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Minimum and Maximum Metabolic Rates of Sorex sinuosus

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The minimal and maximal metabolic rates of *Sorex sinuosus* are similar to other species of shrews. These metabolic rates showed considerable variability depending upon the season, nutritional state, sex behavior and time of day. The average minimal metabolic rate at 20°C is 4.5 kcal/day while the average maximum metabolic rate at 20°C is 6.0 kcal/day. Only under extreme fasting conditions did minimal metabolic rates approach predicted basal values for small mammals. The constantly active nature of shrews contributes to the high metabolic rates observed in *S. sinuosus*.

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I. INTRODUCTION

Opinion is divided as to why the observed »basal« metabolic rates of shrews are higher than the predicted basal metabolic rates derived from Kleiber's (1967) allometric equation for mammals of similar size. One group of investigators believes that these observed high metabolic rates are characteristic of shrews (Pearson, 1948; Gębczyński, 1965, 1971a; Gębczyńska & Gębczyński, 1965; Poczopko, 1971; Vogel, 1976). Vogel (1976) compared the metabolism of 13 species of shrews and concluded that only the tribe *Soricini* have a uniquely higher metabolic rate. The subfamily *Crocidurinae* is characterized by relatively low metabolic rates. The tribes *Neomyini* and *Blarinini* have intermediate metabolic rates. Other investigators attribute these observed high values to experimental conditions such as *SDA* and activity (Morrison, *et al.*, 1959; Hawkins *et al.*, 1960; Buckner, 1964; Martinsen, 1969; Platt, 1974).

Several factors are known to significantly affect the metabolism of small mammals including size, shape, sex, reproductive condition, circadian variation, season, activity and temperature (Gessaman, 1973; Grodziński & Wunder, 1975). Detailed studies on the metabolism and factors affecting the metabolism of the genus of *Sorex* have been conducted on five species: *S. araneus* (Gębczyński, 1965); *S. arcticus*; *S. cinereus* (Buckner, 1964); *S. minutus* (Gębczyński, 1971b). Additional studies on other species are needed to further explain the metabolic uniqueness of shrews (Poczopko, 1971). The objectives of this study were to measure the minimum and maximum metabolic rates of *S. sinuosus* and to determine some factors influencing the metabolic rate of this species.

II. MATERIAL AND METHODS

Sorex sinuosus is a small insectivore which occurs in the northern salt marshes of San Pablo Bay and Suisun Bay, of California (Rudd, 1955). At birth *S. sinuosus* weighs about 0.5 grams and grows to an average weight of 4.5 grams. Reproductively active shrews may weigh as much as 7 grams (Rudd, 1955). Reproductive activity starts in late February, reaches a peak in May, and declines sharply in early June (Johnston & Rudd, 1957). *S. sinuosus* has a life expectancy of less than one year although a small number of individuals do survive through the second year. There is a turnover in age classes of adults born the previous year to adults born in the calendar year during the summer. At this time three age classes can be identified: juveniles, young adults, and old adults (Rudd 1955). Because of the defined breeding season and seasonal change in age classes, three seasons were recognized for analysis: spring (March, April, May, and June), late summer (July, August, September, and October), and winter (November, December, January, and February). *S. sinuosus* was captured using Sherman live traps (22×8×8 cm) during 1967 to 1970. Captured shrews were maintained in the laboratory under the normal lighting regime of the salt marsh and fed a mixture of beef brains and Purina Cat Chow (Registered trademark). The animal room approximated the normal temperature regime of the salt marshes to within 5°C.

Oxygen consumption was measured in a metabolism chamber using a Beckman model F-3 paramagnetic oxygen analyzer with a span of 19—21 percent oxygen in an open-circuit system. The millivolt output of the analyzer was continuously monitored on a Honeywell Stripchart recorder. The animals were supplied with carbon dioxide-free air and oxygen analysis was also performed on carbon dioxide-free air. Oxygen consumption values were calculated according to the formula of Depocas & Hart (1957) for open-circuit systems. This procedure has been found to produce accurate results (Hill, 1972).

The metabolism chamber was a 0.33 liter glass chamber. The floor of the chamber was wired with micro-switches which detected any locomotor activity. This activity was recorded simultaneously with oxygen consumption on an Esterline-Angus Event recorder. By comparing oxygen consumption values with activity recordings the metabolic rates during periods of activity and inactivity could be determined. During the experiments the metabolism chamber was submerged in a constant temperature water bath kept at 20°C. Food and water were provided *ad libitum* during each experiment. Metabolic measurements were made within three weeks of capture. The minimal metabolism was calculated to be the mean of the lowest oxygen consumption values observed in each 15-minute interval through 24 hours. Maximum metabolism was the mean of the highest values observed in each 15-minute interval through 24 hours.

III. RESULTS

The metabolic rate of *S. sinuosus* exhibited considerable variability depending upon the season, nutritional state, behavior and time of day. The minimal daily metabolic rate at 20°C ranged from 3.3 ± 1.2 kcal/day in the winter to 6.9 ± 1.2 kcal per day in the spring (Table 1).

Comparison of seasonal metabolic rates reveal a significant decline $[t_{(.01)(44)}=3.214]$ in minimal daily metabolic rates from late summer to winter. There is a significant increase $[t_{(.01)(31)}=3.645]$ in the metabolic rates from winter to spring. No significant differences existed between the seasonal body weights of these experimental animals. Fasting metabolic rates were observed in three shrews during experiments in which food was deprived (Table 2). All experiments ended in the death of the animal with measurement times lasting from 5 to 23 hours. Fasting animals lost between 8 and 10% of their body weights. The minimal metabolism observed three hours before death (considered post-absorptive) was significantly greater than the predicted basal values. These values were 3 to 6 times greater than predicted basal values. At one hour before death only one animal showed a metabolic rate significantly higher than predicted basal values. At 15 minutes before death the fasting metabolic rates of the three shrews were not significantly different from the predicted basal values.

Table 1

Comparison of the seasonal minimal daily metabolic rate at 20°C of *S. sinuosus* with predicted basal metabolic rates.

Sex	No.	Wt. (g)	Observed minimal metabolic rate ($ccO_2g^{-1}hr^{-1}$)	(kcal day^{-1})[a]	Predicted[b] basal metabolic rate (kcal day^{-1})	Percent[c] difference
			Late Summer			
Males	12	5.4±0.8	7.1±2.2	4.4±1.4	1.4	214
Females	10	5.3±0.5	8.6±2.4	5.2±1.4	1.4	271
Both	22	5.4±0.7	7.8±2.1	4.9±1.3	1.4	250
			Winter			
Males	15	5.0±0.8	5.6±2.5	3.2±1.4	1.3	146
Females	9	4.8±0.6	6.2±1.2	3.4±0.6	1.3	162
Both	24	5.0±0.7	5.8±2.1	3.3±1.2	1.3	154
			Spring			
Males	7	6.8±1.5	8.6±3.4	6.7±2.6	1.6	318
Females	2	5.4	10.1	7.5	1.4	435
Both	9	6.4±1.4	9.4±3.5	6.9±2.6	1.6	331

[a] kcal $day^{-1}=ccO_2g^{-1}\,hr^{-1}\times 24\,hr\times wt(g)\times 4.8\div 1000$. Kleiber (1961).

[b] kcal/day = $69W^{.75}\pm 1.2$ kcal where W=kg. Kleiber (1961).

[c] (Minimal metabolic rate-predicted basal metabolic rate/predicted basal metabolic rate)×100.

Table 2

Comparison of minimal metabolic rates of *S. sinuosus* during fasting, one hour before death, and the last fifteen minutes before death.

Individual	Initial Weight (g)	Weight Loss (g)	Duration of Metabolic Trial (hours)	Minimal Metabolic Rate ($ccO_2g^{-1}\,hr^{-1}$) 3 Hours Before Death	1 Hour Before Death	15 Minutes Before Death	Predicted[a] Basal Metabolic Rate ($ccO_2g^{-1}\,hr^{-1}$)
E-9	7.4	0.7	18	7.6±1.7[b]	13.0±3.6[c]	3.6±.09	2.5±1.4
E-8	4.7	0.5	5	8.0±0.7[d]	6.1±0.4	1.4±2.0	2.3±2.3
C-17	3.7	0.3	23	14.8±0.8[e]	10.1±0.7	2.6±2.4	2.5±2.9

[a] $ccO_2^{-1}\,hr^{-1} = .3936\ wt^{.75}/(24\ hrs. \times 4.7 \times wt \times 1000)$, where wt=g. Adapted from Kleiber (1961).

Significantly different when compared with predicted basal values.

[b] $t_{(.05)(46)} = 3.92$.

[c] $t_{(.05)(38)} = 7.78$.

[d] $t_{(.05)(10)} = 2.45$.

[e] $t_{(.05)(10)} = 4.24$.

Females had an average metabolic rate that was 15% higher than males (Table 1). Although this difference was not significant, the higher metabolic rates of females was observed in each season. Females showed a greater variation in metabolic rate than males from season to season.

Comparison of the minimal metabolic rates of juveniles, young adults, and old adults, showed that juveniles had the highest metabolism, and old adults the lowest. However, this variation was not statistically significant and appears to be weight related (Table 3). One very old female, approximately 22 months old, had a metabolic rate similar to the rest of the population sampled.

Table 3

Comparison of the minimal metabolic rates of various age classes of *S. sinuosus* in late summer.

	Juveniles	Young Adults	Old Adults
Number	7	11	8
Body weight (g)	3.7±0.3	4.9±0.5	5.7±0.6
Minimal metabolic rate (cc $O_2 g^{-1} hr^{-1}$)	9.5±5.7	8.5±2.3	6.6±1.6

Table 4

Comparison of mean minimal and maximum metabolic rates for late summer, winter, and spring.

	Late Summer	Winter	Spring
Number	22	24	9
Minimal metabolic rate (cc $O_2 g^{-1} hr^{-1}$)	7.8±2.1 [b]	5.8±2.1 [c]	9.4±3.5
Maximum metabolic rate (cc $O_2 g^{-1} hr^{-1}$)	9.5±2.1 [b]	8.8±2.1 [c]	12.4±3.3
Percent [a] difference	22	52	32

[a] (max. met. rate — min. met. rate/min. met. rate)×100.

[b] Significantly different; $t_{(.02)(42)} = 2.464$.

[c] Significantly different; $t_{(.001)(46)} = 4.784$.

Activity was recorded in every hour during the metabolic experiments and was a major factor in raising metabolic rate (Table 4). The maximum daily metabolic rates corresponding to periods of activity were significantly higher (22 to 52%) than minimal daily metabolic rates. Although maximum daily metabolic rates of spring were 32% higher than minimal daily metabolic rates of the spring, they were not significantly different [$t_{(.05)(16)} = 1.858$]. Significant differences were observed between the diurnal and nocturnal metabolic rates of winter and spring individuals (Table 5). Individuals from the winter had a slightly greater diurnal metabolic rate while individuals from the spring had a 24% greater nocturnal metabolic rate. There was no significant difference between the diurnal and nocturnal metabolism of late summer.

IV. DISCUSSION

Minimal metabolic rates of *Sorex sinuosus* are similar to the minimal metabolic rates observed in other species of shrews, especially the genus *Sorex* (Fig. 1). Vogel (1976) derived an allometric equation for the minimal metabolism of *Soricinae* ($M=82.6W^{0.53}$, where M equals cal./hr. and W equals grams). It best describes the late summer minimal metabolism of *S. sinuosus*. The observed minimal metabolism of spring and winter animals are respectively higher and lower than the metabolism described by this allometric relationship. At thermal neutrality, the minimal metabolic rates in other species of shrews are considerably higher than predicted basal values (Morrison *et al.*, 1959; Hawkins *et al.*, 1960; Gębczyńska & Gębczyński, 1965). Minimal metabolic rates measured under post-absorptive conditions in *S. sinuosus*, *Cryptotis parva* (Pfeiffer & Gass, *op. cit.*), *S. araneus*, *S. minutus*, and *Neomys fodiens* (Gębczyński, 1971b) were found to be significantly higher than predicted. Only under extreme fasting conditons resulting in death of the animal did the observed metabolic rates of *S. minutus* and *S. araneus* significantly drop to near »basal« levels. This lowering of metabolism was associated with a reduction in activity of the fasting shrews (Gębczyński, 1971b). *S. sinuosus* showed the same response to extreme fasting. Seasonal variation in the metabolic rates of shrews is common. Winter is a time of energy reduction in *Neomys fodiens* (Gębczyńska & Gębczyński, 1965), *S. araneus and S. minutus* (Gębczyński, 1965). A 34% decline in the metabolic rate from summer to winter is observed in *S. sinuosus* (Table 1).

Table 5

Comparison of the mean diurnal metabolic rate with the mean nocturnal metabolic rate and night/day ratios (N/D) for late summer, winter and spring.

	Late Summer	Winter	Spring
Number	9	24	15
Mean diurnal metabolic rate (cc $O_2 g^{-1} hr^{-1}$)	9.6±0.4	6.8±0.6 [a]	10.2±2.1 [b]
Mean nocturnal metabolic rate (cc $O_2 g^{-1} hr^{-1}$)	9.7±0.3	6.3±0.3 [a]	12.7±1.6 [b]
N/D ratio	1.02	0.93	1.24

[a] Significantly different; $t_{(.05)\,(22)} = 3.395$.
[b] Significantly different; $t_{(.01)\,(13)} = 3.070$.

In European shrews, a reduction in body size and organ weight also occurs during the winter (Dehnel, 1949; Pucek, 1965). An analysis of the body weights of *S. sinuosus* revealed a similar seasonal drop in body weights. The average body weight for *S. sinuosus* is 3.9 ± 0.1 grams (n=43) in the winter compared to 4.3 ± 0.1 grams (n=50) for the summer and 5.9 ± 0.2 grams (n=120) for the spring. This seasonal reduction in metabolic rates and body weights of shrews is hypothesized as an adaptation for physiological conservation during periods of the year with high energy demands (Gębczyński, 1965; Mezhzherin, 1969).

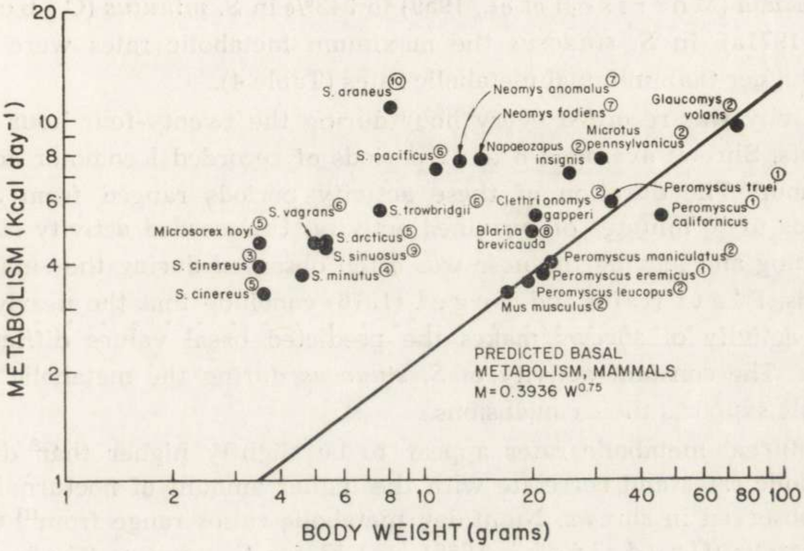

Fig. 1. Comparison of the observed minimal metabolic rates of shrews with other small mammals: 1-McNab & Morrison, 1963; 2-Pearson, 1947; 3-Morrison *et al.*, 1959; 4-Gębczyński, 1971a; 5-Buckner, 1964; 6-Pearson, 1948; 7-Gębczyńska & Gębczyński, 1965; 8-Martinson; 1969; 9-Author; 10-Gębczyński, 1965.

An increase in spring metabolic rates is observed in *N. fodiens* (Gębczyńska & Gębczyński, 1965) and *S. araneus* (Gębczyński, 1965). *S. sinuosus* shows a 67% increase in metabolic rate from winter to summer. These increases in energy expenditure of shrews are associated with increases in body size resulting in part from reproductive maturation (Johnston & Rudd, 1955; Rudd, 1955; Pucek, 1965; Brown, 1974) and increased activity associated with the reproduction (Buckner, 1969; Croin-Michielsen, 1966; Newman, 1976). In the autumn metabolic rates of *S. araneus* and *S. minutus* are intermediate between the metabolic rates of spring and winter (Gębczyński, 1965; 1971). A similar pattern exists in *S. sinuosus* for late summer metabolic rates (Tab. 1).

The metabolic sensitivity of shrews to activity can be seen in the differences between the differences in maximum (active) and minimum (resting) metabolic rates. Shrews are active twenty-four hours a day with greatest amount of activity occurring at night (Hamilton, 1940; Clothier, 1955; Crowcroft, 1957; Ingles, 1960; Shillito, 1963; Buchalczyk, 1972; Newman, 1976). The difference in maximum and minimum metabolic rates of shrews range from 28% in *Blarina brevicauda* (Morrison *et al.*, 1959) to 343% in *S. minutus* (Gębczyński, 1971a). In *S. sinuosus* the maximum metabolic rates were 20 to 52% higher than minimal metabolic rates (Table 4).

Activity was recorded every hour during the twenty-four hour experiments. Shrews averaged 8 to 12 periods of recorded locomotor activity per hour. The duration of these activity periods ranged from a few seconds to 10 minutes of sustained activity. Unrecorded activity such as twitching and moving the nose was often observed during the »inactive« periods. Platt (1974) and Vogel (1976) conclude that the nearly constant activity of shrews makes the predicted basal values difficult to obtain. The constant activity of *S. sinuosus* during the metabolic experiments supports their conclusions.

Nocturnal metabolic rates appear to be slightly higher than diurnal metabolic rates and correlate with the higher amount of nocturnal activity observed in shrews. Night/day metabolic ratios range from 1.04 for *S. cinereus* (Grodziński, 1965) to 1.17 for *S. minutus* (Gębczyński, 1971a). *S. sinuosus* showed a similar pattern during the spring and late summer with night/day ratios of 1.24 and 1.02, respectively. During the winter, diurnal energy expenditure is slightly higher (Table 5). Seasonal variation in the night/day ratios is also observed in *S. araneus* (Gębczyński, 1965).

Investigations into the metabolic patterns of *S. sinuosus* and other species of shrews reveal a number of significant factors affecting their metabolic rates. Efforts at developing daily and annual energy budget for shrews should account for these factors, especially seasonal and behavioral influences.

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TEMPO METABOLIZMU MINIMALNEGO I MAKSYMALNEGO U *SOREX SINUOSUS*

Zbadano minimalne i maksymalne tempo metabolizmu u *Sorex sinuosus*. Obydwa te parametry charakteryzują się dużą zmiennością i zależą od sezonu, płci, wieku, okresu doby i stopnia najedzenia. Minimalne, średnie tempo metabolizmu, mierzone przy 20°C wynosi 4.5 kcal/dobę, maksymalne, mierzone w tej samej temperaturze — 6.0 kcal/dobę (Tabela 1). Samice mają średnio o 15% wyższy metabolizm niż samce. W zależności od sezonu tempo metabolizmu ulega istotnym zmianom: obniżeniu w okresie od końca lata do zimy i podwyższeniu od zimy do wiosny (Tabela 4).Tylko głodzone ryjówki, tuż przed śmiercią głodową, wykazują niższy metabolizm minimalny niż oszacowany dla nich metabolizm podstawowy (Tabela 2).

Najwyższym tempem metabolizmu charakteryzują się osobniki młode a najniższym stare (Tabela 3). Ustalono, że największy wpływ na tempo metabolizmu wywiera aktywność ryjówek (Tabela 4) — stąd maksymalne dobowe tempo metabolizmu połączone z dużą aktywnością ruchową jest do 55% wyższe niż minimalne. Obserwowano również istotne różnice w tempie metabolizmu dziennego i nocnego u zwierząt w różnych sezonach (Tabela 5).