

## Ventilatory accommodation of changing oxygen demand in sciurid rodents

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**Summary.** Ventilation was measured across a range of  $O_2$  consumption rates in four sciurid rodents: *Tamias minimus* (47 g), *Spermophilus lateralis* (189 g), *S. beecheyi* (531 g), and *Marmota flaviventris* juveniles (1054 g) and adults (2989 g). Maximum thermogenic oxygen consumption was measured for all but adult *M. flaviventris*. Aerobic scopes (maximum/minimum  $O_2$  consumption rates) were 4.6, 3.8, 5.4, and 4.8 in *T. minimus*, *S. lateralis*, *S. beecheyi*, and juvenile *M. flaviventris*, respectively. Aerobic scope was at least 4.1 in adult *M. flaviventris*. Ventilatory accommodation of changing  $O_2$  consumption rate was qualitatively similar in the four species, with the bulk of accommodation resulting from changes in minute volume. Nevertheless, there were significant differences in the relative importance of frequency, tidal volume, and  $O_2$  extraction in accommodation. In all species, frequency and minute volume were strongly correlated to  $O_2$  consumption rate. Tidal volume was significantly correlated to  $O_2$  consumption rate in *T. minimus* and *S. beecheyi*, but not in the other species. Oxygen extraction was not significantly correlated to  $O_2$  consumption rate in any species. Analysis of factorial ventilation changes across a standardized 3.8-fold change in  $O_2$  consumption rate revealed significant differences among species in frequency and  $O_2$  extraction, but not in tidal or minute volume. When compared to a generalized allometry for mammalian resting ventilation, the four sciurid species had consistently lower respiration frequency and higher  $O_2$  extraction than predicted, perhaps because the sciurid measurements were made on unrestrained animals. There was no indication that ventilation constrained maximum  $O_2$  consumption rate.

**Key words:** Aerobic scope – Oxygen consumption – Respiration – Ventilation – Sciurid rodents

**Abbreviations:** BMR, basal metabolic rate; BTPS, body temperature and pressure, saturated;  $EO_2$ , oxygen extraction;  $f$ , respiration frequency; MMR, minimal metabolic rate; RH, relative humidity; STPD, standard pressure and temperature, dry;  $T_a$ , ambient temperature;  $T_b$ , body temperature;  $\dot{V}_j$ , minute volume;  $\dot{V}_t$ , tidal volume;  $\dot{V}O_{2max}$ , maximum rate of oxygen consumption

### Introduction

Mammals use aerobic respiration to sustain high levels of metabolic power output. In euthermic mammals  $\dot{V}O_2$  ranges from the minimum needed to support BMR to the maximum attained during intense exercise or thermogenesis ( $\dot{V}O_{2max}$ ). Power outputs higher than  $\dot{V}O_{2max}$  must be supported by anaerobic pathways which usually cannot be maintained for long durations. Hence, the ratio  $\dot{V}O_{2max}/BMR$ , usually termed aerobic scope or factorial scope, is a useful index of the limits to sustainable power output.

Changes in  $\dot{V}O_2$  must be supported by equivalent changes in  $O_2$  transport. The first step in the  $O_2$  transport pathway is pulmonary ventilation. Mammalian respiratory systems can adjust to changing  $O_2$  demand (ventilatory accommodation) by adjusting  $\dot{V}_i$ ,  $EO_2$ , or both. In turn,  $\dot{V}_i$  can be changed by adjusting  $f$ ,  $V_t$ , or both. The extent to which animals rely on different accommodation mechanisms presumably reflects constraints related to size, morphology, phylogeny, and possibly adaptations to particular environmental or ecological regimes.

Despite its importance in supporting aerobic metabolism, relatively little is known about mammalian ventilatory accommodation. Stahl (1967) provides baseline allometric data on respiratory parameters in resting mammals, but complete ventilation data ( $f$ ,  $\dot{V}_t$ ,  $V_t$ ,  $EO_2$ ) across a wide range of  $\dot{V}O_2$  are scarce. Species that have been studied show considerable intra- and interspecific variation and few obvious patterns. In small mammals, accommodation is often accomplished by adjusting  $\dot{V}_i$  with relatively little change in  $EO_2$ , with changing  $f$  usually accounting for most of the change in  $\dot{V}_i$  (Withers 1977; Casey et al. 1979; Thomas 1984; Chappell 1985). Large mammals, including humans, seem to rely more on changes on  $V_t$  with smaller adjustment to  $f$  (Ingram and Legge 1969; Flandrois et al. 1971; Cerretelli and di Prampero 1987). The role of  $EO_2$  is highly variable; in some species it remains relatively constant but in others it is as important to accommodation as changes in  $f$  or  $V_t$  (Ingram and Legge 1969; Thomas and Fregin 1981; Chappell and Roverud 1990).

This paper describes the ventilation patterns of four sciurid rodents ranging in body mass from 47 to almost 3000 g. The primary goal was to examine mechanisms of accommodation across as wide a range of  $\dot{V}O_2$  as possible, including  $\dot{V}O_{2\max}$ . Comparing accommodation mechanisms in closely related species covering a wide range of body mass should reveal the influence of mass while minimizing any confounding effects of taxonomic differences. Ventilatory data from these sciurids was compared with Stahl's allometry for resting placentals, and with reported data from other mammals measured over a range of  $\dot{V}O_2$ . A secondary goal was to examine ventilation patterns near  $\dot{V}O_{2\max}$ , to explore the possibility that ventilatory constraints limit aerobic scope.

## Materials and methods

**Animals.** The four species used in this study (Rodentia: Sciuridae) are native to western North America. Three species were studied at the Rocky Mountain Biological Laboratory in Colorado (RMBL; elevation 2900 m). These were least chipmunks, (*Tamias minimus*;  $n=7$ , mean mass 47 g), golden-mantled ground squirrels (*Spermophilus lateralis*;  $n=6$ , mean mass 189 g), and yellow-bellied marmots (*Marmota flaviventris*). The marmots consisted of four juveniles (mean mass 1054 g) and four adults (mean mass 2989 g). California ground squirrels (*Spermophilus beecheyi*;  $n=6$ , mean mass 531 g) were studied at the University of California, Riverside (UCR; elevation 340 m). Animals were live-trapped in natural habitats (under the provisions of California and Colorado collecting permits) and measurements were performed within 24 h of capture.

**Metabolic measurements.**  $\dot{V}O_2$  was measured using an open-circuit respirometry system with metabolism chambers constructed from acrylic plastic and aluminum. Chamber volumes were approximately 0.6 l for *T. minimus*, 2 l for *S. lateralis*, 4 l for *S. beecheyi*, 6 l for juvenile *M. flaviventris*, and 11 l for adult *M. flaviventris*. An environmental cabinet maintained  $T_a$  within  $\pm 0.5^\circ\text{C}$  (monitored as the temperature of the gas stream exiting the metabolism chamber). For most measurements air was used as the respiratory gas. To elicit high rates of heat loss and  $O_2$  consumption a 21%  $O_2/79\%$  He mixture (heliox) was used. The flow of dry gas through the respirometer was regulated to within  $\pm 1\%$  with Tylan and Applied Materials mass flow controllers periodically calibrated against a Singer American dry volume meter. Flow rates ( $0.9\text{--}2.1 \cdot \text{min}^{-1}$  for *T. minimus*,  $1.2\text{--}3.2 \cdot \text{min}^{-1}$  for *S. lateralis*,  $2.2\text{--}6.5 \cdot \text{min}^{-1}$  for *S. beecheyi*, and  $3.5\text{--}12.1 \cdot \text{min}^{-1}$  for *M. flaviventris*) were adjusted to keep  $O_2$  concentration in excurrent air above 20.3%.

$O_2$  concentrations were measured with an Applied Electrochemistry S-3A  $O_2$  analyzer and RH with a Viasala HT-100 probe. Roughly  $100 \text{ ml} \cdot \text{min}^{-1}$  of the excurrent gas stream was diverted through the RH sensor, dried, scrubbed of  $CO_2$ , and pumped through the  $O_2$  analyzer. Analyzer outputs were sampled at 20, 30, or 60 Hz and averaged and recorded every 5 s by a Macintosh computer equipped with a National Instruments LabNB analog-to-digital converter and custom software. With digital signal averaging, the effective resolution of the system was 0.001%  $O_2$  and 0.1% RH. Accuracy was approximately  $\pm 0.005\%$   $O_2$  and  $\pm 1\%$  RH. Analyzers were referenced against incurrent gas before and after each measurement period.  $\dot{V}O_2$  was calculated as  $\dot{V}O_2 = F \cdot (F_iO_2 - F_eO_2)/(1 - F_eO_2)$ , where  $F$  is flow rate,  $F_iO_2$  is the fractional concentration of  $O_2$  in incurrent gas, and  $F_eO_2$  is the fractional concentration of  $O_2$  in excurrent gas.

**Ventilation measurements.** Metabolism chambers were converted into whole-body plethysmographs (Malan 1973) by placing high-resistance orifices in the incurrent and excurrent gas lines. This arrangement allowed simultaneous measurements of ventilation

and gas exchange (Bucher 1981). Pressure changes associated with the warming and humidification of tidal air were detected by an Omega PX 164-010 pressure transducer, sampled at rates of 20, 30, or 60 Hz, and displayed in real time by the Macintosh computer. These rates provided a minimum of 11-12 data points per inhalation-exhalation cycle at the highest ventilation rates observed. Ventilation records lasting 32, 21.3, or 10.7 s (at sampling rates of 20, 30, or 60 Hz, respectively) could be selected and stored on disk. After measurements were completed at a given combination of gas mixture and  $T_a$ , the system was calibrated by injecting known volumes of gas into the chamber at rates yielding pressure change kinetics similar to those observed during inhalation. To calculate  $V_t$  at  $T_a 0^\circ\text{C}$ , the following assumptions were made: ambient water vapor pressure was equal to that in excurrent air, lung temperature was equal to  $T_b$ , and gas in the respiratory tract was 100% saturated with water vapor. For  $V_t$  calculations at  $T_a \leq 0^\circ\text{C}$  ambient RH was assumed to be 100%; other assumptions were unchanged. Accuracy of  $V_t$  measurements increases as the gradient between  $T_b$  and  $T_a$  increases (Malan 1973). Estimated errors in measurements of  $V_t$ , based on repeatability of calibration injection volumes, accuracy of  $T_a$ ,  $T_b$  and RH measurements, and noise levels in the plethysmograph signal, reach a maximum of 15% at  $30^\circ\text{C}$ , declining to  $< 5\%$  at  $T_a$  of  $10^\circ\text{C}$  and colder.  $EO_2$  was computed as  $\frac{100 \cdot \dot{V}O_2}{F_eO_2 \cdot f \cdot V_t}$ , where  $\dot{V}O_2$  and  $V_t$  are corrected to STPD.

**Protocols.** Animals were weighed immediately prior to experimental runs, then placed in the metabolic chamber and allowed 40-60 min to adjust to chamber conditions at the desired  $T_a$  before measurements were attempted. For experiments using heliox, the adjustment interval was reduced to 20-30 min. The highest  $T_a$  used was  $20\text{--}23^\circ\text{C}$  for *M. flaviventris* and  $30^\circ\text{C}$  for all other species. Measurements were made at intervals of  $10^\circ\text{C}$  (e.g., 30, 20, 10, 0, and  $-10^\circ\text{C}$  for *S. beecheyi*). The minimal  $T_a$  in air was  $0^\circ\text{C}$  for *T. minimus*,  $-20^\circ\text{C}$  for *M. flaviventris*, and  $-10^\circ\text{C}$  for *S. lateralis* and *S. beecheyi*.

Ventilation data were recorded only during periods when animals were inactive and  $\dot{V}O_2$  was stable. For each animal, 5-12 ventilation records were obtained at every combination of gas mixture and  $T_a$ . The elapsed time between ventilation records was at least 1 min. When ventilation records were stored, the computer automatically placed time markers in the respirometry data files. By referring to the markers the rate of gas exchange at the time of each ventilation record ( $\pm 5$  s) could be calculated. At the end of the measurement period the animal was quickly removed from the chamber and  $T_b$  was measured rectally ( $\pm 0.1^\circ\text{C}$ ) with a thermocouple attached to a Bailey BAT-8 thermometer. Measurement periods were 30-100 min at most  $T_a$ s. Experiments were terminated if indications of hypothermia were observed (i.e., steady declines in  $\dot{V}O_2$ , apparent  $V_t$ , or  $f$ ).  $\dot{V}O_{2\max}$  was assumed to have been attained if hypothermia occurred ( $T_b < 35^\circ\text{C}$ ) or if reduction of  $T_a$  did not elicit increased  $\dot{V}O_2$ .

**Units and data analysis.** Calculations involving  $\dot{V}O_2$  are based on units of millilitres per minute STPD or millilitres per gram per minute STPD. Ventilation volumes ( $V_t$  in millilitres and  $\dot{V}_t$  in millilitres per minute) are in BTPS units (i.e., actual volumes in the respiratory tract). STPD units for  $V_t$  and  $\dot{V}_t$  can be computed using the  $T_b$  and barometric pressure data in Tables 1-4. The units for  $f$  are breaths per minute.

Because of non-overlapping and highly significant mass differences between juvenile and adult marmots, these two age classes were treated separately in most analyses. To avoid problems of unequal numbers of ventilation records among individuals, mean values were calculated for each individual at each combination of  $T_a$  and gas mixture ( $n=35$  for *T. minimus*, 30 for *S. lateralis*, 36 for *S. beecheyi*, and 16 each for juvenile and adult *M. flaviventris*). Analyses (repeated-measures ANOVA, least-squares and multiple regression, and covariance analysis) were performed with Statistical Analysis System (SAS) software. Results are presented as mean  $\pm$  SD; the significance level was 0.05.

## Results

### Oxygen consumption, respiratory quotient, and body temperature

In all four species the lowest measured  $\dot{V}O_2$  (MMR) occurred at a  $T_a$  of 20–30 °C. Lower  $T_a$  elicited progressively higher  $\dot{V}O_2$  (Tables 1–4). The  $\dot{V}O_2$  in heliox was

substantially higher than in air at equal  $T_a$ .  $\dot{V}O_{2\max}$  was induced in *T. minimus*, *S. lateralis*, *S. beecheyi*, and juvenile *M. flaviventris*, but not in adult *M. flaviventris*. Mass-specific values of  $\dot{V}O_{2\max}$  (all in heliox) were: *T. minimus*, 0.164 ml · g<sup>-1</sup> · min<sup>-1</sup> at 5–10 °C; *S. lateralis*, 0.0878 ml · g<sup>-1</sup> · min<sup>-1</sup> at -5–0 °C; *S. beecheyi*, 0.0612 ml · g<sup>-1</sup> · min<sup>-1</sup> at -12 to -8 °C; and juvenile

**Table 1.** Metabolic and ventilatory parameters of *Tamias minimus* (mean mass 47.1 ± 7.4 g) in different thermal regimes

$T_a$ (°C)	gas	$T_b$ (°C)	$\dot{V}O_2$ (ml · g <sup>-1</sup> · min <sup>-1</sup> )	$V_t$ (ml)	f (br · min <sup>-1</sup> )	$V_i$ (ml · min <sup>-1</sup> )	EO <sub>2</sub> (%)
5 to 10	heliox	36.3 ± 0.8	0.164 ± 0.026	1.75 ± 0.26	235 ± 30	411 ± 66	16.0 ± 2.7
0	air	38.1 ± 0.5	0.111 ± 0.012	1.50 ± 0.33	165 ± 25	247 ± 60	19.0 ± 4.5
10	air	37.9 ± 0.4	0.0843 ± 0.0107	1.52 ± 0.25	139 ± 31	207 ± 47	17.0 ± 2.9
20	air	38.0 ± 0.8	0.0516 ± 0.0066	1.17 ± 0.31	101 ± 18	116 ± 29	18.8 ± 3.6
30	air	38.3 ± 0.8	0.0352 ± 0.0040	0.857 ± 0.195	93.0 ± 20.1	79.6 ± 21.5	19.0 ± 4.2

Values of  $V_t$  and  $V_i$  are in BTPS units; barometric pressure in the metabolism chamber was 550–555 torr. Data are presented as mean ± S.D.;  $n = 7$  in all cases. The helium-oxygen mixture (heliox) was 21% O<sub>2</sub> and 79% He

**Table 2.** Metabolic and ventilatory parameters of *Spermophilus lateralis* (mean mass 189 ± 30 g) in different thermal regimes

$T_a$ (°C)	gas	$T_b$ (°C)	$\dot{V}O_2$ (ml · g <sup>-1</sup> · min <sup>-1</sup> )	$V_t$ (ml)	f (br · min <sup>-1</sup> )	$V_i$ (ml · min <sup>-1</sup> )	EO <sub>2</sub> (%)
-5 to 0	heliox	35.2 ± 1.1	0.0878 ± 0.015	3.87 ± 0.84	114 ± 35	441 ± 173	33.7 ± 6.4
0	air	37.0 ± 1.2	0.0459 ± 0.0072	3.45 ± 1.08	85.0 ± 22.2	289 ± 93	28.9 ± 7.9
10	air	37.6 ± 1.3	0.0372 ± 0.0072	3.77 ± 0.98	71.8 ± 21.8	256 ± 59	24.1 ± 6.2
20	air	37.8 ± 1.2	0.0286 ± 0.0044	3.19 ± 0.91	66.7 ± 22.9	209 ± 68	24.3 ± 4.0
30	air	37.1 ± 1.2	0.0232 ± 0.0040	3.15 ± 1.00	58.9 ± 13.4	176 ± 26	22.1 ± 2.4

Values of  $V_t$  and  $V_i$  are in BTPS units; barometric pressure in the metabolism chamber was 550–555 torr. Data are presented as mean ± S.D.;  $n = 6$  in all cases. The helium-oxygen mixture (heliox) was 21% O<sub>2</sub> and 79% He

**Table 3.** Metabolic and ventilatory parameters of *Spermophilus beecheyi* (mean mass 531 ± 75 g) in different thermal regimes

$T_a$ (°C)	gas	$T_b$ (°C)	$\dot{V}O_2$ (ml · g <sup>-1</sup> · min <sup>-1</sup> )	$V_t$ (ml)	f (br · min <sup>-1</sup> )	$V_i$ (ml · min <sup>-1</sup> )	EO <sub>2</sub> (%)
-10	heliox	35.6 ± 1.3	0.0612 ± 0.0134	9.43 ± 1.78	81.8 ± 18.5	747 ± 93	26.3 ± 5.6
-10	air	37.7 ± 0.1	0.0429 ± 0.0110	8.62 ± 2.23	64.7 ± 23.2	545 ± 244	27.6 ± 9.5
0	air	37.5 ± 0.3	0.0355 ± 0.0056	8.43 ± 2.22	45.2 ± 19.5	353 ± 122	38.9 ± 15.6
10	air	37.3 ± 0.5	0.0251 ± 0.0065	7.59 ± 1.52	41.3 ± 19.6	297 ± 123	30.0 ± 10.5
20	air	37.7 ± 0.7	0.0179 ± 0.0052	6.26 ± 2.09	44.2 ± 31.2	238 ± 120	33.4 ± 18.8
30	air	37.6 ± 0.6	0.0114 ± 0.0019	6.12 ± 1.95	24.0 ± 7.8	137 ± 31.4	28.7 ± 9.8

Values of  $V_t$  and  $V_i$  are in BTPS units; barometric pressure in the metabolism chamber was 735–740 torr. Data are presented as mean ± S.D.;  $n = 6$  in all cases. The helium-oxygen mixture (heliox) was 21% O<sub>2</sub> and 79% He

**Table 4.** Metabolic and ventilatory parameters of juvenile and adult *Marmota flaviventris* (mean mass 1054 ± 190 and 2989 ± 404 g, respectively) in different thermal regimes

$T_a$ (°C)	gas	$T_b$ (°C)	$\dot{V}O_2$ (ml · g <sup>-1</sup> · min <sup>-1</sup> )	$V_t$ (ml)	f (br · min <sup>-1</sup> )	$V_i$ (ml · min <sup>-1</sup> )	EO <sub>2</sub> (%)
<i>juveniles</i>							
-20 to -15	heliox	36.7 ± 0.4	0.0502 ± 0.0073	16.6 ± 2.2	92.3 ± 19.2	1519 ± 316	29.5 ± 6.2
-15	air	37.2 ± 0.3	0.0258 ± 0.0031	20.3 ± 7.8	51.2 ± 20.4	939 ± 189	24.5 ± 2.3
0	air	37.5 ± 0.4	0.0180 ± 0.0030	26.6 ± 13.1	32.4 ± 5.3	869 ± 462	22.8 ± 11.3
23	air	37.4 ± 0.4	0.0105 ± 0.0010	24.4 ± 9.5	25.7 ± 5.7	657 ± 324	18.9 ± 11.3
<i>adults</i>							
-23 to -18	heliox	36.8 ± 0.6	0.0289 ± 0.0077	56.0 ± 24.6	46.8 ± 14.5	2378 ± 597	30.6 ± 8.2
-18	air	37.1 ± 0.3	0.0144 ± 0.0025	39.9 ± 23.6	35.7 ± 18.2	1511 ± 1222	36.9 ± 22.1
0	air	37.0 ± 0.5	0.00896 ± 0.00195	41.6 ± 19.5	23.1 ± 7.0	891 ± 224	27.8 ± 5.0
21	air	37.3 ± 0.4	0.00712 ± 0.00169	30.2 ± 3.1	23.0 ± 7.8	708 ± 279	23.8 ± 8.0

Values of  $V_t$  and  $V_i$  are in BTPS units; barometric pressure in the metabolism chamber was 550–555 torr. Data are presented as mean ± S.D.;  $n = 4$  in all cases. The helium-oxygen mixture (heliox) was 21% O<sub>2</sub> and 79% He

*M. flaviventris*,  $0.0502 \text{ ml} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$  at  $-20$  to  $-15^\circ\text{C}$ . The measured aerobic scopes ( $\dot{V}\text{O}_{2\text{max}}/\text{MMR}$ ) were 4.6, 3.8, 5.4, and 4.8, respectively. The highest  $\dot{V}\text{O}_2$  measured for adult marmots was  $0.0289 \text{ ml} \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ , at  $-23$  to  $-18^\circ\text{C}$  in heliox, or about 4.1-fold larger than MMR.

#### Ventilation and oxygen extraction

Ventilation was analyzed primarily as a function of  $\text{O}_2$  consumption. Ventilatory changes associated with changing  $\dot{V}\text{O}_2$  followed roughly similar patterns in the four species, although there were obvious quantitative differences in  $f$  and  $V_i$  (Fig. 1). To compensate for the influence of body mass or other species-specific effects on accommodation patterns,  $\dot{V}\text{O}_2$ ,  $f$ ,  $V_t$ ,  $\dot{V}_i$ , and  $\text{EO}_2$  were converted into factorial values by dividing each parameter by its value at MMR (Figs. 2, 3).

In *T. minimus*,  $f$ ,  $V_t$ , and  $V_i$  were all positively and significantly correlated with  $\dot{V}\text{O}_2$  ( $F > 36$ ,  $n = 35$ ,  $P < 0.001$  in all cases).  $\text{EO}_2$  and  $\dot{V}\text{O}_2$  were not significantly correlated.  $\dot{V}_i$  changed approximately 5-fold between MMR and  $\dot{V}\text{O}_{2\text{max}}$  due to a 2.5-fold change in  $f$  and a 2-fold change in  $V_i$  (Fig. 2). Maximum  $f$  was  $311 \text{ breaths} \cdot \text{min}^{-1}$ .

In *S. lateralis*,  $f$  and  $V_i$  were positively and significantly correlated with  $\dot{V}\text{O}_2$  ( $F > 10$ ,  $P \leq 0.003$ ). However, the correlations between  $V_t$  and  $\dot{V}\text{O}_2$  and  $\text{EO}_2$  and  $\dot{V}\text{O}_2$  were not significant. Modulation of  $f$  accounted for most of the change in  $\dot{V}_i$  between MMR and  $\dot{V}\text{O}_{2\text{max}}$  (Fig. 2). The maximum  $f$  was  $184 \text{ breaths} \cdot \text{min}^{-1}$ .

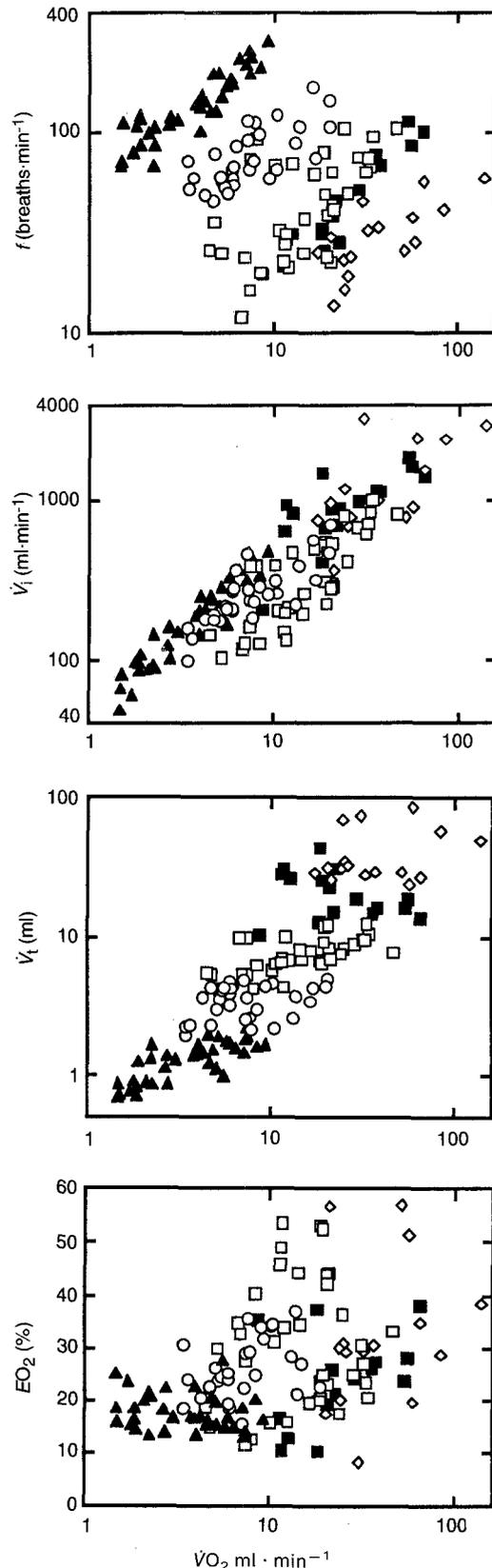
In *S. beecheyi*,  $f$ ,  $V_t$ , and  $\dot{V}_i$  were positively and significantly correlated with  $\dot{V}\text{O}_2$  ( $F > 14$ ,  $n = 36$ ,  $P < 0.001$  in all cases), but the correlation between  $\dot{V}\text{O}_2$  and  $\text{EO}_2$  was not significant. The 5-fold change in  $\dot{V}_i$  between MMR and  $\dot{V}\text{O}_{2\text{max}}$  was largely due to modulation of  $f$ , with a much smaller adjustment of  $V_i$  (Fig. 2). Maximum  $f$  was  $125 \text{ breaths} \cdot \text{min}^{-1}$ .

In juvenile *M. flaviventris*,  $f$  and  $\dot{V}_i$  were positively and significantly correlated with  $\dot{V}\text{O}_2$  ( $F > 100$ ,  $n = 16$ ,  $P < 0.001$  in both cases). There was no significant correlation between  $\dot{V}\text{O}_2$  and either  $V_t$  or  $\text{EO}_2$ . Maximum  $f$  was  $119 \text{ breaths} \cdot \text{min}^{-1}$ .

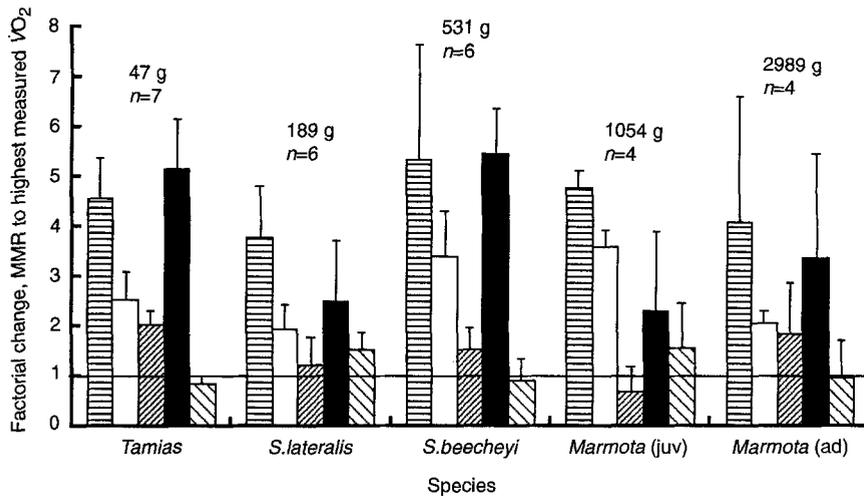
In adult *M. flaviventris*,  $f$  and  $V_i$  were positively and significantly correlated with  $\dot{V}\text{O}_2$  ( $F > 16$ ,  $n = 16$ ,  $P < 0.001$  in both cases). There was no significant correlation between  $\dot{V}\text{O}_2$  and either  $V_t$  or  $\text{EO}_2$ . Maximum  $f$  was  $64 \text{ breaths} \cdot \text{min}^{-1}$ .

Covariance procedures (SAS General Linear Models) were used to estimate the effects of species and  $\dot{V}\text{O}_2$  on ventilatory parameters. These analyses demonstrated highly significant species differences in  $f$ ,  $V_t$ ,  $\dot{V}_i$ , and  $\text{EO}_2$  ( $F_{5,128} > 8.5$ ,  $P < 0.001$  in all cases). Exclusive of species effects,  $\dot{V}\text{O}_2$  significantly affected  $f$  ( $F = 21.3$ ,  $P < 0.001$ ) and  $\dot{V}_i$  ( $F = 116$ ,  $P < 0.001$ ), but not  $V_t$  ( $F = 2.27$ ,  $P = 0.13$ ) or  $\text{EO}_2$  ( $F = 1.05$ ,  $P = 0.306$ ).

To test for interspecific differences in ventilatory accommodation without the confounding effects of different aerobic scope, regression-based predictions of factorial changes in ventilation were compared across a standardized 3.8-fold change in  $\dot{V}\text{O}_2$  (equal to the smallest measured aerobic scope, that of *S. lateralis*). This was



**Fig. 1.** Relationship between ventilatory parameters ( $f$ ,  $V_t$ ,  $\dot{V}_i$ , and  $\text{EO}_2$ ) and  $\text{O}_2$  consumption ( $\dot{V}\text{O}_2$ ) in *Tamias minimus* ( $\blacktriangle$ ), *Spermophilus lateralis* ( $\circ$ ), *S. beecheyi* ( $\square$ ), juvenile *Marmota flaviventris* ( $\blacksquare$ ), and adult *M. flaviventris* ( $\diamond$ ). Each point is the mean value for one combination of ambient temperature and respiratory gas. Note that all plots are log-log except for  $\text{EO}_2$  which is semi-log. For all species, the highest  $\dot{V}\text{O}_2$  were attained in heliox (see text and Tables 1–4)



**Fig. 2.** Mean factorial change in ventilatory parameters between MMR and  $\dot{V}O_{2\max}$ . Factorial changes were computed by dividing each parameter by its MMR value (see text). Symbols:  $\square$  Oxygen Consumption,  $\square$  Frequency,  $\square$  Tidal Volume,  $\blacksquare$  Minute Volume,  $\square$  Oxygen Extraction. Error bars show 1 SD

accomplished for all individuals by regressing each ventilation parameter against  $\dot{V}O_2$  and calculating ventilation at a  $\dot{V}O_2$  of  $3.8 \cdot \text{MMR}$  from the regression equation. Factorial changes between MMR and  $3.8 \cdot \text{MMR}$  were computed by dividing by MMR values (Fig. 4) and compared among species (ANOVA). There was no significant difference for  $V_i$  or  $\dot{V}_i$  ( $P=0.22$  and  $P=0.17$ , respectively), probably because of high within-species variance of  $V_i$ . Significant  $V_i$  changes between MMR and  $\dot{V}O_{2\max}$  for *T. minimus* and *S. beecheyi* became insignificant across the smaller 3.8-fold range of  $\dot{V}O_2$ . There was a significant interspecific difference in  $f$  ( $F_{4,22}=0.2$ ;  $P=0.011$ ) and a marginally significant difference in  $EO_2$  ( $F_{4,22}=3.17$ ;  $P=0.034$ ). The predicted change in  $f$  was approximately 2- to 3-fold in all species. The predicted change in  $EO_2$  was minimal in *T. minimus* and *S. beecheyi*, while *S. lateralis* and *M. flaviventris* had predicted  $EO_2$  changes of 1.4-to 1.8-fold.

## Discussion

### Effects of gas mixture and altitude

Use of both air and heliox introduces a potential complication: the gas mixture might have an influence on ventilation or extraction independent of its effects on heat loss and  $\dot{V}O_2$ . However, other studies (Brice and Welch 1983; DeWeese et al. 1983; M.A. Chappell and T.J. Dawson, unpublished data) revealed few significant effects of gas mixture on ventilation other than those attributable to different  $\dot{V}O_2$  (i.e., at equal  $\dot{V}O_2$ , ventilation in air was similar to ventilation in heliox). Although the sciurids were not tested at equal  $\dot{V}O_2$  in air and heliox, there were no abrupt changes in ventilation patterns associated with the shift between gas mixtures (Fig. 1, 3).

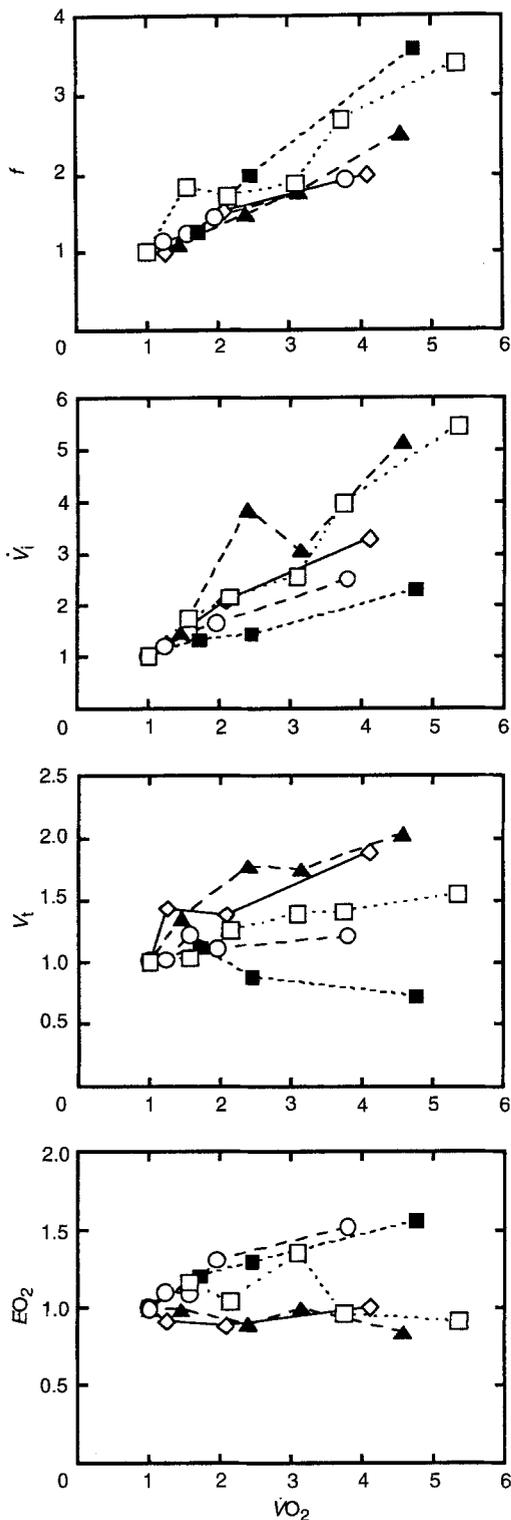
The barometric pressure in metabolism chambers at RMBL was about 25% lower than at UCR (555 and 740 torr, respectively). Hence, inspired  $PO_2$  was higher for *S. beecheyi* than for the other species, which could affect ventilation parameters and  $\dot{V}O_{2\max}$ . Without measurements on each species at different altitudes it is difficult to assess the importance of altitudinal effects, but two studies of deer mice (*Peromyscus maniculatus*) are

relevant. First, Chappell (1985) reported that captive-reared mice acclimatized to 340 and 3800 m compensated for the 36% pressure difference largely by proportional adjustments in  $f$  and  $\dot{V}_i$ . The second study (Hayes 1989a) demonstrated that the  $\dot{V}O_{2\max}$  of wild-caught mice tested within 24 h of capture did not differ between 340 and 3800 m as long as both populations were experiencing similar environmental temperatures when tested. Hence, the altitudinal difference between UCR and RMBL should not influence  $\dot{V}O_{2\max}$  (exclusive of any temperature differences between the sites) but might affect the relationship between ventilation and  $\dot{V}O_2$ . Studies of captive animals at a single altitude could control for altitude effects but would introduce the complications of acclimatization to captivity and to non-native altitudes, both of which affect aerobic scope (Chappell 1985; Hayes 1989b). Since the purpose of the present study was to examine ventilatory accommodation across a "natural" aerobic scope, it seemed most appropriate to perform measurements on freshly-captured individuals at the species' native altitudes.

Did the lower altitude experienced by *S. beecheyi* affect its ventilation patterns compared to those of the high-altitude species? Data in Fig. 1 and results from covariance analysis suggest that *S. beecheyi* has a somewhat lower air convection requirement ( $\dot{V}_i/\dot{V}O_2$ ) than the other species when  $\dot{V}_i$  is measured in BTPS units. However, considerable overlap exists, and there is no indication that *S. beecheyi* has an unusually high or low  $EO_2$ . Similarly, patterns of accommodation for *S. beecheyi* (Figs. 2, 3, 4) overlap with those of the other species.

### Metabolism and aerobic scope

The MMR values obtained may not actually represent BMR, since time constraints and other considerations precluded the long-duration measurements required for rigorous assessment of BMR. Also, measurements were restricted to the active phases of the four species' circadian cycles. Knowledge of BMR is not crucial for assessing ventilatory accommodation but is needed to accurately determine aerobic scope. Willems and Armitage (1975) and Heller and Gates (1971) reported BMRs for *T. minimus* of 0.021 and 0.027 ml  $O_2 \cdot g^{-1} \cdot$



**Fig. 3.** Factorial changes in ventilatory parameters ( $f$ ,  $V_t$ ,  $\dot{V}_i$ , and  $EO_2$ ) as a function of factorial changes in  $O_2$  consumption ( $\dot{V}O_2$ ) in *Tamias minimus* (▲), *Spermophilus lateralis* (○), *S. beecheyi* (□), juvenile *Marmota flaviventris* (■), and adult *M. flaviventris* (◇). Factorial changes were computed by dividing each parameter by its MMR value (see text). Each point is the mean value for each species at one combination of ambient temperature and respiratory gas. For all species, the highest  $\dot{V}O_2$  were attained in heliox (see text and Tables 1–4)

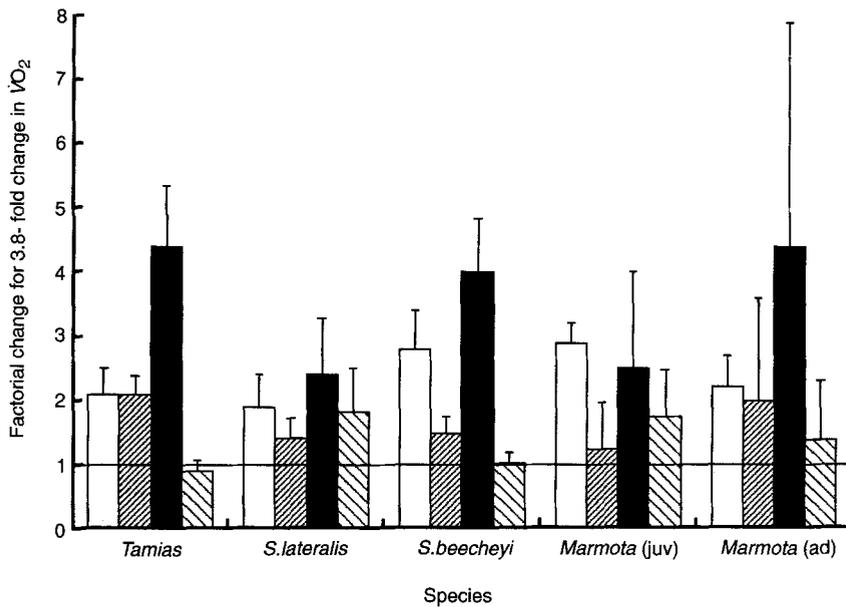
$\text{min}^{-1}$ , respectively, or about 32–41% lower than the MMR measured in this study (Table 1). For *S. lateralis*, Heller et al. (1974) obtained a BMR of  $0.022 \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{min}^{-1}$ , or about 96% of MMR in the present study (Table 2). Baudinette (1972) reported BMR of  $0.009 \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{min}^{-1}$  in *S. beecheyi*, about 27% lower than MMR in the present study (Table 3). Armitage et al. (1990) measured a BMR of  $0.0059 \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{min}^{-1}$  in adult *M. flaviventris*, or about 21% lower than the MMR in this study (Table 4). In the absence of published values of BMR for juvenile marmots, it is assumed that MMR values for juveniles in this study are also 21% higher than actual BMR.

Using mean BMR values from the literature, calculated aerobic scopes are 7.1 in *T. minimus*, 4.0 in *S. lateralis*, 6.8 in *S. beecheyi*, and 5.8 in juvenile *M. flaviventris*. The aerobic scope of adult *M. flaviventris* ( $\dot{V}O_{2\text{max}}$  not measured) exceeds 4.9. Thus, all four sciurid species have thermogenic aerobic scopes consistent with the range 4–7 typical for small placentals (Wunder 1970; Bartholomew 1982; Dawson and Dawson 1982).  $\dot{V}O_{2\text{max}}$  for *S. lateralis* is only 53% of the  $\dot{V}O_{2\text{max}}$  elicited by treadmill exercise in the closely related (perhaps conspecific) *S. saturatus* (Hoyt and Kenagy 1988). The higher  $\dot{V}O_{2\text{max}}$  for *S. saturatus* might be due to interspecific differences, altitudinal effects [Hoyt and Kenagy (1988) made their measurements near sea level], exercise conditioning, or the use of exercise instead of cold exposure. Exercise  $\dot{V}O_{2\text{max}}$  is often reported to be higher than thermogenic  $\dot{V}O_{2\text{max}}$  (Seeherman et al. 1981), although the reverse may be true after cold acclimation (Hayes and Chappell 1986).

#### Ventilatory accommodation of changing $\dot{V}O_2$

Qualitatively, the four species had roughly similar overall ventilatory responses to changing  $\dot{V}O_2$ : increasing  $\dot{V}O_2$  at low  $T_a$  was accommodated largely by increasing  $\dot{V}_i$ , with smaller and usually insignificant changes in  $EO_2$  (Figs. 2, 4). Dependence of  $\dot{V}_i$  on  $f$  and  $V_t$  varied considerably, but with no obvious pattern with respect to body mass (Figs. 2, 4). The species in which  $V_t$  varied most were the smallest (*T. minimus*) and the largest (adult *M. flaviventris*). Adult and juvenile marmots had contrasting patterns, with juveniles showing relatively little change in  $V_t$ .

How does ventilation in sciurids compare with that of other mammals? Minimal resting values (i.e., at thermoneutral  $T_a$ ) are compared to a generalized allometry for resting placentals (Stahl 1967) in Table 5. The sciurids have consistently lower  $f$  (by 1.26- to 2.86-fold) and higher  $EO_2$  (by 1.3- to 2.3-fold) than predicted values. The differences may derive from measurement technique. Ventilation data for the sciurids were measured from unrestrained animals, while many of the data used by Stahl (1967) were obtained from restrained animals. Studies by Bucher (1981, 1985) have clearly shown that restraint or other disturbance greatly increases  $f$  and decreases  $EO_2$  in birds, and it is likely that similar responses occur in mammals.



**Fig. 4.** Factorial change in ventilatory parameters predicted for a 3.8-fold change in oxygen consumption (MMR to 3.8 times MMR). Factorial changes for the different variables were computed from regressions for each individual (see text). □ Frequency, ▨ Tidal Volume, ■ Minute Volume, ▩ Oxygen Extraction. Error bars show 1 SD

**Table 5.** Comparison of observed minimal metabolic rates (MMR) and associated ventilatory parameters (means for 4–7 individuals) for *Tamias minimus*, *Spermophilus lateralis*, *S. beecheyi*, and adult

and juvenile *Marmota flaviventris* with allometric predictions of resting values for placental mammals (from Stahl 1967)

Species	MMR (ml O <sub>2</sub> · min <sup>-1</sup> )	V <sub>t</sub> (ml)	f (breaths · min <sup>-1</sup> )	V <sub>i</sub> (ml · min <sup>-1</sup> )	EO <sub>2</sub> (%)
<i>T. minimus</i>	1.65	0.517	93.0	50.1	19.0
47 g, predicted	1.14	0.320	118	37.8	14.4
observed/predicted	1.45	1.62	0.79	1.33	1.32
<i>S. lateralis</i>	4.38	1.90	28.9	106	22.1
189 g, predicted	3.27	1.36	82.5	112	13.9
observed/predicted	1.34	1.40	0.35	0.95	1.59
<i>S. beecheyi</i>	6.05	3.69	24.0	112	28.7
531 g, predicted	7.17	3.98	63.1	251	13.6
observed/predicted	0.84	0.93	0.38	0.44	2.11
<i>M. flaviventris</i> (juv)	11.1	14.7	25.7	396	18.9
1054 g, predicted	12.1	8.12	52.8	429	13.5
observed/predicted	0.91	1.81	0.49	0.92	1.4
<i>M. flaviventris</i> (ad)	21.3	18.2	23.0	427	23.8
2989 g, predicted	26.7	24.0	40.2	965	13.2
observed/predicted	0.80	0.76	0.57	0.44	1.80

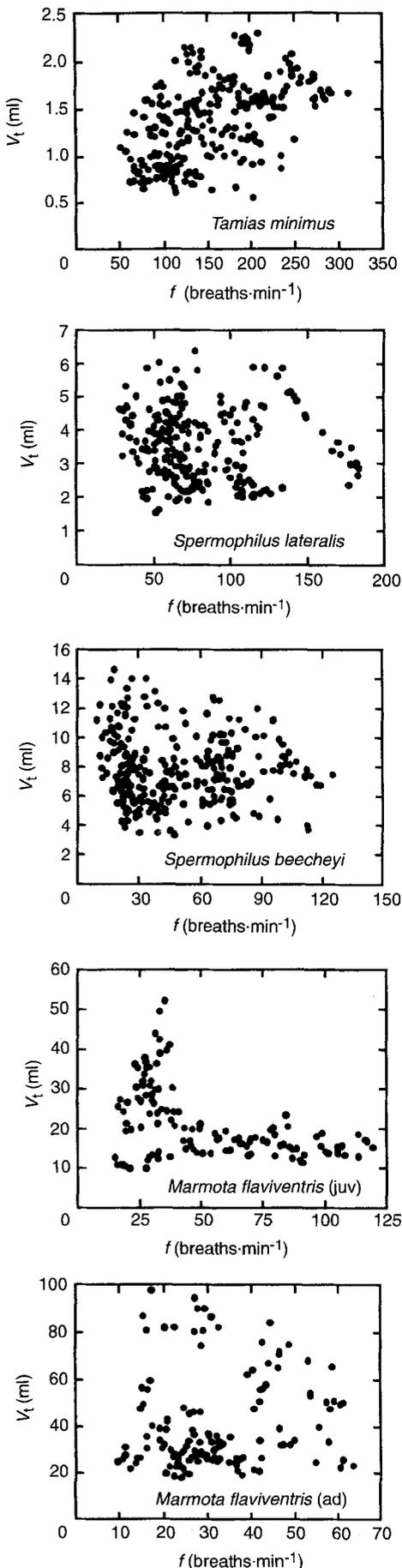
All data are computed for STPD conditions.

Note: the predicted V<sub>i</sub> is computed as f · V<sub>t</sub>, not directly from Stahl's allometric equations. Predicted EO<sub>2</sub> is computed as 100 · MMR / (0.2095 · V<sub>i</sub>)

In addition to their higher than predicted EO<sub>2</sub> at MMR, most of the sciurids attained surprisingly high EO<sub>2</sub> at intermediate and high V̇O<sub>2</sub>. Mammalian EO<sub>2</sub>s are typically 15–25% (Stahl 1967; Withers et al. 1979; Chappell 1985), but EO<sub>2</sub> species means at different T<sub>a</sub> regularly approached or exceeded 30% in *S. lateralis*, *S. beecheyi*, and *M. flaviventris* (Tables 2–4). Individual means for the latter two species occasionally reached 50–55% (Fig. 1), only slightly less than the highest EO<sub>2</sub>s reported from birds (Brent et al. 1984; Stahel and Nicol 1988; Bucher and Chappell 1989). These observations suggest that the mammalian alveolar lung with tidal flow can exchange gas nearly as efficiently as the avian parabronchial lung with unidirectional flow (Piiper and Scheid 1977).

In several small dasyurid marsupials [5.4–144 g; M.A. Chappell and T.J. Dawson, unpublished data; Hallam (1991)], EO<sub>2</sub> increases with increasing body mass. No indication of a similar mass effect on EO<sub>2</sub> in sciurids was found, either for MMR or at elevated V̇O<sub>2</sub> (Tables 1–4). Comparable data from very small (ca. 5 g) placentals are lacking, but the resting EO<sub>2</sub> of little pocket mice [*Perognathus longimembris*, 10 g; Withers (1977)] and deer mice [*Peromyscus maniculatus*, 18.5 g; Chappell (1985)] is 16–22%, similar to that of *T. minimus*, *S. lateralis*, and juvenile *M. flaviventris*.

It is more difficult to compare patterns of ventilatory accommodation between sciurids and other mammals, since few comparable ventilation measurements across a large range of V̇O<sub>2</sub> are available. Most data from large



mammals were obtained during exercise, while most data from small mammals were obtained via cold exposure. Generally, sciurid accommodation resembles that reported for other small mammals including little pocket mice, deer mice, tundra voles [*Microtus oeconomus*, 32 g, Casey et al. (1979)], collared lemmings [*Dicrostonyx groenlandicus*, 47 g, Casey et al. (1979)], brown lemmings [*Lemmus trimucronatus*, 64 g; Casey et al. (1979)], least weasels [*Mustela rixosa*, 75 g; Casey et al. (1979)], and the bats *Pteropus gouldii* and *Phyllostomus hastatus* [870 and 110 g; Thomas et al. (1984)]. Correlations between  $\dot{V}O_2$  and  $EO_2$  are generally insignificant or negative in sciurids and small non-sciurids (Withers et al. 1979). An exception is the lesser bulldog bat, *Noctilio albiventris* (40 g), which supports a large thermogenic aerobic scope ( $> 7$ ) by substantial and roughly equivalent changes in  $f$ ,  $V_t$ , and  $EO_2$  (Chappell and Roverud 1990).

Like that of small mammals, accommodation in humans (70 kg) results mainly from changes in  $\dot{V}_i$  (Levine 1978; Cerretelli and di Prampero 1986), with relatively constant  $EO_2$ . In contrast, horses [476 kg; Thomas and Fregin (1981)], young pigs [23 kg; Ingram and Legge (1969)] and sheep (Joyce and Blaxter 1964) substantially increase  $EO_2$  at elevated  $\dot{V}O_2$ . The role of  $EO_2$  in accommodation in dogs (20–24 kg) is uncertain; it has been reported to be stable (Flandrois et al. 1971) or to change considerably (Wagner et al. 1977). Unlike many small mammals, humans, pigs, and normothermic (i.e., non-panting) dogs adjust  $V_i$  primarily by changing  $V_t$ , with proportionally smaller changes in  $f$ .

To summarize, changes in  $f$  always have an important role in accommodation, modulation of  $V_t$  shows considerable interspecific variation but is generally more important in large species, and adjustment of  $EO_2$  is usually minor but in some species may be nearly as important in accommodation as  $f$ . Body mass strongly influences the magnitude of  $f$ ,  $V_t$ , and  $\dot{V}_i$ , but it apparently does not consistently affect the magnitude of  $EO_2$  (at least in placentals larger than 15–20 g). The role of  $EO_2$  in accommodation shows no obvious relationship to mass. Together with the high variance typical of ventilation parameters (Fig. 1), these observations emphasize the large degree of plasticity inherent in ventilatory accommodation. High variance (within and between individuals as well as among species) indicates that a variety of accommodation patterns may be equally effective in supporting changing  $\dot{V}O_2$ .

#### Limits to ventilation and $\dot{V}O_2$

The factors that determine maximal  $\dot{V}O_2$  are controversial but are probably related to  $O_2$  transport capability (Weibel and Taylor 1981). Limitations to  $O_2$  transport are often assumed to result from constraints on pulmonary diffusion capacity, cardiovascular transport, or diffusion from capillaries to mitochondria (Weibel 1984).

Fig. 5. Relationship between respiratory frequency and tidal volume. Each point represents a single ventilation measurement

Ventilation is also a potential limiting factor. For example, the contractile characteristics of ventilatory muscles limit  $f$ , lung dimensions set an upper limit to  $V_t$ , and mechanical constraints would be expected to reduce the  $V_t$  attainable at high  $f$ . Data from the present study provides little indication that any sciurid ventilation parameter approaches an upper limit at  $\dot{V}O_{2\max}$ . Frequency (the parameter playing the largest and most consistent role in accommodation in sciurids) increased linearly with increasing  $\dot{V}O_2$  with no evidence of a plateau at high  $\dot{V}O_2$  (Figs. 1, 3).  $V_t$  generally increased slightly or remained stable with increasing  $\dot{V}O_2$ ; only in juvenile marmots did it decline somewhat at high  $\dot{V}O_2$  (Fig. 3). Plots of  $V_t$  as a function of  $f$  (Fig. 5) do suggest that the highest  $V_t$  were not attained at high  $f$ . However, there was no indication of a plateau in  $\dot{V}_i$  or a sudden increase in  $EO_2$  at  $\dot{V}O_{2\max}$ , suggesting that ventilation was not a limiting factor in these species.

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