど減少しな かった。絶食後5日間飽食させると、クモの呼吸率および生体重は、 ほとんど絶食前と同じレベルまで回復 した。また、絶食条件下では飽食条件下に比較して、代謝基質として脂肪が使わるれ割合の高いことが示唆 された。したがって、飢餓条件下における呼吸率の低下は、クモの衰弱または老化によるものではなく、 行 動や代謝様式が変化するためであると考えられた。これらの結果をもとに、外温性捕食者の捕食戦略につい て考察した。