

Effects of temperature and altitude on ventilation and gas exchange in chukars (*Alectoris chukar*)

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Summary. The effects of ambient temperature (T_a) on ventilation and gas exchange in chukar partridges (*Alectoris chukar*) were determined after acclimation to low and high altitude (LA and HA; 340 and 3,800 m, respectively).

At both LA and HA, oxygen consumption (\dot{V}_{O_2}) increased with decreasing T_a at T_a from 20 to -20°C . At T_a of 35 to 40°C , \dot{V}_{O_2} increased above thermoneutral values at HA but remained constant and minimal at LA. Water loss rates increased rapidly at $T_a > 30^\circ\text{C}$ at both altitudes as birds began to pant. Ventilation rates (f) during panting were 5- to 23-fold greater than the minimal f at thermoneutral T_a .

Increased \dot{V}_{O_2} at T_a below thermoneutrality was supported by increased minute volume (\dot{V}_I) at both altitudes. The change in \dot{V}_I was primarily a function of changing tidal volume (V_T), although f increased slightly as T_a declined. Oxygen extraction (E_{O_2}) remained fairly constant at T_a below 20°C at both altitudes. Both V_T and E_{O_2} were considerably lower when birds were panting than at lower T_a .

Chukars showed few obvious ventilatory adaptations to HA. The 35% change in P_{O_2} between 340 and 3,800 m was accommodated by a corresponding change in \dot{V}_I (BTPS), most of which was accomplished by increased f at HA, along with a slight increase in E_{O_2} .

(\dot{V}_{O_2}) as heat production requirements change with changing ambient temperature (T_a). Modulation of \dot{V}_{O_2} may be accomplished by adjusting lung ventilation and/or oxygen extraction efficiency (E_{O_2}). Lung ventilation (minute volume, \dot{V}_I) is itself a function of tidal volume (V_T) and respiration frequency (f). Considerable data exist on the relationship between T_a and f in birds (e.g., Lasiewski 1972), but less is known about interactions between \dot{V}_{O_2} , \dot{V}_I , V_T , and E_{O_2} , particularly at very low T_a where rates of oxygen consumption are high and it is advantageous to minimize rates of heat loss (Bernstein and Schmidt-Nielsen 1974; Bucher 1981; Bech et al. 1984; Brent et al. 1983, 1984). A contrasting situation occurs at high T_a , when panting transforms the respiratory system into a major pathway for heat loss, in addition to its primary gas exchange function.

At high altitudes, the respiratory system is challenged because of reduced oxygen availability. An additional problem is the low T_a often characteristic of high altitudes. Ventilatory changes between low and high altitude or during isobaric hypoxia have been described for several birds (Bouverot et al. 1976; Colacino et al. 1977; Bouverot and Hildwein 1978; Brackenbury et al. 1982; Boggs and Kilgore 1983; Bouverot 1985). However, there are few data from acclimated, unrestrained animals and relatively little is known about the combined effects of altitude and temperature.

This report describes patterns of respiratory gas exchange and ventilation in chukar partridges (*Alectoris chukar*) exposed to a range of ambient temperatures after acclimation to altitudes of 340 and 3,800 m. From an ecological and evolutionary viewpoint, chukars are appropriate subjects for such a study. They are native to mountainous semidesert regions in southern and western Asia. While chukars are not normally found at the extreme altitudes reported for some birds (e.g.,

Introduction

The avian respiratory system must accommodate large variations in rates of oxygen consumption

Abbreviations and symbols: HA high altitude; LA low altitude; \dot{m}_{H_2O} rate of evaporative water loss; E_{O_2} oxygen extraction efficiency; f respiratory frequency; V_T tidal volume; \dot{V}_I minute volume; BMR basal metabolic rate; MHP metabolic heat production

> 8,000 m for bar-headed geese, *Anser indicus*; Black and Tenney 1980), wild flocks of chukars have been observed at altitudes from near sea level to over 4,000 m in western North America, where they have been widely introduced. Our study addresses three major questions about respiratory function: (1), Do chukars increase E_{O_2} at low T_a in order to minimize ventilation and hence respiratory heat loss at high \dot{V}_{O_2} ? (2), Do chukars acclimated for several weeks to 3,800 m compensate for the reduced P_{O_2} by means of increased E_{O_2} , augmented ventilation, or both? (3), Does T_a affect ventilatory parameters differently at low *vs* high altitude?

Materials and methods

Animals. Chukars ($n=7$) were purchased as adults (mean mass 475 g, range 385–568 g) from commercial breeders. At the low altitude site (LA; Riverside, California; elevation 340 m) they were housed in an aviary in an outdoor greenhouse. At the high altitude site (HA; the Barcroft Laboratory of the University of California's White Mountain Research Station; elevation 3,800 m), birds were housed in an aviary in a well ventilated, unheated building. Food and water were available ad libitum. Low altitude work took place in April and May 1985 and high altitude work was performed in August and September 1985, following 1.5 months of acclimation to local altitude. Natural photoperiods were used throughout the experiments.

Measurements. Metabolism was measured in a plexiglas respirometry chamber (volume 11 l) placed in an environmental cabinet which controlled temperature $\pm 0.5^\circ\text{C}$. At each altitude, six chukars were measured at -20 , -10 , 0 , 10 , 20 , 30 , and 35°C and three birds were measured at 40°C . The T_a was measured with thermocouples in the excurrent air line at its junction with the metabolism chamber. Birds were unrestrained and stood on a screen-wire platform over a layer of mineral oil which covered voided excreta. At each T_a , body temperature (T_b) was obtained with a cloacal thermocouple within 45 s (usually within 20 s) after completing measurements and removing the bird from the chamber. To check the accuracy of this method, we handled 4 chukars for up to a minute after the initial T_b measurement. Little T_b change ($<0.4^\circ\text{C}$) occurred during this interval.

Oxygen consumption, carbon dioxide production (\dot{V}_{CO_2}), and evaporative water loss (\dot{m}_{H_2O}) were determined with an open-circuit respirometry system. Flow rates of dry air varied from 2.5 l/min STP at high T_a to 5 l/min STP at $T_a < 0^\circ\text{C}$, and were regulated $\pm 1\%$ with mass flow controllers (Applied Materials AFC-550). A fraction of the excurrent air was diverted through a humidity sensor (Weather Measure HT-100), dried and passed through a CO_2 sensor (Applied Electrochemistry CD-3A), passed through CO_2 absorbent and redried, and passed through an O_2 sensor (Applied Electrochemistry S-3A). All instruments were periodically referenced against dry air diverted from upstream of the respirometry chamber. The humidity probe resolved 0.1% relative humidity (R.H.) and was calibrated over salt solutions to within 1% of actual R.H. The CO_2 and O_2 analyzers resolved concentrations of 0.01% and 0.001%, respectively. During experiments, O_2 concentration was always $>20.4\%$, CO_2 concentration was always $<0.5\%$, and R.H. in the metabolism chamber never exceeded 40%. Ven-

tilation and gas exchange data were taken after animals had been held at one T_a for at least 1 h and \dot{V}_{O_2} was low and stable. All measurements were made during the daylight portion of the photoperiod.

The respirometry chamber functioned as a whole-body plethysmograph allowing simultaneous measurements of ventilation and gas exchange, as described by Bucher (1981). Pressure changes caused by the warming and wetting of tidal air were measured with a pressure transducer connected to a polygraph or microcomputer. Measurable signals in the open-circuit system were obtained by inserting high resistance valves upstream and downstream of the respirometer. The pressure in the chamber was 4–8 Torr over ambient, so that actual pressures experienced by the birds were approximately 748 Torr at 340 m and 488 Torr at 3,800 m. These chamber pressures correspond to altitudes of approximately 100 m and 3,600 m, respectively. The system was calibrated by serial injections of known volumes of air into the chamber before completion of each set of ventilation measurements at a particular T_a . Inspiratory tidal volume was calculated by comparing ventilation deflections with calibration deflections according to Malan (1973), using a computer program that assumed lung temperature = T_b . Percent oxygen extraction was calculated from $\dot{V}_I (=f \times VT)$ and \dot{V}_{O_2} as $E_{O_2} = [\dot{V}_{O_2}/0.2095 \dot{V}_I] \times 100$, after accounting for ambient humidity and CO_2 concentration. The CO_2 concentration in expired air was calculated as $[\dot{V}_{CO_2}/\dot{V}_I] \times 100$, after accounting for humidity.

Unless otherwise stated, values of \dot{V}_{O_2} and \dot{V}_{CO_2} are corrected to STP; VT and \dot{V}_I are calculated at BTPS and therefore indicate actual volumes in the respiratory tract. STPD values for VT and \dot{V}_I are shown in brackets ([]). The E_{O_2} was computed using STPD volumes for \dot{V}_I .

Data reduction and statistical tests. At a given T_a , we made two to four measurements on each bird. To avoid biasing results in favor of individuals with many data points, a single average value was obtained for each individual for comparisons between different temperatures (e.g., Figs. 1 and 2). For other comparisons between ventilation parameters, all the data points were used. In most cases (except at $T_a > 30^\circ\text{C}$), individual variation was slight. Results are given as mean \pm SEM. ANOVA's or *t*-tests were used to compare means; 2-way ANOVAS were used to examine the interactions between T_a and altitude. Regressions were fitted by the method of least squares. The significance level for all tests was $P < 0.05$.

Results

Chukars adapted well to the experimental apparatus and protocols. They seldom struggled or attempted to escape and were often observed sleeping or standing quietly on one leg. Nevertheless, unusual noises, even of low amplitude, often elicited sudden changes in respiration rate lasting from a few seconds to several minutes.

Body temperature and water loss

Body temperatures showed significant differences ($P=0.004$), but little absolute variation, over a wide range of T_a (Fig. 1 A). At LA, T_b varied from a minimum of $40.1 \pm 0.4^\circ\text{C}$ at $T_a = 0^\circ\text{C}$ to a maximum of $42.2 \pm 0.19^\circ\text{C}$ at $T_a = 40^\circ\text{C}$. At HA, T_b

was even more stable, ranging between 40.4 ± 0.21 °C at $T_a = -20$ °C and 41.7 ± 0.17 °C at $T_a = 35$ °C. When T_a was below 35 °C, T_b 's at HA were always slightly but significantly higher (by 0.5 to 0.8 °C) than at equivalent T_a at LA.

We calculated \dot{m}_{H_2O} at all T_a of 0 °C or greater (at subzero T_a , measurements were inaccurate because water vapor froze onto the metabolism chamber walls). Water loss rates were low between 0 and 30 °C, but increased at higher T_a (Fig. 1B). At 0 °C there was no difference in \dot{m}_{H_2O} between LA and HA, but at higher T_a \dot{m}_{H_2O} was always significantly lower at HA. The maximum observed \dot{m}_{H_2O} (at 40 °C) was about 0.85% of body mass per hour at LA and 0.53% of body mass per hour at HA.

Oxygen consumption and carbon dioxide production

At both LA and HA, \dot{V}_{O_2} was minimal at $T_a = 30$ °C and increased with decreasing T_a . There was a significant effect of altitude (\dot{V}_{O_2} at HA was greater than corresponding LA values at all $T_a < 30$ °C), but no significant interaction between T_a and altitude (2-way ANOVA; Table 1). The thermoneutral zone extended from 20 °C to 30–35 °C at HA and from 20 °C to at least 40 °C at LA. Resting metabolism at 30 °C was about 0.0137 ± 0.0009 ml/[g·min], about 85% of predicted daytime BMR of a 475 g nonpasserine (Aschoff and Pohl 1970) and 94% of predicted BMR for a galliform bird of similar mass (data in Bucher 1986).

Carbon dioxide production closely paralleled \dot{V}_{O_2} at all combinations of temperature and altitude. The respiratory exchange ratio (R) averaged over all T_a was 0.90 ± 0.018 at LA and 0.86 ± 0.024 at HA. The difference is significant ($P = 0.011$), but at any particular T_a the R at HA was never significantly different from the corresponding value at LA.

Non-panting ventilation

Ventilation parameters are plotted against T_a in Fig. 2 and \dot{V}_{O_2} in Fig. 3. To facilitate comparisons between altitudes, Figs. 2B and 2D show the \dot{V}_T and \dot{V}_I data for 3,800 m when corrected to the barometric pressure at 340 m, in addition to the BTPS data.

Tidal volume was strongly and inversely correlated to T_a at both LA and HA (Fig. 2B). The change in \dot{V}_T with T_a was greater at LA: at -20 °C the \dot{V}_T was approximately twice the 30 °C value at LA, but at 3,800 m the -20 °C \dot{V}_T was only 54% greater than \dot{V}_T at 30 °C. Nevertheless, a

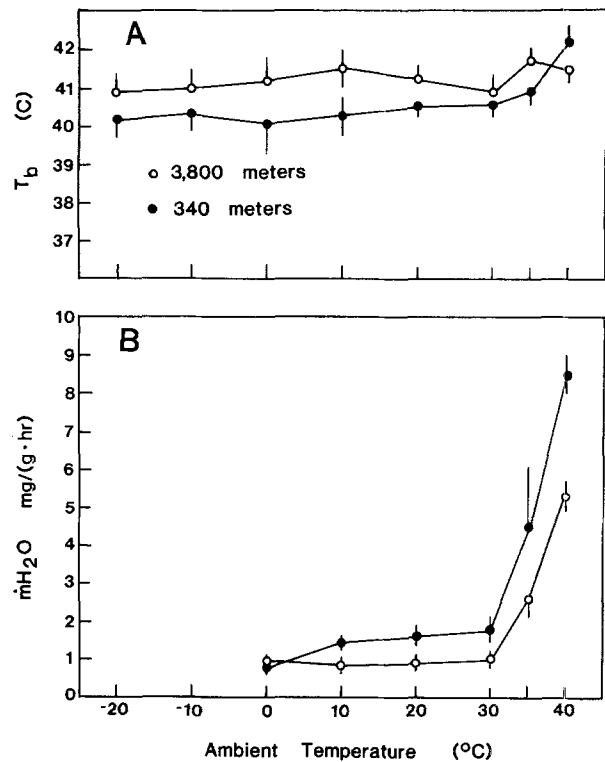


Fig. 1. **A** Body temperature of chukars at low and high altitude at different ambient temperatures. Vertical lines indicate 2 SEM; $n = 6$ individuals for all ambient temperatures except 40 °C, where $n = 3$. **B** Evaporative water loss of chukars at low and high altitude at different ambient temperatures. Symbols and sample sizes as above

Table 1. Results from 2-way ANOVAS showing significance levels for the individual and combined effects of ambient temperature and altitude on ventilatory parameters in chukars. The data set included six temperatures (-20 to 30 °C) and two altitudes (340 and 3,800 m); six birds were measured at each combination of T_a and altitude

Source	\dot{V}_{O_2}	\dot{V}_T	f	\dot{V}_I	E_{O_2}
Temperature	0.000	0.000	0.066	0.000	0.014
Altitude	0.002	0.384	0.214	0.000	0.000
Interaction	0.422	0.052	0.036	0.089	0.059

2-way ANOVA revealed no significant effects of altitude, and no interaction effects between T_a and altitude for non-panting birds (Table 1). Significant positive relationships between \dot{V}_T and \dot{V}_{O_2} occurred at both altitudes ($r^2 = 0.445$ at LA; $r^2 = 0.486$ at HA; Fig. 3C, 3H).

Ventilation frequency changed only slightly between -20 and 30 °C at either altitude. The f at -20 °C was significantly higher (by a factor of about 1.5) than the minimal f observed in thermoneutrality at each altitude (23.3 ± 0.9 breaths/min at 20 °C at 340 m, and 28.0 ± 1.6 breaths/min at

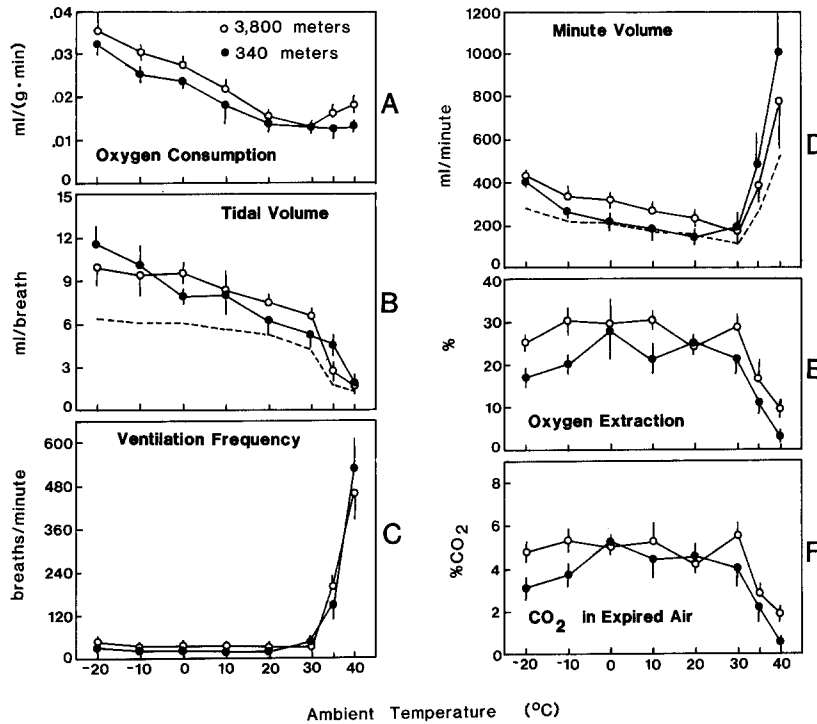


Fig. 2A–F. Respiratory parameters of chukars at low and high altitude as a function of ambient temperature. Symbols and sample sizes as in Fig. 1. Oxygen consumption is expressed as ml/[g·min] STP. All other volumes are BTPS, except dashed lines in B and D, which represent the 3,800 m data corrected to the barometric pressure at 340 m

30 °C at 3,800 m). At all T_a below 20 °C, the f at 3,800 m was higher by a factor of 1.2–1.36 than the corresponding f at LA. However, 2-way ANOVA showed no significant effects of either T_a or altitude on f , and a marginally significant interaction term (Table 1). The relationship between f and \dot{V}_{O_2} was weak but significant at both altitudes, with only a slight tendency for higher f at high \dot{V}_{O_2} ($r^2=0.137$ at LA; $r^2=0.224$ at HA; Fig. 3B, 3G).

Minute volume was strongly affected by both T_a and altitude, but significant interactions were not observed between -20 and 30 °C (Table 1). The \dot{V}_I was minimal at 20 and 30 °C at LA and HA, respectively, and increased at higher and lower T_a (Fig. 2D). At -20 °C, \dot{V}_I was 2.7 times greater than the minimal value at LA (408 ± 11 vs. 150 ± 15 ml/min [353 and 130 ml/min STPD]); at HA, \dot{V}_I changed 2.4 times from its minimal value (438 ± 23 vs. 182 ± 9 ml/min [266 and 110 ml/min STPD]). As with V_T , \dot{V}_I was significantly correlated to \dot{V}_{O_2} ($r^2=0.590$ at LA; $r^2=0.638$ at HA; Fig. 3D, 3I).

The relationship between V_T and f is shown in Fig. 4. When birds were not panting, f remained below 70 breaths/min and there was considerable variability in V_T . The largest V_T (12–20 ml) were associated with low f (17–40 breaths/min); at f between 45 and 65 breaths/min the maximum V_T was somewhat reduced. Throughout the range of f , there was little difference between the V_T data from LA and HA.

Ventilation during panting

At LA, several individuals panted intermittently at 30 °C and all birds panted vigorously at higher T_a ; in contrast, at HA panting was never observed at 30 °C. The f during panting increased by 5 to 23 times minimal values, attaining rates of 500–600 breaths/minute at 40 °C. We found no significant difference in f between HA and LA at T_a 's of 30 °C and above. The V_T of panting birds was very low (1.5–5.5 ml). Nevertheless, ventilation increased rapidly as birds began to pant, and at $T_a=40$ °C, \dot{V}_I was $1,007 \pm 114$ ml/min and 782 ± 48 ml/min [871 and 475 ml/min STPD] at LA and HA, respectively.

Oxygen extraction

Oxygen extraction was significantly affected by both altitude and T_a (Table 1; Fig. 2E, 3E, 3J), but the interaction term was not significant for nonpanting birds. At T_a of -20 to 30 °C, E_{O_2} averaged $22.5\% \pm 0.7\%$ at LA and $28.3\% \pm 0.6\%$ at HA ($P < 0.0001$). During panting (T_a 35–40 °C), E_{O_2} averaged $11.2\% \pm 1.6\%$ at LA and $14.8\% \pm 1.2\%$ at HA ($P = 0.045$), reaching minimum values of 2–3% at LA and 7–8% at HA. Somewhat surprisingly, E_{O_2} showed weak or non-significant relationships to V_T and f at both altitudes, except for the decreased E_{O_2} during panting. The relationship between E_{O_2} and \dot{V}_I was clearer (Fig. 5). The high-

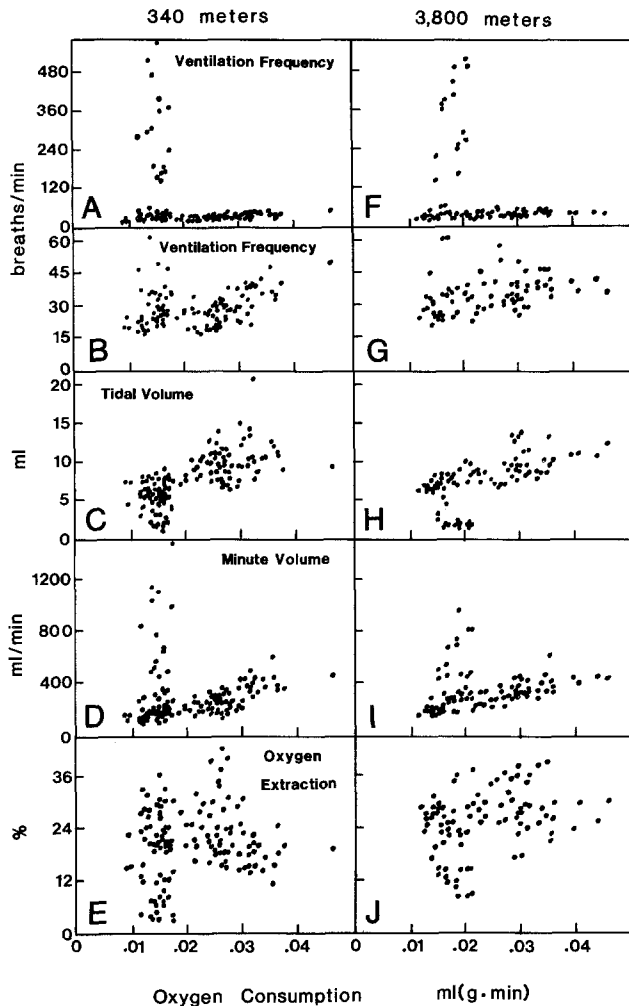


Fig. 3 A–J. Respiratory parameters of chukars at low and high altitude, plotted as a function of oxygen consumption. Oxygen consumption is expressed at STP; all respiratory volumes BTPS. Figs. 3 B and 3 J are enlarged versions of 3 A and 3 F, respectively, showing non-panting ventilation only

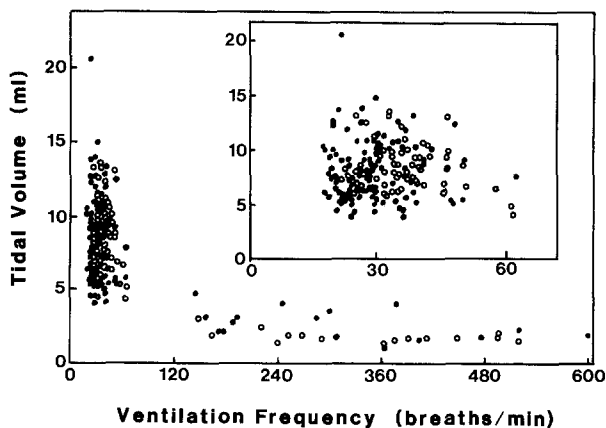


Fig. 4. Tidal volume (BTPS) expressed as a function of ventilation frequency at 340 m (closed circles) and 3,800 m (open circles). The insert shows an enlarged version of the data for non-panting ventilation frequencies

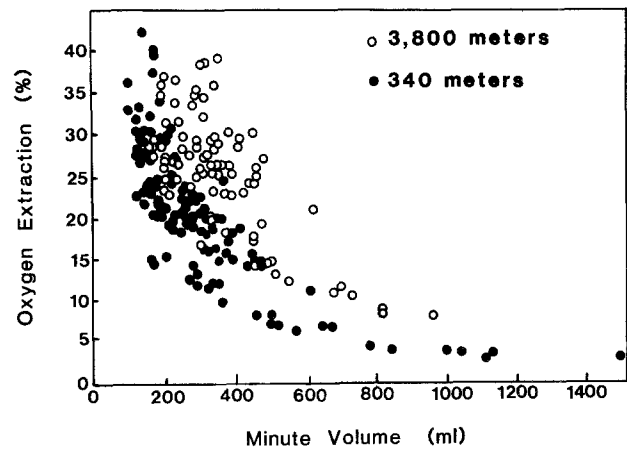


Fig. 5. Oxygen extraction expressed as a function of minute volume (BTPS)

est E_{O_2} occurred at low to moderate \dot{V}_I , with rapid decline at the high \dot{V}_I associated with panting.

The concentration of CO_2 in expired air closely paralleled the E_{O_2} values as T_a changed (Fig. 2F), remaining between 3% and 5% except when birds were panting.

Discussion

In chukars, the lowest ventilation frequencies occurred within the thermoneutral zone (i.e., \dot{V}_{O_2} constant and minimal). At LA the minimum f (23.3 breaths/min) was approximately as predicted for a resting 475 g nonpasserine (Lasiewski 1972) but less than expected for an unrestrained bird of like mass (Bucher 1985). These comparisons must be interpreted cautiously. Most allometric analyses of ventilatory parameters (e.g., Lasiewski 1972) have been based on measurements in thermoneutral but otherwise unspecified conditions. Ventilatory parameters may change dramatically within the thermoneutral zone (e.g., many birds pant without significantly increasing \dot{V}_{O_2}), so it is difficult to determine a proper basis for comparison (Bucher 1985).

Temperature effects on ventilation

For T_a at or below thermoneutrality, chukars accommodated changing oxygen demands for heat production primarily by adjusting total ventilation (\dot{V}_I). Changes in E_{O_2} were relatively unimportant (Fig. 2, 3). Most of the change in \dot{V}_I was accomplished by modulating V_T , although f increased at high \dot{V}_{O_2} (particularly at 3,800 m).

Other birds show a variety of ventilatory patterns at different T_a . Pigeons (*Columba livia*; Bech et al. 1985), prairie falcons (*Falco mexicanus*; Kai-

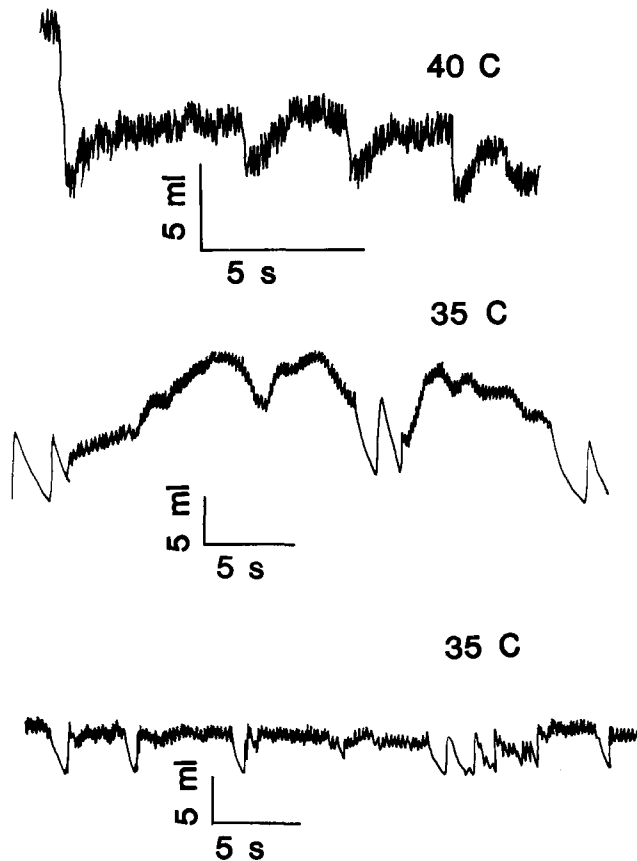


Fig. 6. Typical ventilation traces from panting chukars, showing high frequency, low volume respiratory movements periodically interrupted by deep ventilations ("flushouts")

ser and Bucher 1986) and parrots (*Bolborhynchus lineola* and *Amazona viridigenalis*; Bucher 1981, 1985) respond similarly to chukars: high thermogenic \dot{V}_{O_2} is accommodated by increases in \dot{V}_I , with relatively high and stable E_{O_2} . At low T_a , E_{O_2} may decline slightly (however, except for the present study, none of these investigations included $T_a < 0^\circ\text{C}$). The change in \dot{V}_I is mostly due to modulation of \dot{V}_T with relatively stable f in *Columba*, *Alectoris*, *Falco*, and *Amazona*; in *Bolborhynchus* the reverse is true. In contrast, mallard ducks (*Anas platyrhynchos*; Bech et al. 1984) and European coots (*Fulica atra*; Brent et al. 1984) are considerably more reliant on adjustments of E_{O_2} . In *Fulica*, \dot{V}_I increases only 50% as T_a is reduced from thermoneutrality (20–30 °C) to -25°C , but E_{O_2} increases by a factor of 2.4 (from 18 to 42%) over the same range of T_a . The pattern in *Anas* is qualitatively similar. In both *Fulica* and *Anas* at $T_a < 0^\circ\text{C}$, the change in \dot{V}_I results from a relatively larger increase in f than in \dot{V}_T . The diversity of responses observed in the relatively small number of birds that have been studied suggests that the

avian ventilatory system shows great flexibility in mechanisms for coping with changing thermogenic oxygen demand.

High E_{O_2} at T_a below thermoneutrality is often interpreted as an adaptation to reduce respiratory heat loss (Johansen and Bech 1983). Such an adaptation might be valuable for chukars, which regularly experience severe winter cold in their natural habitats. Accordingly, we calculated rates of respiratory heat loss for chukars at low T_a . At -20°C , the metabolic heat production (MHP) is about 305 J/min at LA. We did not measure expired air temperature but assume it was near 0°C , as reported for the European coot at T_a below 0°C (Brent et al. 1984). If so, chukars at 340 m exposed to -20°C lost about 5.0 J/min as respiratory water loss (assuming expired air was saturated), and approximately 10.1 J/min as heat transferred to tidal air and not recovered on exhalation. Respiratory heat loss was thus 5% of total heat loss. At 3,800 m, the corresponding values were: MHP, 335 J/min; respiratory water loss, 5.4 J/min; heat loss from warming tidal air, 7.3 J/min; respiratory heat loss 4% of total heat loss. We conclude that respiration is not a major avenue for heat loss in *Alectoris* at low T_a , although the E_{O_2} of chukars (18–24% at -20°C) is relatively modest compared to values reported for other birds (e.g., 42% at -25°C in the European coot; Brent et al. 1984). Even if chukars doubled their E_{O_2} , they would reduce MHP requirements by only 2–3% at -20°C .

In addition to winter cold, chukars must deal with high heat loads during the summer. During panting, E_{O_2} is low because the birds are moving large volumes of air to facilitate evaporative heat loss. The transition from a low-volume, high E_{O_2} ventilatory mode into a high-volume, low E_{O_2} mode occurred at T_a between 30 and 35°C (Figs. 1, 2). The greatly elevated \dot{V}_I during panting was due entirely to a 5- to 23-fold increase in f , which is similar to f increases of 29-, 26-, and 23-fold, respectively, in the mute swan *Cygnus olor* (Bech and Johansen 1980), Pekin duck (Bouverot et al. 1974), and greater flamingo *Phoenicopterus ruber* (Bech et al. 1979).

The \dot{V}_T during panting was considerably lower than during normal ventilation in chukars, and was only slightly larger than the predicted 1.6 ml tracheal volume (i.e., anatomical dead space) for a 475 g nonpasserine (Lasiewski and Calder 1971). We often observed occasional large ventilations during sustained panting, or panting superimposed on low-frequency, high-volume respiration (Fig. 6). Similar patterns have been reported for panting pigeons (Ramirez and Bernstein 1976),

pekin ducks (Bouverot et al. 1974), flamingos (Bech et al. 1979), and domestic fowl *Gallus domesticus* (Gleeson 1985). Because f is high in panting chukars, the contribution of deep breaths to overall \dot{V}_I is minor (approximately 5–10% at $T_a = 40^\circ\text{C}$). Ramirez and Bernstein (1976) and Bech et al. (1979) point out that restricting \dot{V}_T to dead space volume during panting would ameliorate the potential for hypocapnia during hyperventilation. Periodic deep breaths ('flushouts') may allow adequate pulmonary gas exchange, which might otherwise be compromised during panting by the low mean \dot{V}_T .

Effects of high altitude

Physiological compensation for the reduced partial pressure of oxygen at high altitudes may involve increased ventilation, increased oxygen extraction from tidal air, or both. Many avian species and several mammals apparently use increased ventilation as the primary compensatory mechanism at high altitudes (Lenfant 1973; Frisncho 1975; Bouverot 1985), although few studies have included long-term acclimation. The change in \dot{V}_I at HA is accomplished in various ways. Humans depend primarily on increased \dot{V}_T (except at extreme altitudes), while deer mice rely almost exclusively on increased f (Chappell 1985). Pigeons change both \dot{V}_T and f approximately equally when acclimated to 4,000 m (Bouverot et al. 1976). In contrast, bar-headed geese (*Anser indicus*), which fly at altitudes exceeding 8,000 m, show little change in \dot{V}_I between sea level and 6,100 m, relying instead on increased E_{O_2} to maintain \dot{V}_{O_2} (computed from Table 6 in Black and Tenney 1980). Bar-headed geese substantially increase ventilation rates only when altitudes exceed 7,000–8,000 m.

Chukars compensated for the 37% reduction in oxygen partial pressure at 3,800 m mainly by a matching increase in \dot{V}_I (Fig. 2D). In this respect they are similar to the majority of birds and mammals thus far studied. Elevated \dot{V}_I in chukars was accomplished by increasing f , with only minor changes in \dot{V}_T (Fig. 2B, 2C). In addition to the greater ventilatory flow at HA, a slight increase in E_{O_2} , averaging about 4–5%, was also apparent. Besides these adjustments, chukars showed remarkably few changes in respiration and ventilation after 1.5 months of acclimation to 3,800 m. Few interactive effects between altitude and temperature were noted at thermoneutral or lower temperatures. The most significant interaction occurred in panting birds. At HA, panting began at higher T_a and involved lower \dot{V}_I than at LA

(Fig. 2). This implies that the thermoregulatory drive for panting at high T_a may be inhibited by requirements for adequate gas exchange at the low P_{O_2} at HA, as reported for pekin ducks (Bouverot and Hildwein 1978). However, in chukars exposed to $T_a = 40^\circ\text{C}$, the T_b at HA was lower than at LA, suggesting that the HA birds were not experiencing significant heat stress.

Oxygen consumption was slightly higher at HA (except at 20 and 30 °C). The difference could reflect higher costs of breathing at HA, due to the increase in \dot{V}_I . This hypothesis is not supported by data obtained from panting birds (when ventilatory costs were presumably maximal). Here, \dot{V}_I was greater at LA than at HA, but the opposite was true for \dot{V}_{O_2} (Fig. 2A, 2D). Increased \dot{V}_{O_2} at HA might also result from reduced insulation, as our birds were molting during the experiments at HA. Reduced insulation could also account for the lower \dot{V}_I and \dot{m}_{H_2O} of panting chukars at HA. Insulation decreases during molt because of near-surface vascularization in growing feathers and because of reduced plumage density (Lustick 1970). Molt may also explain the elevated T_b we observed at HA (Newton 1968).

In summary, chukars adjust several ventilation parameters as oxygen demand and oxygen availability change. As T_a decreases, increasing oxygen demand is accommodated by increases in \dot{V}_I , which is accomplished primarily through increased \dot{V}_T with minor changes in f . Reduced oxygen availability at high altitude is accommodated primarily by matching increases in \dot{V}_I , which are attained primarily by increased f with relatively unchanged \dot{V}_T when compared to similar T_a at low altitude. The increase in \dot{V}_I at high altitude is accompanied by minor increases in E_{O_2} . The overall ventilatory response to changing T_a is similar at both high and low altitude.

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References

- Aschoff J, Pohl H (1970) Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. *J Ornithol* 111:38–47
- Bech C, Johansen K (1980) Ventilatory and circulatory responses to hyperthermia in the mute swan (*Cygnus olor*). *J Exp Biol* 88:195–204
- Bech C, Johansen K, Maloiy GMO (1979) Ventilation and ex-

- pired gas composition in the flamingo, *Phoenicopterus ruber*, during normal respiration and panting. *Physiol Zool* 52:313–328
- Bech C, Johansen K, Brent R, Nicol S (1984) Ventilatory and circulatory changes during cold exposure in the Pekin Duck *Anas platyrhynchos*. *Respir Physiol* 57:103–112
- Bech C, Rautenberg W, May B (1985) Ventilatory oxygen extraction during cold exposure in the pigeon (*Columba livia*). *J Exp Biol* 116:499–502
- Bernstein MH, Schmidt-Nielsen K (1974) Ventilation and oxygen extraction in the crow. *Respir Physiol* 21:393–401
- Black CP, Tenney SM (1980) Oxygen transport during progressive hypoxia in high-altitude and sea-level waterfowl. *Respir Physiol* 39:217–239
- Boggs DF, Kilgore DL (1983) Ventilatory responses of the Burrowing Owl and Bobwhite to hypercarbia and hypoxia. *J Comp Physiol* 149:527–533
- Bouverot P (1985) Adaptation to altitude-hypoxia in vertebrates. Springer, New York Berlin Heidelberg
- Bouverot P, Hildwein G (1978) Combined effects of hypoxia and moderate heat load on ventilation in awake pekin ducks. *Respir Physiol* 35:373–384
- Bouverot P, Hildwein G, Le Goff D (1974) Evaporative water loss, respiratory pattern, gas exchange and acid-base balance during thermal panting in Pekin ducks exposed to moderate heat. *Respir Physiol* 21:255–269
- Bouverot P, Hildwein G, Oulhen PH (1976) Ventilatory and circulatory O₂ convection at 4,000 m in pigeon at neutral or cold temperature. *Respir Physiol* 28:371–385
- Brackenbury JH, Gleeson M, Avery P (1982) Control of ventilation in running birds: effects of hypoxia, hyperoxia, and CO₂. *J Appl Physiol* 53:1397–1404
- Brent R, Rasmussen JG, Bech C, Martini S (1983) Temperature dependence of ventilation and O₂-extraction in the kittiwake, *Rissa tridactyla*. *Experientia* 39:1092–1093
- Brent R, Pedersen PF, Bech C, Johansen K (1984) Lung ventilation and temperature regulation in the European coot (*Fulica atra*). *Physiol Zool* 57:19–25
- Bucher TL (1981) Oxygen consumption, ventilation and respiratory heat loss in a parrot, *Bolborhynchus lineola*, in relation to ambient temperature. *J Comp Physiol* 142:479–488
- Bucher TL (1985) Ventilation and oxygen consumption in *Amazona viridigenalis*: a reappraisal of 'resting' respiratory parameters in birds. *J Comp Physiol B* 155:269–276
- Bucher TL (1986) Ratios of hatchling and adult mass-independent metabolism: A physiological index to the altricial-precocial continuum. *Respir Physiol* 65:69–83
- Chappell MA (1985) Effects of ambient temperature and altitude on ventilation and gas exchange in deer mice (*Peromyscus maniculatus*). *J Comp Physiol B* 155:751–758
- Colacino JM, Hector DH, Schmidt-Nielsen K (1977) Respiratory responses of ducks to simulated altitude. *Respir Physiol* 29:265–281
- Frisancho (1975) Functional adaptation to high altitude hypoxia. *Science* 187:313–319
- Gleeson M (1985) Analysis of respiratory pattern during panting in fowl, *Gallus domesticus*. *J Exp Biol* 116:487–491
- Johansen K, Bech C (1983) Heat conservation during cold exposure in birds (vasomotor and respiratory implications). *Polar Research* 1 n.s.:259–268
- Kaiser T, Bucher TL (1985) The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation and water loss in relation to ambient temperature in the Prairie Falcon, *Falco mexicanus*. *Physiol Zool* 58:748–758
- Lasiewski RC (1972) Respiratory function in birds. In: Farner DS, King JR (eds) *Avian biology*, vol 2. Academic Press, New York, pp 287–342
- Lasiewski RC, Calder WA (1971) A preliminary allometric analysis of respiratory variables in resting birds. *Respir Physiol* 11:152–166
- Lenfant C (1973) High altitude adaptation in mammals. *Am Zool* 13:447–456
- Lustick S (1970) Energy requirements of molt in cowbirds. *Auk* 87:742–746
- Malan A (1973) Ventilation measured by body plethysmography in hibernating mammals and in poikilotherms. *Respir Physiol* 17:32–44
- Newton I (1968) The temperatures, weights, and body composition of molting Bullfinches. *Condor* 70:323–332
- Ramirez JM, Bernstein MH (1976) Compound ventilation during thermal panting in pigeons: a possible mechanism for minimizing hypocapnic alkalosis. *Fed Proc* 35:2562–2565