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Effects of ambient temperature and altitude on ventilation and gas exchange in deer mice (*Peromyscus maniculatus*)

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Summary. The effects of different ambient temperatures (T_a) on gas exchange and ventilation in deer mice (*Peromyscus maniculatus*) were determined after acclimation to low and high altitude (340 and 3,800 m).

At both low and high altitude, oxygen consumption ($\dot{V}_{O_2}$) decreased with increasing T_a at T_a from −10 to 30 °C. The $\dot{V}_{O_2}$ was 15–20% smaller at high altitude than at low altitude at T_a below 30 °C.

Increased $\dot{V}_{O_2}$ at T_a below thermoneutrality was supported by increased minute volume ($\dot{V}$I) at both low and high altitude. At most T_a, the change in $\dot{V}$I was primarily a function of changing respiration frequency (f); relatively little change occurred in tidal volume (VT) or oxygen extraction efficiency (O_2EE). At $T_a = 0$ °C and below at high altitude, $\dot{V}$I was constant due to declining VT and O_2EE increased in order to maintain high $\dot{V}_{O_2}$.

At high altitude, $\dot{V}$I (BTP) was 30–40% higher at a given T_a than at low altitude, except at T_a below 10 °C. The increased $\dot{V}$I at high altitude was due primarily to a proportional increase in f, which attained mean values of 450–500 breaths/min at T_a below 0 °C. The $\dot{V}$I (STP) was equivalent at high and low altitude at T_a of 10 °C and above. At lower T_a, $\dot{V}$I (STPD) was larger at low altitude.

At both altitudes, respiratory heat loss was a small fraction (<10%) of metabolic heat production, except at high T_a (20–30 °C).

Abbreviations: *EHL* evaporative heat loss; f respiration frequency; HL_a heat loss from warming tidal air; HL_e evaporative heat loss in tidal air; HL_r total respiratory heat loss; *MHP* metabolic heat production; *O_2EE* oxygen extraction efficiency; *RQ* respiratory quotient; T_a ambient temperature; T_b body temperature T_{lc} lower critical temperature; $\dot{V}_{CO_2}$ carbon dioxide production; $\dot{m}_{H_2O}$ evaporative water loss; $\dot{V}_{O_2}$ oxygen consumption; $\dot{V}$I minute volume; VT tidal volume

Introduction

At low ambient temperatures (T_a), most small mammals maintain relatively constant body temperature by means of elevated metabolic heat production supported by concomitant increases in the rate of oxygen consumption ($\dot{V}_{O_2}$). Increases in $\dot{V}_{O_2}$ may be accommodated through augmented lung ventilation and/or increased oxygen extraction efficiency (O_2EE). In turn, lung ventilation (minute volume, $\dot{V}$I) may be elevated via increased tidal volume ($\dot{V}$I) and/or increased respiration frequency (f). Considerable data exist on the relationship between T_a and f in mammals (e.g., Hargrove and Gessaman 1973), but less information is available on the relationships between $\dot{V}_{O_2}$, $\dot{V}$I, and O_2EE, particularly for small mammals exposed to a range of T_a (Casey et al. 1979; Withers et al. 1979). Few consistent patterns are apparent from the data that do exist: some species depend primarily on increases in $\dot{V}$T to augment $\dot{V}$I when $\dot{V}_{O_2}$ increases at low T_a, while others adjust f. Oxygen extraction also shows considerable variation, both at different T_a and interspecifically.

Within a species, the functional ranges of f, $\dot{V}$T, and O_2EE are constrained by biochemical, morphological, and/or mechanical considerations. Presumably, some of these limits may be approached when $\dot{V}_{O_2}$ is near maximum during severe cold stress. High altitudes also challenge the respiratory system, because low atmospheric pressure reduces oxygen availability. Ventilatory changes between low and high altitude have been described for man and a few other species, but little is known about the combined effects of cold exposure and high altitude on respiration in small mammals. This report describes patterns of respiratory gas exchange and ventilation in deer mice (*Peromyscus*

maniculatus) exposed to a range of ambient temperatures at both high and low altitude.

Deer mice are particularly appropriate subjects for such a study. This species inhabits the widest altitudinal range of any native North American mammal, occurring from sea level in coastal areas to above 4,000 m in the Sierra Nevada and Rocky Mountains. At 4,000 m the barometric pressure is only 60% of the sea-level value, and the resulting hypoxia severely limits aerobic metabolism (Chappell and Snyder 1984). Cold exposure is also an important factor in *Peromyscus* ecology. In winter these mice apparently do not hibernate for long periods and may be active above ground in very cold weather. Even in summer the nighttime temperatures experienced by montane populations of deer mice often drop below 0 °C.

Materials and methods

Animals. Deer mice were housed in unisexual groups of 3–5 in 30 × 18 × 12 cm plastic cages containing sawdust and cotton bedding. The animals were provided with laboratory mouse chow and water ad libitum, supplemented occasionally with fresh fruit or vegetables. The mice (subspecies *sonoriensis*) were obtained from populations in eastern California. Some individuals were wild-caught at altitudes of 3,150 m and 3,800 m; the rest were from laboratory lines derived from and periodically outbred to wild-caught stock collected at altitudes of 2,000–4,000 m but born and reared at 340 m. All animals were adults (mean body mass was approximately 18.5 g).

Most of the individuals were used at both low and high altitudes. During low-altitude studies, mice were housed in a 22 °C room at the University of California, Riverside (elevation 340 m). The animal room was kept on photoperiods approximately matched to the prevailing natural light-dark cycle. All laboratory lines were bred and maintained in Riverside. High-altitude work was performed at the Barcroft Laboratory of the University of California's White Mountain Research Station (elevation 3,800 m). At Barcroft, mice were kept in an unheated room (~17 °C) exposed to prevailing photoperiods through windows. Animals were acclimated to each test altitude for at least three months before experiments began.

Measurements. Metabolic measurements were performed in an aluminum and plexiglas respirometry chamber (internal volume ~800 ml). The respirometer was placed in a large environmental chamber which controlled temperature within 0.5 °C. The T_a in the respirometer was measured with thermocouples. During runs, the mice were unrestrained and stood on a screen-wire platform over a layer of mineral oil which covered voided urine and feces. Animals were kept in the apparatus for a maximum of 4 h at at time; each individual required several runs to obtain data at all T_a. Body temperatures (T_b) were obtained after runs by quickly removing mice from the chamber and taking readings with rectal thermocouples. All T_b readings were obtained within 30 sec (usually <15 s) after opening the chamber. The respirometry data were rejected if animals became hypothermic (T_b <34 °C).

Oxygen consumption ($\dot{V}_{O_2}$), carbon dioxide production ($\dot{V}_{CO_2}$), and evaporative water loss ($\dot{m}_{H_2O}$) were determined in an open-circuit flow system. Flow rates (800–1,200 ml/min STPD) of dry, CO_2-free air were maintained (plus or minus 1%) with Applied Materials mass flow controllers. Approximately 100 ml/min of excurrent air from the chamber was diverted through a humidity sensor (Weather Measure HT-100), dried, passed through a CO_2 sensor (Applied Electrochemistry CD-3A), passed through CO_2 absorbent, dried again, and passed through an O_2 sensor (Applied Electrochemistry S-3A). The humidity probe resolved 0.1 % R.H. and was calibrated over salt solutions to within 0.5% of actual R.H.. The CO_2 and O_2 analyzers could resolve concentrations of 0.01% and 0.001%, respectively. During experiments, the CO_2 and O_2 sensors were periodically referenced against air diverted from upstream of the respirometer. The concentration of O_2 in the chamber never fell below 20.4%, CO_2 concentration never exceeded 0.5%, and chamber relative humidity never exceeded 50%.

The respirometry chamber also functioned as a whole-body plethysmograph as described by Withers (1977a, b) and Bucher (1981). Volume changes caused by the warming and wetting of tidal air were measured with a volumetric pressure transducer (Grass PT5) connected to a Grass polygraph. Measurable signals in the open-circuit system were obtained by inserting high resistance valves upstream and downstream of the respirometer. The resulting pressure increase in the chamber amounted to 4–6 Torr over ambient pressure (measured with a manometer), and the chamber pressures experienced by the mice were approximately 745 Torr at 340 m and 485 Torr at 3,800 m. The system as a whole was calibrated by injecting known volumes of air into the respirometer before and after each ventilation measurement at each T_a. Injection rates were adjusted so that the slopes of polygraph signals for calibration and animal ventilation were similar (Malan 1973; Bucher 1981). Volume change during inspiration was calculated by comparing the magnitude of deflections on the polygraph record during ventilation with those obtained from calibration injections. Ventilation measurements were taken after animals had been held at one temperature for at least 45 min, and $\dot{V}_{O_2}$ (which was measured simultaneously) had been stable for at least 10 min.

Tidal volume was determined by comparing the observed volume change during inspiration to the expected proportional change due to (a) the volume change of dry air due to the difference between ambient and lung temperature, and (b) the change in water vapor volume between the air in the chamber and 100% saturation at lung temperature (Malan 1973). The air temperature in the lungs was assumed to equal T_b. The computer program that performed these calculations took into account the ambient humidity and CO_2 concentration, and the volume change due to respiratory exchange ratios (RQ) of less than 1.0. Unless otherwise stated, V_T and $\dot{V}_I$ were computed for ambient pressure and the prevailing body temperature. Oxygen extraction efficiency was calculated from $\dot{V}_I$ and $\dot{V}_{O_2}$ (ml/min) as $O_2EE = [\dot{V}_{O_2}/0.2095\ \dot{V}_I)] \times 100$. A minimum of ten individuals (usually 12–15) were tested at each combination of altitude and air temperature.

Measurement accuracy and statistical tests. The maximum cumulative error in gas exchange calculations, due to resolution limits and calibration errors of sensors and inaccuracies of the flow controllers, was about 3% for $\dot{V}_{O_2}$ and 5–6% for $\dot{V}_{CO_2}$ and $\dot{m}_{H_2O}$. Water loss measurements at temperatures below 0 °C may have been underestimated because of the freezing of water vapor on the chamber walls ($\dot{m}_{H_2O}$ measurements were discarded if significant frost formation was noted during a run). According to Malan (1973) and Epstein and Epstein (1978), the barometric technique used for determining tidal volume should be accurate to within 10–15% at T_a's near 30 °C. At lower T_a accuracy should increase, since the temperature change

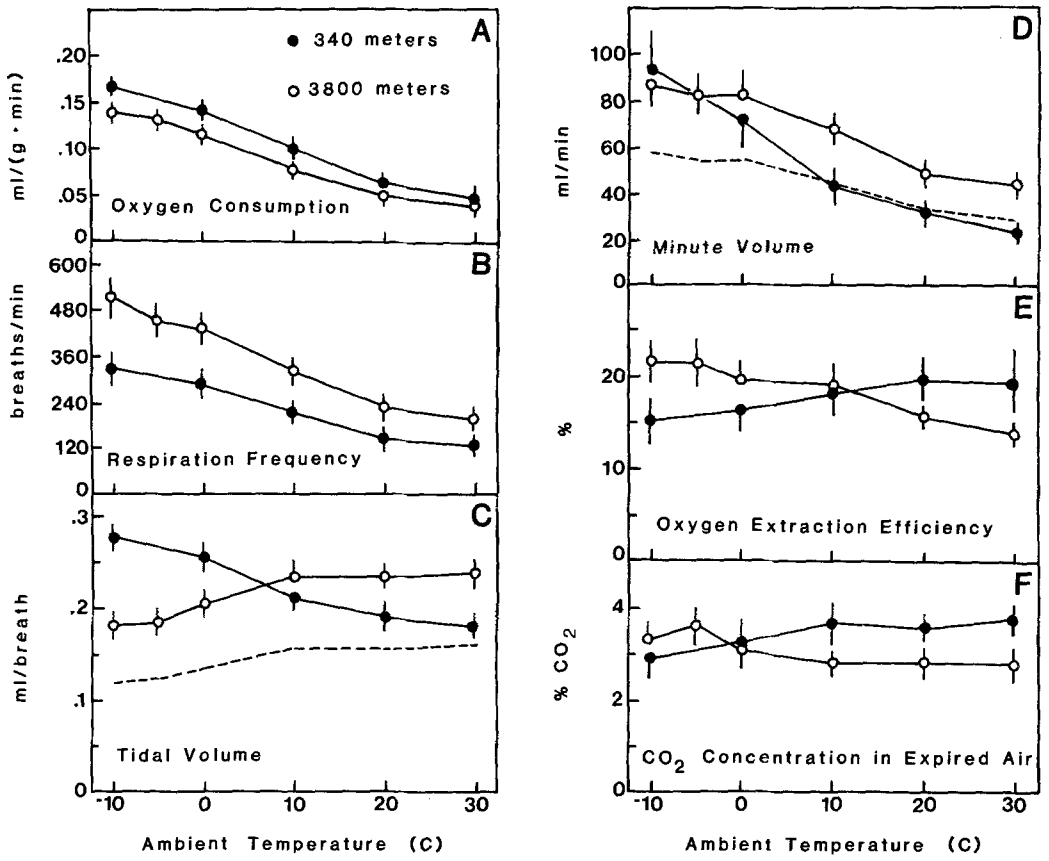

Fig. 1A–F. Respiratory parameters of deer mice at low and high altitude, expressed as a function of ambient temperature. Vertical lines indicate two SE above and below the mean. Oxygen consumption is expressed as ml/[g·min] STP. All other volumes are BTPS except dashed lines in **C** and **D**, which represent the 3,800 m data corrected to the barometric pressure at 340 m

of inspired air is larger and errors in estimating lung temperature are proportionally less important.

Most of the data analysis involved least-squares and multiple regression and one- and two-way ANOVA. Differences were assumed significant at $P<0.05$. For two-way ANOVAs involving both ambient temperature and altitude, the 5 °C data taken at 3,800 m were not included, since no low-altitude measurements were made at that T_a.

Results

No significant differences were observed in metabolic or ventilatory responses between wild-caught and lab-reared animals at either low or high altitude. Accordingly, data from all mice were combined for analysis at each combination of temperature and altitude.

Average body temperatures (39 °C at T_a= 30 °C, 37.5 °C at T_a=20 °C, 36 °C at T_a=10 °C, and 35 °C at T_a below 10 °C; S.E. about 0.4 °C at all T_a) were similar to those reported elsewhere (Hill 1983; Chappell and Holsclaw 1984). No significant altitudinal differences were observed in the relationship between T_b and T_a, except that at −10 °C a higher proportion of animals became hypothermic at high altitude than at low altitude (6 of 14 runs at 3,800 m; 3 of 12 runs at 340 m).

Oxygen consumption, carbon dioxide production, and water loss

At both low and high altitude, $\dot{V}_{O_2}$ was lowest at 30 °C and increased with decreasing T_a (Fig. 1A). That observation is consistent with other studies (Chappell and Holsclaw 1984), which report a lower critical temperature (T_{lc}) for *P. maniculatus* of about 25 °C in the absence of forced convection. At all T_a, the $\dot{V}_{O_2}$ was higher at 340 m than at 3,800 m; the differences were significant except at 30 °C. Assuming that 30 °C is within the thermal neutral zone, basal metabolic rate (BMR) averaged 0.041 ml/[g·min], or about 35% greater than predicted for an 18.5 g mammal (Stahl 1967). The highest $\dot{V}_{O_2}$, obtained at −10 °C (0.17 ml/[g·min] STP at 340 m and 0.14 ml/[g·min] STP at 3,800 m),

Table 1. Comparison of mean respiratory parameters of deer mice at thermoneutral T_a (30 °C) between low and high altitudes and with predicted values for 18.5 g mammals (Stahl 1967). Volumetric data are shown for ambient pressure (745 Torr at 340 m and 485 Torr at 3,800 m) and corrected to STP

	$\dot{V}_{O_2}$ (ml [g·min])	V_T (ml)	f (breaths/min)	$\dot{V}_I$ (ml/min)	O_2EE (%)
Predicted	0.0302	0.121	151	15.6	17.1
340 m: measured (BTPS)	–	0.183	122	22.2	19.4
corrected to STP	0.0434	0.157	–	19.2	–
3,800 m: measured (BTPS)	–	0.231	181	41.8	14.3
corrected to STP	0.0379	0.129	–	23.4	–
Ratio: 3,800 m/340 m (BTPS)	–	1.26	1.48	1.88	0.74
Ratio: 3,800 m/340 m (corrected to STP)	0.87	0.82	–	1.22	–

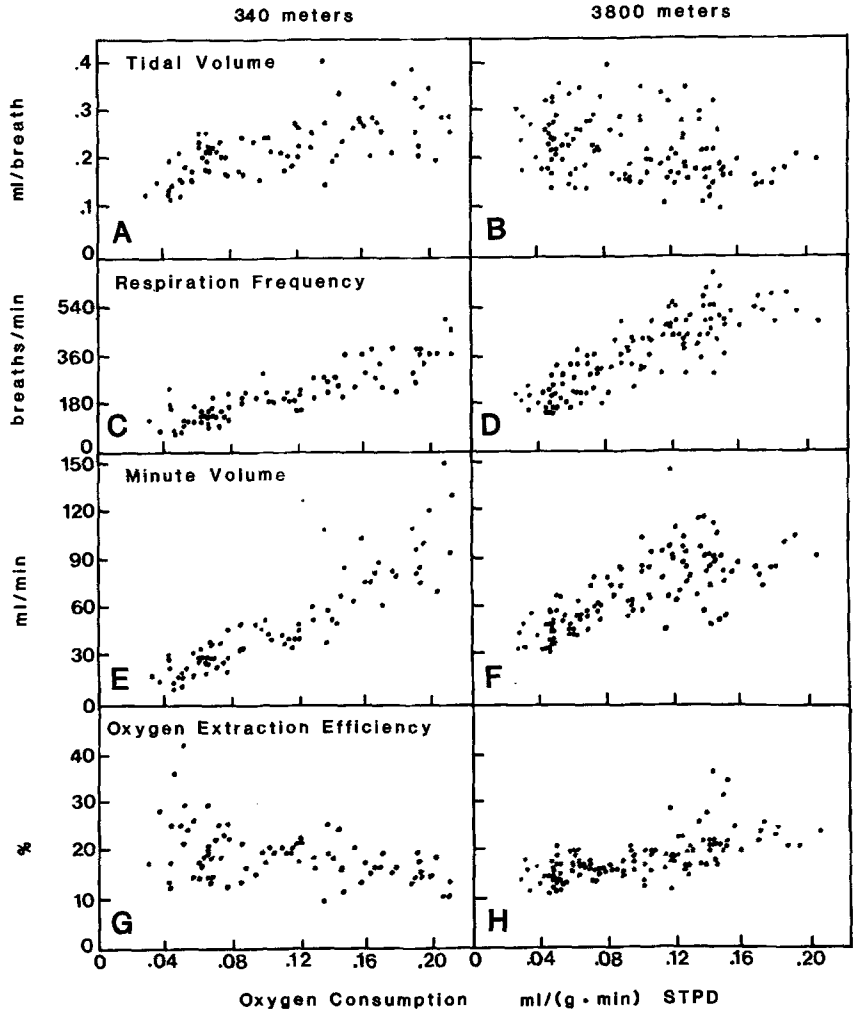

Fig. 2A–H. Respiratory parameters of deer mice at low and high altitude, plotted as a function of $\dot{V}_{O_2}$. The $\dot{V}_{O_2}$ is expressed at STP: all respiratory volumes BTPS

are approximately equivalent to the species' maximum oxygen consumption (Chappell 1984; Chappell and Snyder 1984).

Carbon dioxide production closely paralleled $\dot{V}_{O_2}$ at all combinations of temperature and altitude. Values of RQ averaged 0.7–0.8; occasionally a mouse would show an RQ of 0.9–1.0 for short periods at the start of a run. Water loss rates showed considerable variation, but usually were low at low T_a and increased with increasing T_a. The maximum observed $\dot{m}_{H_2O}$ was about 6–8 mg H_2O/[g·h] at 30 °C.

Respiratory parameters

Respiratory parameters are plotted as a function of T_a in Fig. 1, and as a function of $\dot{V}_{O_2}$ in Fig. 2. Tidal and minute volumes shown are calculated at BTPS and therefore indicate actual volumes in the respiratory tract. In order to facilitate comparison between altitudes, Figs. 1C and D also show the V_T and $\dot{V}_I$ data for 3800 m when corrected to the barometric pressure at 340 m (745 Torr).

Measured respiratory parameters at $T_a = 30$ °C (within the thermoneutral zone) are compared to predicted values for an 18.5 g mammal (Stahl 1967) in Table 1. At low altitudes, deer mice had greater V_T, lower f, and larger $\dot{V}_I$ than predicted; O_2EE was slightly higher than predicted. At high altitudes, V_T, f, and $\dot{V}_I$ were considerably greater than predicted, even after correction to STPD conditions. Oxygen extraction at high altitude was lower than either low-altitude measurements or predictions.

At T_a below T_{lc}, f increased linearly with decreasing T_a at both low and high altitude (Fig. 1B). Mean values of f were about 2.5-fold higher at −10 °C than at 30 °C at low altitude; the corresponding change was approximately 2.7-fold at high altitude. At all T_a, f was substantially (30–40%) higher at 3,800 m than at 340 m. The effects of both altitude and temperature were significant (D.F. = 1, $F = 69.8$, $P < 0.001$ for altitude; D.F. = 4, $F = 71.1$, $P < 0.001$ for temperature; D.F. = 4, $F = 3.16$, $P = 0.016$ for interaction; 2-way ANOVA). In contrast, there was relatively little modulation of V_T as T_a changed (Fig. 1C). Slight but significant decreases in V_T with declining T_a were observed at high altitude, while the reverse was true at low altitude.

Minute volume increased with decreasing T_a at both low and high altitude (D.F. = 1, $F = 20.6$, $P < 0.001$ for altitude; D.F. = 4, $F = 45.6$, $P < 0.001$ for temperature; D.F. = 4, $F = 3.79$, $P < 0.01$ for interaction; 2-way ANOVA). However, the factorial increase in $\dot{V}_I$ between 30 °C and −10 °C was 4.1× at low altitude compared to 2.2× at high altitude (Fig. 1D), and the slopes of least-squares regressions of $\dot{V}_I$ on T_a for low- and high-altitude data are significantly different ($P < 0.01$; analysis of covariance). At low altitude, O_2EE increased with increasing T_a; the opposite was true at high altitude (P for both altitude and temperature not significant, D.F. = 4, $F = 10.8$, $P < 0.001$ for interaction; 2-way ANOVA). The O_2EE at low T_a (−10 to 0 °C) was significantly higher at 3,800 m than at 340 m, while at high T_a (20 to 30 °C) the O_2EE was significantly higher at 340 m (1-way ANOVA). The concentration of CO_2 in expired air paralleled changes in O_2EE; significant differences between values for low and high altitude occurred only at high T_a.

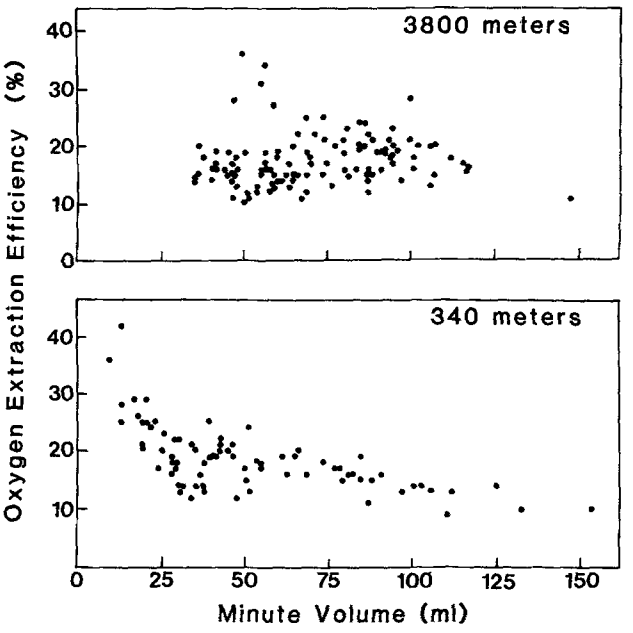

Fig. 3. Oxygen extraction plotted as a function of minute volume (BTPS) at low and high altitude

Since $\dot{V}_{O_2}$ was strongly correlated to T_a over the range of T_a used in this study (Fig. 1A), the relationships between $\dot{V}_{O_2}$ and the respiratory parameters (V_T, f, $\dot{V}_I$, and O_2EE; Fig. 2) were similar to the relationships observed between these variables and T_a. There was a slight increase in V_T with increasing $\dot{V}_{O_2}$ at low altitude, while at high altitude V_T decreased slightly with increasing $\dot{V}_{O_2}$; the slopes of these regressions are significantly different ($P < 0.01$; analysis of covariance). Both f and $\dot{V}_I$ were strongly and positively correlated to $\dot{V}_{O_2}$ at both low and high altitude (Fig. 2C, D, E, F). The slopes of regressions of f and $\dot{V}_I$ against $\dot{V}_{O_2}$ do not differ between high and low altitude, but at any $\dot{V}_{O_2}$ the values for both f and $\dot{V}_I$ at high altitude were usually 30–40% greater than at low altitude. Oxygen extraction declined as $\dot{V}_{O_2}$ increased at low altitude, but increased with increasing $\dot{V}_{O_2}$ at high altitude, and the slopes of the regressions are significantly different ($P < 0.01$; analysis of covariance). The relationship between ventilation and oxygen extraction is clarified if O_2EE is plotted as a function of $\dot{V}_I$ (Fig. 3). No interaction was apparent between $\dot{V}_I$ and O_2EE at high altitude, but at low altitude O_2EE increased substantially at low $\dot{V}_I$ and was lowest at high $\dot{V}_I$. However, it should be noted that minimum values of $\dot{V}_I$ at low altitude (where O_2EE was greatest)

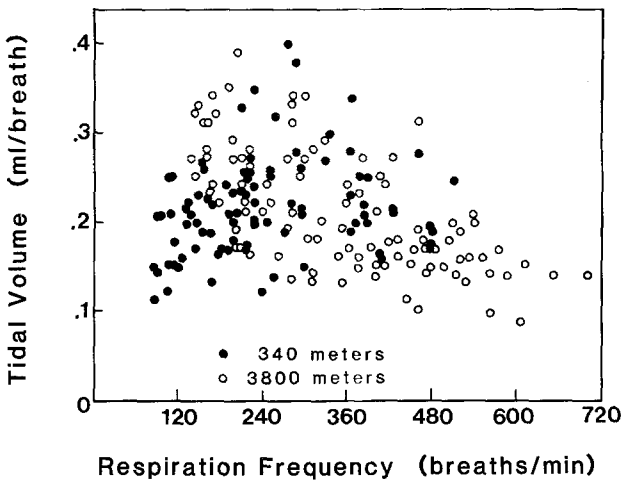

Fig. 4. Tidal volume (BTPS) as a function of respiration frequency at low and high altitude

were considerably smaller than at high altitude. Within the range of $\dot{V}_I$ common to both altitudes there was little difference in O_2EE.

Figure 4 shows V_T plotted against f. Considerable variability in V_T was apparent at low to moderate f. For example, at f's of 240–360 breaths/min, there was a 3–4-fold range of V_T at both low and high altitude. A decline in both the range and magnitude of V_T occurred at high f, such that at $f > 500$ breaths/min the maximum V_T was only half that observed at moderate f.

Discussion

Respiration at low T_a

The ventilatory responses of deer mice subjected to temperatures below T_{lc} were qualitatively similar at low and high altitudes. Cold-exposed animals accommodated increased oxygen demand primarily by increasing total ventilation ($\dot{V}_I$), although changes in O_2EE had some influence. A stepwise multiple regression incorporating V_T, f, and O_2EE accounted for 91.3% of the variation in $\dot{V}_{O_2}$ (ml[g·min]) at low altitude (partial r^2 values were 0.606 for V_T, 0.849 for f, and 0.423 for O_2EE). At high altitude, a similar regression explained 87.4% of the variation in $\dot{V}_{O_2}$ (partial $r^2 = 0.435$ for V_T, 0.780 for f, and 0.399 for O_2EE). At both 340 m and 3,800 m, most of the change in $\dot{V}_I$ was accomplished by adjusting f; changes in V_T were much less important (V_T actually declined at high $\dot{V}_I$ at 3,800 m).

In several species of small arctic mammals, increased $\dot{V}_{O_2}$ at low T_a was accompanied by elevated $\dot{V}_I$, as observed for deer mice (Casey et al. 1979; Withers et al. 1979). However, in many of the arctic species the increase in $\dot{V}_I$ was accomplished by augmenting both f and V_T. The few birds for which data are available show mixed reactions to low T_a. Responses occur in both $\dot{V}_I$ and O_2EE, and some species increase $\dot{V}_I$ mostly by increasing f while others rely heavily on changing V_T (Bernstein and Schmidt-Nielsen 1974; Bucher 1981; Brent et al. 1984).

Effects of high altitude

Despite an overall similarity in ventilation responses to T_a, a number of significant differences were apparent between deer mice tested at low and high altitude. Perhaps the most obvious were the consistently higher f at all T_a at high altitude (Fig. 1B), and a correspondingly larger $\dot{V}_I$ at high altitude at all but the lowest T_a. Expressing $\dot{V}_I$ as a function of $\dot{V}_{O_2}$ (Figs. 2E, 2F) indicates that deer mice compensate for reduced oxygen availability at high altitude primarily by means of a proportional increase in total ventilation. In general, the increase in $\dot{V}_I$ seen at high altitude (approximately 40%) was about the same as the 35% change in barometric pressure between 340 m and 3,800 m (see also Fig. 1D).

This pattern changed at low ambient temperatures. Minute volume at high altitude was relatively constant at $T_a < 10$ °C (Fig. 1D). Respiration frequency continued to increase as T_a declined (Fig. 1B); the plateau in $\dot{V}_I$ resulted from concomitant decreases in V_T (Fig. 1C). The reason for the decline of V_T is unclear. One possibility is that mechanical or muscular limitations deriving from the extremely high f at these low T_a (9–10 breaths/s at −10 °C) interfered with lung filling. Observations of reduced range and magnitude of V_T at high f (Fig. 4) are consistent with that hypothesis. In any event, mice subjected to $T_a < 0$ °C at high altitude were able to maintain the $\dot{V}_{O_2}$ necessary for thermoregulatory heat production by increasing O_2EE, despite the unchanging $\dot{V}_I$ (Fig. 1E). The mechanism for increasing O_2EE is unclear, but may involve increased perfusion of alveolar capillaries or perhaps a reduction in venous P_{O_2}.

Other mammals, including humans, also use increased ventilation as the primary respiratory mechanism to compensate for reduced oxygen availability at high altitude (Lenfant 1973; Frisancho 1975), and the same pattern occurs in birds (Bouverot et al. 1976; Colacino et al. 1977). Increased $\dot{V}_I$ at high altitude is almost exclusively a result of increased f in deer mice. However, other species may change V_T, f, or both. For example, humans primarily depend on increased V_T (except

at extremely high altitudes), while in pigeons both V_T and f increase by roughly equivalent factors.

Many investigators report that species or individuals native to high altitudes have different respiratory characteristics than low-altitude natives, even after the latter have been extensively acclimated (e.g., Lenfant 1973). Often the differences are attributed to developmental, rather than genetic factors (Frisancho 1975). The present study did not directly address the question of acclimation vs genetic adaptation, but it is noteworthy that I observed no differences at either high or low altitude between wild-caught mice collected at 3,150–3,800 m and animals native to 2,000–4,000 m but born and reared at 340 m. The similarity is not simply due to the statistical limitations inherent with small sample sizes – in all cases there was extensive data overlap between these groups.

Respiratory heat loss

The respiratory system is a pathway for heat loss as well as gas exchange. Body heat is lost when tidal air is warmed above ambient temperature and by evaporation of water into tidal air. Respiratory heat loss (HL_r) is usually a significant fraction of metabolic heat production (MHP) only when T_a is high and evaporative cooling from the respiratory tract becomes important. However, accumulating evidence (Withers 1977b; Bucher 1981; Brent et al. 1984) suggests that birds may decrease air convection requirements, and hence HL_r, by increasing O_2EE at T_a below thermoneutrality.

Respiration in deer mice shows few characteristics consistent with an attempt to reduce HL_r at low T_a, although the increased O_2EE at very low T_a observed at high altitude could be interpreted as such a mechanism. Heat loss through the respiratory tract is a small fraction of the total heat production of a deer mouse in cold conditions. Figure 5A shows total MHP and total evaporative heat loss (EHL) at different T_a, and total EHL and the maximum heat loss due to warming tidal air (HL_a, calculated by multiplying $\dot{V}_I$ by the specific heat of air and the temperature change assumning air is expired at T_b) are shown as fractions of MHP in Fig. 5B. These are maximal estimates of the heat lost through respiration and are unrealistic, since total EHL includes cutaneous as well as respiratory evaporation (HL_e) and much of the heat and water lost to inspired air is recovered in nasal heat exchangers (Schmidt-Nielsen et al. 1970; Welch 1984). Exact values of HL_a and HL_e cannot be determined without knowledge of the

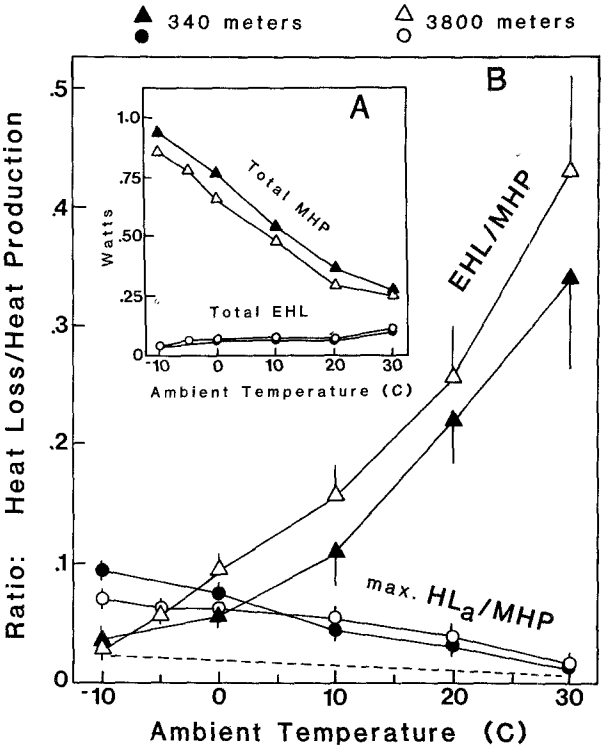

Fig. 5. **A** Total metabolic heat production (MHP) and evaporative heat loss (EHL) at different T_a at low and high altitude. **B** Ratio of EHL to MHP (triangles), ratio of maximum heat loss from warming inspired air to MHP (max HL_a/MHP, circles), and probable HL_a after recovery of heat in nasal heat exchanger (dashed line) at different T_a. See text for details of calculations. Vertical lines indicate two SE on each side of the mean

temperature of expired air. Welch (1984) gives a regression of expired air temperature as a function of T_a for deer mice, which indicates that the animals can recover 60–70% of the heat lost in warming and wetting inspired air. Hence, at T_a of 0 °C or below, HL_a and HL_e are probably 1–2% and 2–3%, respectively, of MHP, and total HL_r amounts to at most 4–5% of MHP.

Curiously, the requirements for MHP at any temperature below T_{lc} were significantly greater at low altitude than at high altitude (Fig. 1A), even though average body temperatures were similar at both elevations. The low- and high-altitude tests took place at different times of the year and the mice were housed at slightly different T_a, so seasonal or short-term temperature acclimation may have occurred. That explanation is unlikely, since mean T_a's at the two sites differed by only 5 °C, and high altitude testing took place in summer when fur insulation should have been at its annual minimum (Wickler 1981). Furthermore, changes in thermogenic capacity, rather than changes in insulation, play the major role in seasonal and cold acclimation in *Peromyscus* (Conley and Porter

1983; unpublished data). Another possible explanation for the reduced MHP at high altitude is that rates of heat loss (i.e., thermal conductance), and therefore MHP requirements, were lower at high altitude due to the reduced heat capacity of air at low barometric pressures (Tracy et al. 1980). The reduction in MHP requirements (roughly 15–20%) was not directly proportional to the 35% difference in barometric pressure and heat capacity between 340 m and 3,800 m, presumably because (a) only the convective heat loss pathway is affected by changes in air density (radiative exchange is unaffected), and (b) decreased viscosity at low pressures increases the thermal conductivity of air and partly compensates for reduced heat capacity.

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