

Cold exposure increases running $\dot{V}O_{2\max}$ and cost of transport in goats

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Schaeffer, P. J., J. F. Hokanson, D. J. Wells, and S. L. Lindstedt. Cold exposure increases running $\dot{V}O_{2\max}$ and cost of transport in goats. *Am J Physiol Regulatory Integrative Comp Physiol* 280: R42–R47, 2001.—We inadvertently subjected a group of goats to 5 mo of cold exposure (mean minimum temperature less than -13°C) during an experiment designed to examine the effects of training by daily running on one member of each sibling pair. During the three coldest months, the sedentary but cold-exposed goats experienced a 34% increase in maximal oxygen uptake ($\dot{V}O_{2\max}$, $P < 0.01$) and a 29% increase in running speed at maximal ($P < 0.05$). When temperatures increased in the spring, both oxygen uptake and running speed decreased. We interpret these findings as evidence that cold is a sufficient stimulus to invoke the development of aerobic structures in muscle and that these structures subsequently can be utilized for the novel task of running. When the experiment was subsequently repeated without the cold exposure, running speed and $\dot{V}O_{2\max}$ of trained animals increased less than in either group of cold-exposed animals. However, the cost of transport of these warm runners was lower than either group of cold-exposed animals (from 13–19%, $P < 0.0001$). Thus, although aerobic capacity was increased with acclimation to severe winter weather, cold-acclimated goats operated with lower efficiency during locomotion.

shivering thermogenesis; nonshivering thermogenesis; muscle adaptability; cross-adaptation.

MUCH OF OUR CURRENT KNOWLEDGE of mammalian adaptation to cold environments is traceable to the pioneering experiments of Hammel, Hart, Irving, Scholander and their associates decades ago (9, 12, 20, 25–28). The fundamental forms of adaptation to cold described therein are still widely accepted today. For warm-blooded animals in the cold, three qualitatively different kinds of adaptation are recognized: 1) hypothermic, 2) insulative, and 3) metabolic (30). First, animals may adapt by a relative reduction in metabolism and decrease in body temperature, which in its most extreme form results in hibernation. Alternatively, exposure to cold is met with either an increase in insulation and thus a decrease in heat loss so that changes in metabolism are not necessary for the maintenance of body temperature or by an increase in metabolism sufficient to protect body temperature. This increase in metabolism may be by nonshivering heat production occurring

primarily in brown adipose tissue (BAT) (19) as well as in muscle (2) and other organs (especially those that support aerobic metabolism such as heart and lungs) or by shivering thermogenesis in skeletal muscle (see Ref. 2 for review).

Although all metabolically active tissues generate heat, in mammals, skeletal muscle is one of two tissues capable of significant heat production (thermogenesis) in excess of basal rates, the other being BAT. However, whereas skeletal muscle accounts for about 40% of body weight in all mammals, only adult mammals ≤ 10 kg have BAT throughout their lifetime (10, 14). Hence, whether by shivering or nonshivering means, skeletal muscle is a potential source of elevated thermogenesis in all mammals and may be nearly the sole source in large mammals. Furthermore, given the high capacity of muscle for aerobic metabolism, muscle has a great capacity for heat production.

The adaptability of muscle, coupled with its capability to generate a large heat flux, preadapts it for a major role in whole animal acclimation to cold. Vertebrate skeletal muscle, once thought to possess limited phenotypic plasticity, is now known to be highly adaptable to changes in both the nature and intensity of the demands placed on it. Thus there are a suite of phenotypic adaptations that have been demonstrated in response to strength training, endurance training, as well as detraining effects or responses to disuse (see, e.g., Ref. 1). The cumulative outcome of numerous studies is the understanding that both the metabolic and contractile properties of skeletal muscle are continually subject to use-induced structural and functional modifications. Thus chronic exposure to cold environments, with a sufficient stimulus and if energy supplies are adequate, will result in an increase in the ability to produce heat in animals lacking BAT (5, 13, 16). Hence, summit metabolism [the maximum rate of oxygen uptake ($\dot{V}O_{2\max}$) in the cold] increases in response to chronic cold exposure, just as the $\dot{V}O_{2\max}$ during exercise increases in response to chronic endurance exercise training. It appears that muscle responds adaptively to chronic cold exposure, much as it does to strength and endurance training. However, the cross-adaptation, or lack thereof, of either training effect has

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not been investigated. Here we examine the functional outcomes of skeletal muscle adaptations that accompany a cold-induced seasonal increase in metabolism. Specifically, we investigate the question, do global, whole animal, functional responses resulting exclusively from cold exposure have any impact on an animal's metabolic capacity and locomotor performance during exercise?

MATERIALS AND METHODS

Experimental animals, Wyoming. Five sets of sibling pairs of (preweaned) goat kids were purchased at a livestock auction. The animals were housed in outdoor pole and rail pens at the Red Buttes Field Station operated by the University of Wyoming 10 miles south of Laramie. This facility is at 2,200-m elevation where the winters are long and extreme. The only shelter was an uninsulated plywood lean-to in the corner of the pen. All animals were provided with food (alfalfa and grain as adults) and water ad libitum. These animals constituted our cold-exposed groups.

Experimental animals, Arizona. A second set of five sibling pairs of goats was purchased from a goat breeder in Arizona. These goats were housed in chain-link pens in Flagstaff (similar, 2,100-m elevation, but in a much more moderate climate). The Flagstaff goats had free access to an enclosed heated shelter and were confined to the shelter on all winter nights. All animals were provided with food (alfalfa and grain as adults) and water ad libitum. These animals constituted our temperature-control groups (protected from cold temperatures). All animals were maintained in accordance with the guidelines of the Animal Care Committees of the University of Wyoming and Northern Arizona University, as well as the National Institutes of Health *Guide for the Care and Use of Laboratory Animals*, revised 1985.

Endurance training. In both locations, the goat kids were individually trained to run on a motorized treadmill (by using a baby bottle of milk as an enticement). About 6 wk were required to train all of the animals to run with little encouragement on the treadmill. Once all the animals were accustomed to the treadmill, the goats in each location were randomly divided (by sibling pair) into control (sedentary) and experimental (endurance trained) groups. Thus the four groups constituted a 2×2 experimental design for the comparison of training and temperature effects on aerobic capacity.

Animals in the experimental group were endurance trained by running on the treadmill for 15 min daily (5 days/wk) at a speed calculated to require 85% of their $\dot{V}O_{2\max}$ (as determined at the beginning of the study and every 3 mo subsequently). Because training speeds varied on an individual basis, goats were paired with "training partners" so that two animals could be trained simultaneously. Grain was used as an incentive during the daily training runs. $\dot{V}O_{2\max}$ was determined for both the trained and untrained goats every 3 mo for 1 yr. Measurements were made at the end of September, December, March, and June, representing as 3, 6, 9, and 12 mo of endurance training. The training ceased and the animals were killed at the end of the training year.

$\dot{V}O_{2\max}$ and running speed. $\dot{V}O_{2\max}$ and running speeds for all animals were determined at the beginning of the experimental period and at 3-mo intervals thereafter. Oxygen uptake was determined for each animal using an open-flow system with the animals wearing a loose-fitting polyethylene mask. A constant bias flow of air (~ 500 l/min) was drawn through the mask by a remote shop vacuum. A small sample of the excurrent air was withdrawn for determination of its

oxygen content (Ametek SA-3 analyzer). The oxygen analyzer was calibrated, and $\dot{V}O_2$ was calculated using the technique described by Fedak et al. (7). Constant flow rate out of the mask was obtained by exactly regulating the line voltage (SOLA voltage regulator model MCR 2000) to the vacuum. Flow was monitored by a venturi flowmeter and differential pressure transducer (packed in foam to ensure temperature stability) in the excurrent line. $\dot{V}O_{2\max}$ was determined for each animal by a progressive step test (29). Whereas the animals ran on the treadmill, speed was increased every 2 min with oxygen uptake measured continuously. Treadmill speed was calibrated by measuring the time required for a mark on the treadmill to make a complete circuit. Final treadmill speeds were recorded at the end of each run. End run lactate was determined on whole blood (collected by venapuncture from the jugular vein) with a Yellow Springs Instrument model 27 lactate analyzer. Criteria to establish $\dot{V}O_{2\max}$ included blood lactate in excess of 5 mM, which was usually accompanied by a plateau of oxygen uptake (independent of increased tread speed). Once the speed necessary to elicit $\dot{V}O_{2\max}$ was determined for each animal, repeated runs (of 5-min duration, at least 3 per animal) were performed at that constant speed, $\dot{V}O_{2\max}$ was again calculated, and end-run lactate concentration was determined.

Cost of transport at $\dot{V}O_{2\max}$. A cost of transport at $\dot{V}O_{2\max}$ (COT_M) was then calculated by dividing the oxygen costs ($\dot{V}O_{2\max}$ in $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) by the speed of running at maximum (m/min). Although not a conventional measure of cost of transport, this measure does provide a point of insight into the economy of locomotion in these animals. Furthermore, if end-run lactates are similar then the aerobic and anaerobic contribution to this measure (COT_M) can be assumed to not differ between groups.

Statistical analysis. Five variables (body weight, $\dot{V}O_{2\max}$, running speed at $\dot{V}O_{2\max}$, COT_M , and lactate concentration) were analyzed with ANOVA (GLM model; SAS, ver. 8, SPSS) examining the effects of temperature, training, and individual goat. Data across all time periods were initially considered together, resulting in a conservative test of our main effects. F values for the effect of temperature and training were calculated by dividing the mean square for each by an error term calculated from the mean square for the individual goat term and the mean square error term. The F value for the effect of the individual goat was calculated by dividing the mean square for individual goat by the mean square error term. This tested for variation among different animals within any one training or temperature group. For those variables that showed significant differences, a one-way ANOVA (Sigma-Stat, ver. 2.03; SPSS) was run using the data from all four groups at 9 and 12 mo of training. Pairwise comparisons were then made using Tukey's test. The level of significance was set at $P < 0.05$ in all cases.

RESULTS

Experimental animals. Although the two pairs of animals lived under considerably different environmental conditions, body weight data showed no significant differences (ANOVA, $P > 0.05$). Table 1 shows the mean value for each group at each time point.

$\dot{V}O_{2\max}$. Both endurance exercise training and cold exposure had a significant impact on maximal aerobic capacity (ANOVA, $P < 0.0001$). Individual animal variation within each experimental group was not significant (ANOVA, $P = 0.15$). As a consequence of daily endurance training, the $\dot{V}O_{2\max}$ of the trained and

Table 1. Data for weight, running speed at $\dot{V}O_{2\max}$ and lactate concentration at $\dot{V}O_{2\max}$ in each group of goats

Variable	Time of Training, mo	Warm Sedentary	Warm Trained	Cold Sedentary	Cold Trained
Weight, kg*	3	18.9 ± 1.1(6)	19.2 ± 1.2(6)	18.5 ± 2.8(5)	21.1 ± 2.3(4)
	6	22.8 ± 1.5(5)	22.6 ± 1.1(6)	24.7 ± 2.7(5)	28.5 ± 2.3(5)
	9	26.3 ± 1.5(6)	28.4 ± 0.9(6)	29.2 ± 2.2(5)	33.1 ± 2.5(6)
	12	35.1 ± 2.0(6)	37.4 ± 2.1(5)	36.7 ± 2.5(6)	39.8 ± 2.6(6)
Speed at $\dot{V}O_{2\max}$, m/min†	3	3.51 ± 0.05(6)	3.53 ± 0.05(6)	2.90 ± 0.11(5)	3.67 ± 0.10(4)
	6	3.56 ± 0.04(5)	3.78 ± 0.04(6)	3.35 ± 0.18(5)	4.61 ± 0.08(5)
	9‡	3.68 ± 0.05(6)	4.33 ± 0.07(6) ^f	4.33 ± 0.26(5) ^e	5.28 ± 0.18(6) ^{a,b,c}
	12‡	3.80 ± 0.05(6)	4.87 ± 0.09(5) ^f	4.48 ± 0.26(6)	4.98 ± 0.20(6) ^c
[Lactate], mM*	3	7.0 ± 0.27(6)	7.0 ± 0.10(6)	5.6 ± 0.16(5)	5.4 ± 0.06(4)
	6	9.4 ± 0.16(5)	7.9 ± 0.34(6)	6.8 ± 0.22(5)	7.4 ± 0.04(5)
	9	8.8 ± 0.21(6)	8.8 ± 0.20(6)	6.0 ± 0.18(5)	7.1 ± 0.16(6)
	12	7.3 ± 0.21(6)	7.0 ± 0.26(5)	8.8 ± 0.15(6)	8.8 ± 0.25(6)

Values are means ± SE; no. of animals studied in parentheses. *ANOVA showed no significant effect of treatments ($P > 0.05$). †ANOVA showed significant differences between groups, overall model, $P < 0.001$; temperature effects, $P < 0.05$; training effects, $P < 0.0001$; individual variation, $P = 0.2036$. ‡One-way ANOVA comparing each group within this time point, $P < 0.001$. Individual pairwise differences (Tukey's tests): ^acold trained (CT) ≠ cold sedentary (CS), ^bCT ≠ warm trained (WT), ^cCT ≠ warm sedentary (WS), ^eCS ≠ WS, ^fWT ≠ WS. $\dot{V}O_{2\max}$, maximal oxygen uptake.

control goats began to diverge after 3 mo and continued to do so at 6 mo. After 6 mo of training in Flagstaff $\dot{V}O_{2\max}$ was 9% greater in the trained goats compared with their untrained siblings (see Fig. 2). In contrast, after 6 mo of training in Laramie $\dot{V}O_{2\max}$ was 29% greater in the trained goats than in their untrained siblings. At this point in their training, the goats in Laramie were already beginning to experience winter weather.

During the five coldest months of this year-long study (*months 5 through 9*), the mean ambient temperature had been -6.7°C and the mean minimum temperature -13.5°C (Fig. 1). Each of those 5 mo had one or more days in which the minimum temperature fell below -20°C and the three coldest months had several days in which the minimum temperature dropped be-

low -25°C (Fig. 1). Usually, these cold temperatures were accompanied by strong winds, resulting in "wind chill" equivalence of temperatures often below -50°C .

The pattern of training-induced increase in aerobic capacity changed both quantitatively and qualitatively during the winter months. At the 9-mo time point, there were significant differences among the four groups (ANOVA, $P < 0.001$). In Laramie, the measurements made after 9 mo of training followed the coldest winter months (*months 7 through 9*). $\dot{V}O_{2\max}$ in the untrained, cold-exposed goats increased dramatically (by 34%) and was no longer significantly different from the cold-exposed, trained goats (Fig. 2). In contrast, the temperature-control (Flagstaff) goats showed no disproportionate increase in $\dot{V}O_{2\max}$ between *months 6 and 9* and the difference in $\dot{V}O_{2\max}$ comparing the control and trained goats at 9 mo (17.5%) was statistically significant (Fig. 2). However, at 9 mo, the measured values of $\dot{V}O_{2\max}$ of the Flagstaff goats, both endurance trained and untrained, were significantly lower than those of their activity matched pair of cold-exposed goats (30 and 32% below, respectively; Fig. 2). Among the groups, differences remained significant at the 12-mo time point (ANOVA, $P < 0.001$). $\dot{V}O_{2\max}$ of the trained Flagstaff goats continued to increase between *months 9 and 12* (to 28% higher than their sedentary controls after 12 mo). With the end of winter cold in this period, $\dot{V}O_{2\max}$ decreased slightly in both groups of Laramie goats (despite continued endurance training in the cold-trained animals). At 12 mo, $\dot{V}O_{2\max}$ of the two cold-exposed groups remained statistically equivalent, although both were still significantly higher than the sedentary temperature controls and the cold-trained goats were still significantly higher than their warm-trained counterparts (Fig. 2).

Running speed at $\dot{V}O_{2\max}$. Speed at $\dot{V}O_{2\max}$ was also affected by both endurance exercise training and cold exposure (ANOVA, $P < 0.001$). Individual animal variation within each experimental group was not signifi-

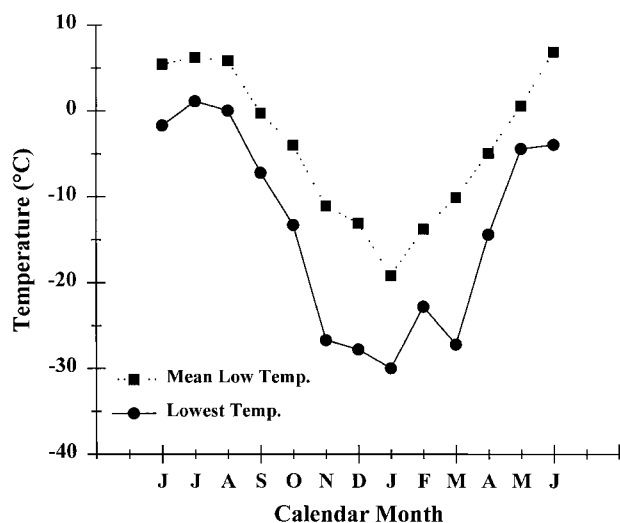


Fig. 1. Two measures of ambient temperature (the monthly mean low temperature and monthly extreme low temperature) are shown over the 12 mo of endurance training for 2 groups of goats maintained in Laramie, Wyoming. November through March constitute the coldest months of the year.

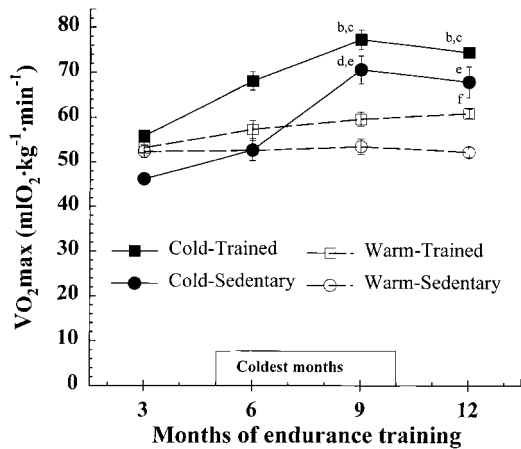


Fig. 2. Maximum oxygen uptake ($\dot{V}O_{2\max}$) is shown as a function of experiment duration. Trained goats (\square , \blacksquare) were run on a motorized treadmill for 15 min daily, 5 days/wk. Their untrained siblings are labeled as sedentary (\circ , \bullet). Cold-exposed goats (\blacksquare , \bullet) were maintained outdoors throughout an entire Wyoming winter (see text for details). Goats that were protected from the cold (in Flagstaff) are labeled as warm (\square , \circ). Symbols are group mean values (the mean of the individual animal means) for 4–6 animals (n of each group same as that for running speed; see Table 1); error bars represent the SE. ANOVA showed significant overall differences as well as significant effects of both temperature and training ($P < 0.001$ in all cases). At both 9 and 12 mo, one-way ANOVA showed significant differences among the 4 groups ($P < 0.001$). CT, cold-trained; CS, cold-sedentary; WT, warm-trained; WS, warm-sedentary) Individual pairwise differences (Tukey's tests) are shown as follows: ^bCT \neq WT; ^cCT \neq WS; ^dCS \neq WT; ^eCS \neq WS; ^fWT \neq WS.

cant ($P = 0.20$). The largest increases in running speed were seen among the endurance-trained animals, but like $\dot{V}O_{2\max}$ also increased dramatically in the cold-exposed, sedentary goats. Significant differences existed between the groups after 9 mo of training and after the Laramie goats had experienced 5 mo of extreme winter weather (Table 1, ANOVA, $P < 0.001$). At this point, the cold-exposed, sedentary goats were running at nearly identical speeds as the warm, exercise-trained goats, both significantly faster (by 18%) than the warm, sedentary goats. At 9 mo, the cold-exposed, trained goats were running significantly faster than all three other groups, 22% faster than the warm-trained or cold-sedentary goats and 43% faster than the warm-sedentary goats. Among the groups, differences remained significant at 12 mo, but the pattern of differences was altered (Table 1, ANOVA, $P < 0.001$). After the removal of the cold stimulus, no further increases in running speed were seen in either cold-exposed group with a slight decline in the cold-exposed, endurance-trained goats. At this point, the cold-trained goats were running at speeds that were similar to both the warm-trained and the cold-sedentary goats, but still faster than the warm-sedentary goats. The warm-trained goats continued to increase running speeds with training, still running faster than the warm-sedentary goats and now equal to the cold-trained goats as well (Table 1).

Cost of transport at $\dot{V}O_{2\max}$. Measurements of running speed at $\dot{V}O_{2\max}$ include the contribution of both aerobic and anaerobic power. To minimize the effect of

anaerobic energy use as a confounding factor in the assessment of COT_M , we analyzed the blood lactate concentrations measured at $\dot{V}O_{2\max}$ after each run. ANOVA showed no significant differences between groups (Table 1; $P > 0.05$). Thus although calculating a cost of transport at $\dot{V}O_{2\max}$ gives an underestimate (because anaerobic ATP production is substantial at $\dot{V}O_{2\max}$), for comparative purposes this is a valid measure of energy costs of running.

Analysis of COT_M showed significant differences (ANOVA, overall model effect, $P < 0.0001$). However, the only significant effects were temperature ($P < 0.05$) and intra-group variation ($P < 0.01$). The effects of endurance training were not significant ($P = 0.06$), although it is likely that a less conservative statistical method would have found this to be a significant effect as well. As with the variables from which COT_M is derived ($\dot{V}O_{2\max}$ and running speed at $\dot{V}O_{2\max}$), ANOVA showed significant differences between groups after 9 mo of exercise ($P < 0.01$). This difference is due to the COT_M being significantly higher in the cold-exposed, sedentary goats compared with either of the two warm groups (13 and 19%, respectively). The cold-exposed, trained goats were intermediate but not different from any of the other groups. After 12 mo, ANOVA again showed significant differences in COT_M ($P < 0.001$). With the end of winter weather, the COT_M of the cold-exposed, sedentary goats appeared to decline but remained significantly elevated compared with the two warm groups. The cold-exposed, trained goats also showed elevated COT_M compared with the warm-trained goats. The COT_M declined throughout the training period in the warm, trained goats such that COT_M of the cold-trained and cold-sedentary goats was 14 and 21% higher, respectively (Fig. 3).

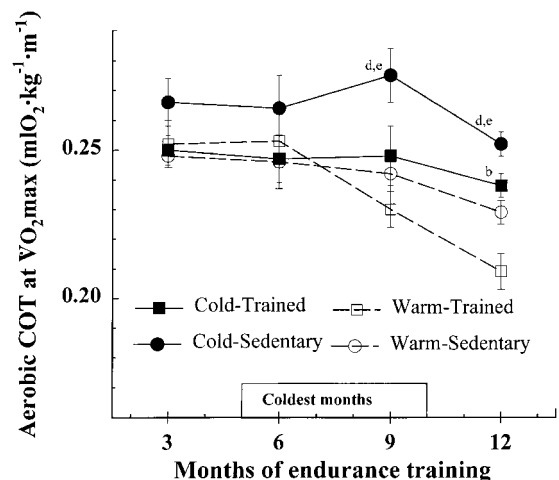


Fig. 3. Cost of transport (COT) at $\dot{V}O_{2\max}$ is shown as a function of experiment duration. Symbols are the same as in Fig. 2. ANOVA showed significant overall differences as well as significant effects of temperature ($P < 0.001$ and $P < 0.01$, respectively). At both 9 and 12 mo, one-way ANOVA showed significant differences among the 4 groups ($P < 0.01$ and $P < 0.001$, respectively). Individual pairwise differences (Tukey tests) are shown as in Fig. 2 with the exception that training effects were not tested because they were found insignificant (ANOVA, $P > 0.05$).

DISCUSSION

To protect body temperature and to compensate for increase heat loss, birds and mammals respond to the cold by increasing their metabolic heat production. This relationship was first quantified by Scholander and colleagues in their classic studies comparing arctic and tropical mammals approximately 50 years ago (26–28). As the ambient temperature drops below thermoneutrality, there is a linear increase in heat production ($\dot{V}O_{2\max}$) with decreasing ambient temperature. Often, in particular in small or young mammals, the task of thermogenesis is shared by BAT and muscle tissue. However, mammals weighing more than about 10 kg lack BAT as adults (10, 14).

In studies of mammals that possess BAT, muscle adaptation appears to have a relatively small role in a metabolic response to cold. Unacclimated rats respond to a cold challenge with an increase in metabolic heat production that is largely due to increased shivering thermogenesis. However, on prolonged exposure to cold, BAT hypertrophy results in the replacement of shivering with nonshivering thermogenesis (11). Similarly, in hamsters, blood flow to muscle is decreased during nonshivering thermogenesis, and the magnitude of this decrease is greater after cold acclimation (15). In the musculature of cold-exposed guinea pigs, Hoppeler et al. (18) found no evidence of structural adaptation to increased energy demand. Thus the vigorous hypertrophy of BAT appears to fully account for the metabolic acclimation to cold exposure in these animals.

Other mammals lacking BAT also show increased metabolic heat production in response to cold acclimation with the exception of humans in whom studies have shown mixed results. Shivering intensity as well as oxygen uptake was higher in both cold-acclimated miniature pigs (5), as well as large white pigs, (13) compared with warm-acclimated controls, although there was also evidence for nonshivering thermogenesis. Studies of human acclimation to various repeated cold-exposure regimens have usually resulted in a diminished metabolic response to a subsequent cold challenge (e.g., 4, 6, 21). These studies typically do not result in a hypothermic response and have been termed tolerance adaptation (4). However, it is difficult to carry out human experiments that are comparable in magnitude to the exposure that animal studies typically use. This problem has been circumvented in studies of Korean women divers who experience severe cold stress on a daily basis. These women show a mix of hypothermic, insulative, and metabolic adaptations after cold acclimation, with impressive increases in aerobic capacity (16). Similarly, Scholander et al. (24) showed increased metabolic capacity in response to cold in a group of men who lived above tree lines in Norway for 2 mo during the late autumn. Thus whereas these species lack BAT, they do acclimate to cold temperatures by increasing their whole body metabolic capacity.

Because goats lack BAT, the primary mechanism available for heat production is shivering and nonshivering thermogenesis by the muscle tissue. Exposure to the extremely low temperatures and strong winds of a cold Wyoming winter provides a powerful and prolonged demand for heat production. How does the suite of adaptive responses to cold differ from those resulting from aerobic training?

First, the magnitude of the response is as great or greater than that typical of endurance training. Hence, the increase in $\dot{V}O_{2\max}$ following chronic cold exposure resulted in over double the increase accruing from daily training. This may not be the result of the intensity, but rather the duration of each of these stimuli. The magnitude of the cold-alone stimulus was great enough that there was no additive (synergistic) response of cold plus training. In other words, cold alone produced the same magnitude of response as cold plus training. In fact, detraining occurred with the return of warm weather, independent of continued, daily running at an estimated 85% of $\dot{V}O_{2\max}$!

Second, in addition to a quantitative shift to increased aerobic capacity, the cold exposure also resulted in a qualitative shift in muscle function as well. Although the increased aerobic capacity of the muscle could be exploited during locomotion (i.e., running $\dot{V}O_{2\max}$ increased greatly following cold exposure), the relationship between running speed and oxygen uptake was significantly altered. Cost of transport (defined as the energy necessary to move 1 kg of body mass 1 m) differed predictably with temperature and less so with endurance training. Hence, those animals subject to the cold but no running had the highest cost of transport. Likewise, daily running with no cold exposure resulted in the lowest cost of transport. The trend was that cold was a greater determinant than running in setting the cost of transport. Again, this may be explainable by the relative durations of each of these stimuli.

Like most other mammals, goats adapt to the cold by increasing their metabolic heat production. Because the winter nights are not only cold, but long as well, the cold exposure was intense and prolonged. This cold exposure served as a particularly severe form of aerobic training. The running aerobic capacity increased in goats that were either exercise trained or cold exposed, demonstrating cross adaptation (i.e., the ability to use those structures resulting from one task for a novel task).

Perspectives

The suite of muscle adaptations resulting from cold exposure in goats is both large in magnitude and seems identical to the kinds of adaptations that result from endurance exercise training. Thus the basic aerobic structures that serve heat production are available to fuel locomotion as well, resulting in large quantitative increases in running $\dot{V}O_{2\max}$ following cold exposure without endurance training. However, these results suggest that muscle from cold-exposed goats

became specialized for heat generation, resulting in a decrease in the efficiency in the coupling of metabolic energy flux to locomotor performance. Alterations in mechano-chemical coupling could be explained by the development of higher basal metabolism in muscle, which could not be eliminated during locomotion, perhaps by addition of uncoupling proteins to mitochondria (8), by increases in the permeability of the mitochondrial inner membrane (3), or by increased futile cycling (2). Likewise, efficiency of ATP utilization could be reduced if the specific myosin expressed in response to cold exposure is poorly suited for locomotion. Inasmuch as we did not measure these variables, more experiments will be required to elucidate a mechanism for this observation.

Variability in the observed maximal aerobic capacity among individuals of a single species is not uncommon. The influence of differing ambient temperatures, especially for studies of wild animals, may explain much of this variation. Temperature influences need not be severe to influence measurements of aerobic capacity and may be an under-appreciated factor in explaining inter-individual variation.

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