Influence of training on sweating responses during submaximal exercise in horses

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McCUTCHEON, L. J., AND R. J. GEOR. Influence of training on sweating responses during submaximal exercise in horses. J Appl Physiol 89: 2463–2471, 2000.—Sweating responses were examined in five horses during a standardized exercise test (SET) in hot conditions (32–34°C, 45–55% relative humidity) during 8 wk of exercise training (5 days/wk) in moderate conditions (19–21°C, 45–55% relative humidity). SETs consisting of 7 km at 50% maximal O2 consumption, determined 1 wk before training day (TD) 0, were completed on a treadmill set at a 6° incline on TD0, 14, 28, 42, and 56. Mean maximal O2 consumption, measured 2 days before each SET, increased 19% [TD0 to 42: 135 ± 5 (SE) to 161 ± 4 ml·kg−1·min−1]. Peak sweating rate (SR) during exercise increased on TD14, 28, 42, and 56 compared with TD0, whereas SRs and sweat losses in recovery decreased by TD28. By TD56, end-exercise rectal and pulmonary artery temperature decreased by 0.9°C, respectively, and mean change in body mass during the SET decreased by 0.1 and 1.2 kg. Mean maximal O2 consumption, determined 2 days before each SET, increased 19% [TD0 to 42: 135 ± 5 (SE) to 161 ± 4 ml·kg−1·min−1]. Peak sweating rate (SR) during exercise increased on TD14, 28, 42, and 56 compared with TD0, whereas SRs and sweat losses in recovery decreased by TD28. By TD56, end-exercise rectal and pulmonary artery temperature decreased by 0.9 ± 0.1 and 1.2 ± 0.1°C, respectively, and mean change in body mass during the SET decreased by 23% (TD0: 10.1 ± 0.9; TD56: 7.7 ± 0.3 kg). Sweat Na+ concentration during exercise decreased, whereas sweat K+ concentration increased, and values for Cl− concentration in sweat were unchanged. Moderate-intensity training in cool conditions resulted in a 1.6-fold increase in sweating sensitivity evident by 4 wk and a 0.7 ± 0.1°C decrease in sweating threshold after 8 wk during exercise in hot, dry conditions. Altered sweating responses contributed to improved heat dissipation during exercise and a lower end-exercise core temperature. Despite higher SRs for a given core temperature during exercise, decreases in recovery SRs result in an overall reduction in sweat fluid losses but no change in total sweat ion losses after training.

sweating rate; sweat ion concentrations; fluid regulation; heat dissipation

IN HUMAN SUBJECTS UNDERGOING physical training in a cool environment, comparisons of pre- and posttraining tests at the same absolute workload have demonstrated reductions in end-exercise core temperature (1). Adaptations that can improve heat dissipation and thereby reduce the rate of increase of core temperature include an earlier onset of sweating (lower sweating threshold), higher sweating rates (SRs) for a given core temperature (increased sweating sensitivity), and an increase in the proportion of cardiac output directed toward the cutaneous circulation (9, 21). Augmentation of these mechanisms requires a repeated, sustained elevation of core temperature and has been induced in human subjects by intense interval training or by more prolonged exercise at an intensity exceeding 50% of the subject’s maximal oxygen consumption (Vo2 max)(7).

In addition to improved heat dissipation, repeated or continuous exposure to hot conditions has also been associated with modifications of sweat fluid that result in more diluted sweat, with ion conservation largely reflecting decreases in sweat Na+ content (26). Whereas such adaptations are more typically associated with repeated or continuous exposure to hot conditions (heat acclimation), modification of sweat fluid composition in horses as a result of sustained elevations of core temperature during repeated moderate- to high-intensity exercise has been reported after training (15).

During exercise in hot conditions, metabolic heat production by skeletal muscle can limit exercise capacity. The reduction in the thermal gradient for heat loss to the environment increases the rate of heat storage and reduces the time to a critical hypothalamic temperature that results in voluntary fatigue (13). In the exercising horse, these limitations are greater than in humans as a result of the use of a larger proportion of body mass during locomotion (greater rate of heat production per unit body mass) and a higher metabolic rate at any given relative workload (13). Conversely, a two- to threefold lower surface area-to-body mass ratio (m2/kg) in horses results in a significantly lower mass-specific area for heat dissipation (9, 27). Consequently, even in cool conditions, the high rate of metabolic heat production combined with physical constraints on convective, conductive, and evaporative heat loss result in elevations in core (rectal) temperature (Tre) of 2.5–3.5°C after <30 min of exercise at 50% of Vo2 max.

Similar to humans, horses are highly reliant on sweating for heat dissipation during exercise. However, SRs per unit surface area are greater in trained equine athletes compared with human counterparts. In fit horses exercising at 40–50% Vo2 max in hot conditions, an earlier onset of sweating was observed, and peak sweating rate increased, both of which are adaptations that can improve heat dissipation during exercise. The increase in sweating rate was associated with a decrease in sweating sensitivity, which suggests that the increased rate of sweating was not due to the increased metabolic heat production alone. Instead, this increase in sweating rate may have been a result of the increased core temperature and the decreased thermal gradient for heat loss to the environment.

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titions, local SRs of 35–40 ml·m⁻²·min⁻¹ (~10 l/h) have been measured (14, 18). However, in contrast to studies of active acclimation in human subjects, in which SRs increase after repeated exposure to humid heat, no increase in the sensitivity of the sweating response in relation to Tₑₚ or pulmonary artery temperature (Tₑₚ) was detected in horses after 15 or 20 days of humid heat acclimation (14, 17). In these studies, horses had been trained in cool conditions before heat acclimation. To date, there have been no equine studies on the effects of training on sweating responses. Inasmuch as submaximal exercise in horses in moderate ambient conditions results in a higher core temperature compared with human subjects exercising at the same workload, the contribution of exercise training to improvements in heat dissipation may be greater in horses than in humans. Furthermore, the high SRs measured in trained horses during heat acclimation, coupled with the absence of a change in sweating sensitivity during this period, would support the hypothesis that exercise training in moderate ambient conditions provides sufficient thermal stimulus to provoke a significant enhancement of mechanisms for heat dissipation. Therefore, this study was designed to determine whether the responses in horses to training in cool conditions were sufficient to result in increases in SR and sweating sensitivity during exercise in hot ambient conditions. A significant augmentation of these responses during training could explain the relatively small improvements in heat dissipatory mechanisms reported during subsequent periods of heat acclimation (14, 17).

In the present study, we examined sweating responses in five untrained Thoroughbred horses at 2-wk intervals throughout an 8-wk training regimen. We hypothesized that 8 wk of training in moderate ambient conditions, at intensities sufficient to cause a sustained increase in Tₑₚ of 2–3°C, would result in alterations to sweating responses during exercise in hot conditions. Specifically, we hypothesized that the thermal stimulus imposed by moderate-intensity exercise training would result in 1) an increased sweating sensitivity, 2) reduction in the Tₑₚ and Tₑₚ for the onset of sweating, 3) a lower end-exercise Tₑₚ and Tₑₚ, and 4) a decrease in the ion content of sweat [as a result of a decrease in sweat Na⁺ concentration ([Na⁺]) during a standardized exercise test (SET) in hot, dry conditions.

MATeRIALS AND METHODS

The care and use of animals followed the Guide to the Care and Use of Experimental Animals (Canadian Council on Animal Care, Ottawa, ON). All animal experiments were conducted after approval by the Animal Care Committee of the University of Guelph and were performed in compliance with their recommendations.

Subjects. Five mature Thoroughbred horses (3–6 yr of age; 3 geldings and 2 mares), weighing 437–498 kg [469.6 ± 10.3 (SE) kg], were used. Horses had been paddock rested for a minimum of 16 wk before the commencement of the study but had been acclimated to exercise on the treadmill before this period. Throughout the study, horses were housed indoors in box stalls maintained at 18–20°C and were fed a diet of timothy grass and alfalfa hay (4–5 kg/day) and a commercially prepared mixed grain ration (Purina, Mississauga, ON) supplemented daily with 100 g NaCl and 50 g KCl. The quantity of mixed grain ration was progressively increased from 2 to 4.5 g/day as the duration and intensity of the training increased. Exercise was restricted to that associated with the training regimen.

Experimental design. The investigation was designed as a longitudinal study, with each horse completing a SET at 2-wk intervals throughout the study. For the training sessions, horses were exercised on a treadmill (Sato) in an environmentally controlled room in moderate conditions [19–21°C, 45–55% relative humidity (RH)]. The training protocol consisted of treadmill exercise (3° incline) for 5 days/wk, with a gradual increase in the duration and intensity of exercise. Horses were exercise trained for 8 wk, with increases in exercise duration and intensity after each week. Initially, horses were required to complete 20 min at 4 m/s, 2 min at 5.5 m/s, and 1 min at 7 m/s (~6,000 m). In successive weeks, training time at 4 m/s was increased (~2 min/wk), and time and speed at higher workloads were also increased gradually such that, at the end of 8 wk of training, a maximum distance of 9–10 km/day at speeds ranging from 4 to 9 m/s was achieved. Tₑₚ was measured continuously at rest and during exercise in each training session. On training days (TD) 0, 14, 28, 42, and 56, horses completed a SET in hot ambient conditions (32–34°C, 45–55% RH). Two days before each SET, the Vₒ₂ max of each horse was measured by using an incremental exercise test.

Exercise protocol. Food was withheld overnight, and water was withheld for 3 h before the start of each SET. A catheter for collection of mixed venous blood and measurement of Tₑₚ was placed in the pulmonary artery (via the left jugular vein; PE 240, Becton Dickinson) after aseptic preparation and local anesthesia of the overlying skin. The position of the catheter in the pulmonary artery was verified by observation of characteristic pressure traces with an oscilloscope monitor (Tecktronix 401, Spacelabs Medical Products, Mississauga, ON) and a pressure transducer (DTX model T36AD-B, Viggo-Spectromed, Oxnard, CA). After measurement of body mass (~0.5 kg; KSL Scales, Kitchener, ON), horses were kept in a holding area (room temperature 20°C) until 15 min before exercise. At that time, horses were moved to an environmentally controlled exercise laboratory and positioned on a high-speed treadmill (Sato). A thermodilimeter (model 3309–60, Cole-Palmer Instruments, Chicago, IL) was used to monitor ambient conditions during all SETs. The room was maintained at 32–34°C and 45–55% RH throughout each SET.

Each SET consisted of 7 km of treadmill exercise (6° incline) at a speed equivalent to 50% of the pretraining Vₒ₂ max (range 3.7–4.1 m/s), followed by a 30-min standing recovery. A fan mounted above and 0.5 m in front of the treadmill was used to maintain an air velocity of 3.5–4 m/s over the anterior and dorsal aspects of the horse. Air velocity was measured with an anemometer (Davis Instruments, Hayward, CA) positioned at three sites: lateral midcervical region, lateral and dorsal thorax, and dorsal to the gluteal region of the hindquarters. During each SET, sweat fluid for determination of local SR was collected at 5-min intervals during exercise and recovery; Tₑₚ and Tₑₚ were also measured at each 5-min interval. Body mass was measured after completion of exercise test. The hair coats of the horses were clipped to a length of ~1.0 cm; no correction was made for trapping of sweat in the hair coat.

Measurement of oxygen consumption. Oxygen consumption (Vₒ₂) for the determination of Vₒ₂ max was measured by using
an open-circuit calorimeter (5). \( \dot{V}O_2 \text{max} \) was determined by use of an incremental step test in which the horses trotted for 5 min at 4 m/s, after which treadmill speed was increased to 6 m/s and was subsequently increased in 1 m/s increments each minute until the horse could no longer keep pace with the treadmill, despite verbal encouragement. \( \dot{V}O_2 \text{max} \) was defined as the value at which \( \dot{V}O_2 \) reached a plateau, despite further increases in speed, and when respiratory exchange ratio was >1.0. A plateau was defined as a change in \( \dot{V}O_2 \) of <4 ml·kg\(^{-1}\)·min\(^{-1}\) with an increase in speed. From linear regression analysis, the running speed that elicited 50% \( \dot{V}O_2 \text{max} \) was calculated for each horse.

**Measurement of body temperature.** T\(_{pa}\) was measured by placing a thermocouple (T-180; Physitemp Instruments) 20–30 cm proximal to the anal sphincter. T\(_{re}\) was measured by inserting a thermocouple into the pulmonary artery within the catheter introduced via the jugular vein. Thermocouples had response times of \( \sim 1\) s when calibrated in a heated water bath with a NIST-traceable thermometer (Fisher Scientific, Mississauga, ON).

**Measurement of sweating responses.** Local SR was based on measurement of the volume of sweat samples obtained from an area of the left lateral thorax by use of a direct sweat collection method, as described elsewhere (19). In brief, a sealed polyethylene pouch enclosing a 150-cm\(^2\) area of skin was attached to an area of shaved skin with a dermal adhesive. The edges of the pouch were further sealed by dermal tape that covered the pouch/skin margin. A ventral reservoir, formed by a deep fold in the polyethylene, separated accumulating sweat from the skin surface and facilitated the formation of a deep fold in the polyethylene, separated accumulating sweat from the skin surface and facilitated the formation of an open-circuit calorimeter (5). Sweat fluid was collected within the pouch at each time point during exercise and recovery. For successive SETs, placement of the pouch was alternated between left and right thorax.

Local SR, expressed as milliliters per square meter per minute, was calculated on the basis of the volume of sweat collected from the measured skin area within the pouch at the end of each 5-min interval. Therefore, the measured SR represents the average rate of sweat production over a 5-min period. Extrapolation of the local SR at each time point during exercise and recovery to the horse's total body surface area was used to calculate a mean whole body SR. Total body surface area (SA) was calculated by using the formula (9)

\[
SA = 1.09 + 0.008 \times \text{body mass (kg)}
\]

Peak SR (SR\(_{\text{peak}}\)) was used to describe the highest rate of sweat production attained during each SET and corresponded with the SR measured at the end of exercise. Total sweat fluid loss for the duration of exercise and recovery was estimated from the total body water losses after correction for fecal and estimated respiratory water losses; this was assumed to represent a constant percentage (\( \sim 15\% \)) of the overall water losses (9). No horse voided urine during any of the SETs. The effect of training on the SR-body temperature relation was evaluated by determining the slope (expressed as ml·m\(^{-2}\)·min\(^{-1}\)·°C\(^{-1}\)) and the x-intercept of the regression line representing the mean SR and temperature (T\(_{pa}\) or T\(_{re}\)) for each 5-min interval during exercise; temperature was the mean of the temperature (T\(_{pa}\) or T\(_{re}\)) at the start and the finish of each 5-min interval. The x-intercept (the temperature at which the regression line of the sweating vs. temperature relation extends to the zero value of the x-axis) was used as an estimate of the sweating threshold (24).

**Measurement of sweat ion concentrations and sweat ion losses.** [Na\(^+\)], K\(^+\) concentration ([K\(^+\)]), and Cl\(^-\) concentration ([Cl\(^-\)]) in sweat were determined with an ion-selective analyzer (Nova Statprofile 9; Nova Biomedical, Boston, MA). All analyses were performed in duplicate. Total losses of Na\(^+\), K\(^+\), and Cl\(^-\) in sweat were calculated based on the ion concentrations of samples collected and the SR during each 5-min interval during exercise and recovery. For each SET, linear regression analysis was used to examine the relation between SR and sweat [Na\(^+\)] for every 5-min interval during exercise.

**Statistical analyses.** Data were analyzed by using two-way ANOVA with repeated measures to compare measures over time among SETs. When a significant F ratio was obtained, the Bonferroni post hoc test was used to test for differences among means. The slope and threshold of each individual's SR vs. sweat [Na\(^+\)] and SR vs. T\(_{pa}\) and T\(_{re}\) relation were determined by least squares linear regression. A one-way repeated-measures ANOVA was used to determine whether differences in slope or intercept data existed among training days. Data are reported as means ± SE. Unless otherwise stated, significance was accepted at \( P < 0.05 \).

## RESULTS

### Environmental conditions.

Mean room temperature and RH during the SETs on TD0, 14, 28, 42, and 56 were 33.5 ± 0.3°C and 48 ± 5%, respectively, with no difference among days for these environmental conditions (\( P > 0.71 \)).

\( \dot{V}O_2 \) and \( \dot{V}O_2 \text{max} \). Before the commencement of the study, mean \( \dot{V}O_2 \text{max} \) was 135 ± 5 ml·kg\(^{-1}\)·min\(^{-1}\). By TD14, mean \( \dot{V}O_2 \text{max} \) had increased (\( P < 0.05 \)) by 13% (153 ± 4 ml·kg\(^{-1}\)·min\(^{-1}\)), with an additional 6% increase (\( P < 0.05 \)) by TD28 (161 ± 4 ml·kg\(^{-1}\)·min\(^{-1}\)) and no further change in the last 4 wk of training. During each SET throughout the study, each horse was required to exercise at the same absolute workload, based on measurement of \( \dot{V}O_2 \). Mean \( \dot{V}O_2 \) during exercise for all SETs during the study did not change (\( P > 0.22 \)) and ranged between 49 and 53% of the value for \( \dot{V}O_2 \text{max} \) achieved before the training protocol.

**Exercise duration and changes in body mass.** Mean time required for subjects to complete the 7-km SETs was 30.2 ± 0.8 min. Whereas mean preexercise body mass was not different after 8 wk of training, mean change in body mass during the SET (including exercise and recovery) decreased from 9.7 ± 0.7 kg (TD0) to 8.6 ± 0.3 kg (TD56) (\( P < 0.05 \); Table 1).

**Body temperatures.** Exercise training resulted in a mean increase in T\(_{pa}\) of 2.5 ± 0.2°C that was sustained for \( \sim 18–25 \) min of the training session. Mean end-exercise temperature decreased (0.6–1.0°C) from 40.2 ± 0.1°C (T\(_{re}\)) and 40.9 ± 0.1°C (T\(_{pa}\)) on TD0 to 39.6 ± 0.1°C (T\(_{re}\)) and 39.9 ± 0.2°C (T\(_{pa}\)) on TD56.

**SR.** During each SET, SR increased continually during exercise, with SR\(_{\text{peak}}\) attained at the end of exercise (Fig. 1). On TD28 and during subsequent SETs, SR early in exercise was higher (\( P < 0.05 \)) compared with that on TD0. Similarly, SR\(_{\text{peak}}\) for TD28, 42, and 56 was higher than for TD0. By TD28 there was also a more rapid decline in SR during recovery, such that SR was lower after 5 min of recovery (Fig. 1).
Individual exercise-associated sweating threshold
and sweating sensitivity values determined for TD0, 28, and 56, based on $T_{re}$ and $T_{pa}$, are presented in
Tables 2 and 3, respectively; and the relation between SR and $T_{re}$ and $T_{pa}$ for all subjects (exercise values) is
illustrated in Fig. 2. Sweating sensitivity, determined for $T_{re}$ and $T_{pa}$, increased significantly by TD28 of the
protocol, with TD56 data not different from TD28 ($P < 0.05$). A significant decrease ($P < 0.05$) in sweating
threshold was detected in TD56 (Tables 2 and 3). Individual correlations between SR and $T_{re}$ and $T_{pa}$ during
exercise for all training days ranged from $r = 0.657$ to $0.993$ with a mean value of $r = 0.881$ for $T_{re}$, and
from $r = 0.657$ to $0.993$ with a mean value of $r = 0.804$ for $T_{pa}$.

Sweat ion composition. Mean [Na$^+$], [Cl$^-$], and [K$^+$]
measured in sweat fluid produced during exercise and recovery on TD0, 28, and 56 are presented in Fig. 3. On
TD0, there was a significant increase in sweat [Na$^+$] during exercise from 95.6 ± 5 mmol/l in the first 5 min
of exercise to 141.0 ± 6 mmol/l at the end of exercise. Sweat [Na$^+$] subsequently declined during recovery
(118.7 ± 5 mmol/l) but was still higher ($P < 0.05$) than values measured at the onset of exercise. This pattern
of change in sweat [Na$^+$] during exercise and recovery was similar during each subsequent SET. By TD56, sweat [Na$^+$] was significantly lower ($P < 0.01$) than TD0 data at all points during exercise and at 15 and 30
min of recovery, with values of 74.6 ± 4 and 123.7 ± 5
mmol/l at the onset and end of exercise, respectively.
The pattern of change in sweat [Cl$^-$] was similar to that of sweat [Na$^+$] (Fig. 3B). However, training did
not result in a significant change ($P > 0.61$) in the [Cl$^-$] in sweat at any given time point during the SET. In
contrast to the pattern of increase in sweat [Na$^+$] and [Cl$^-$] during exercise, there was a gradual but signifi-
cant decline in sweat [K$^+$] throughout exercise (Fig. 3C) and the first 5 min of recovery ($P < 0.05$) during
each SET and an increase to values still less than those
of early exercise by the end of recovery. By TD14, values for sweat [K$^+$] were ~8–10 mmol/l higher ($P < 0.05$) at each sampling interval, compared with TD0, and were unchanged during the remaining SETs.

Fluid and ion losses in sweat. Calculated total sweat
fluid losses and ion losses of Na$^+$, K$^+$, and Cl$^-$ in sweat
during exercise and recovery for TD0, 14, 28, 42, and
56 are presented in Fig. 4. Calculated fluid losses were comparable with measured changes in body mass
after estimated respiratory water losses were sub-
tracted from the total decrease in body mass (14, 16)
(Table 1). By TD42, total sweat fluid losses decreased
by 10.5 ± 0.7% compared with TD0; losses for TD56 were not different from those for TD42 ($P > 0.34$).
Whereas exercise-associated sweat fluid losses in-
creased ($P < 0.05$) on TD14 compared with TD0, these losses were unchanged for the remaining SETs. In
contrast, the calculated loss of fluid in sweat during recovery decreased by TD28 and was 56% lower on
TD56 compared with TD0 (Fig. 4A).

After 4 wk of training, total losses of Na$^+$, K$^+$, and
Cl$^-$ in sweat had increased by ~20% compared with
TD0. In comparison, total sweat ion losses decreased
on TD42 and 56 to values not different from TD0 ($P > 0.15$). Whereas losses of Na$^+$, K$^+$, and Cl$^-$ during
exercise had increased by the end of 8 wk of training,
there was a concomitant decline in ion losses during recovery. Accordingly, exercise-associated ion losses in
sweat represented ~46% of overall losses on TD0 com-

<table>
<thead>
<tr>
<th>TD</th>
<th>Preexercise Body Mass, kg</th>
<th>Change in Body Mass During Entire SET, kg</th>
<th>Calculated Sweat Fluid Losses for SET, liters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
</tr>
<tr>
<td>0</td>
<td>469.6 ± 10.3</td>
<td>9.7 ± 0.7</td>
<td>9.5 ± 0.3</td>
</tr>
<tr>
<td>14</td>
<td>466.8 ± 11.7</td>
<td>9.4 ± 0.3</td>
<td>9.8 ± 0.5</td>
</tr>
<tr>
<td>28</td>
<td>461.2 ± 10.4</td>
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<td>9.3 ± 0.6</td>
</tr>
<tr>
<td>42</td>
<td>463.8 ± 10.2</td>
<td>8.7 ± 0.5$^*$</td>
<td>8.5 ± 0.5$^*$</td>
</tr>
<tr>
<td>56</td>
<td>457.8 ± 7.2</td>
<td>8.6 ± 0.3$^*$</td>
<td>8.2 ± 0.4$^*$</td>
</tr>
</tbody>
</table>

Values are means ± SE; n = 5. SET, standardized exercise test; RH, relative humidity; TD, training day. $^*$P < 0.05, significantly different from TD0.
pared with ~63% of total ion losses in sweat on TD56 (Fig. 4B, Table 4).

Regression analyses performed to determine the relation between [Na\(^+\)] and SR for all subjects indicated that sweat [Na\(^+\)] during exercise was highly correlated to SR during each SET (Fig. 5). Furthermore, by TD28 and 56, the [Na\(^+\)] in sweat was lower at a given SR (intercept values of 76.2 ± 1.3 and 77.2 ± 1.4 mmol/l, respectively), compared with TD0 (104.8 ± 1.8 mmol/l). Individual correlations between SR and [Na\(^+\)] ranged from \(r = 0.845\) to 0.951 on TD0, from \(r = 0.913\) to 0.969 on TD28, and from \(r = 0.915\) to 0.986 on TD56.

**DISCUSSION**

Previous equine studies have utilized trained subjects to examine dissipation of metabolic heat during exercise under various ambient conditions. In this 8-wk study, significant adaptive changes in sweating responses were induced by training horses in moderate conditions. In this group of horses, the effects of moderate-intensity training in a cool environment on sweating responses during submaximal exercise in hot conditions were evident within 2–6 wk of training and included 1) an increase in sweating sensitivity during exercise at the same absolute workload, 2) a decrease in pre- and end-exercise \(T_{re}\) and \(T_{pa}\), 3) a reduction in the rate of sweat fluid loss during recovery that resulted in decreased overall sweat fluid losses for the SETs, and 4) a decrease in sweat [Na\(^+\)] at a given SR during exercise. These findings also support the hypothesis that high heat production in horses during exercise, combined with constraints on heat loss, results in significant improvements in heat dissipatory mechanisms during training in cool conditions and may explain relatively small changes in sweating sensitivity and SR during subsequent training in the heat (14, 17).

**Comment on methods.** The training regimen in this study resulted in a significant enhancement of aerobic capacity, as demonstrated by the ~19% increase in \(V_{O2}^{\text{max}}\) evident by TD28. As each subject performed all SETs at the same absolute workload, the relative workload decreased slightly by TD56 compared with TD0. For each horse, there was no significant change in mean \(V_{O2}\) during exercise on TD14, 28, 42, and 56 compared with TD0. Therefore, it is unlikely that a reduction in metabolic heat production contributed to the lower end-exercise \(T_{re}\) and \(T_{pa}\) in the latter SETs.

Despite cool ambient conditions (19–21°C), the workload for daily training resulted in a substantial, sustained increase in \(T_{re}\) (~2.5°C) but was moderate enough to enable subjects to complete each training session. Similarly, the duration and intensity of the SET provided several sampling intervals while ensuring that all subjects could complete the initial exercise test in the untrained state. Maintaining ambient temperature during each SET ~13–15°C higher than during training sessions enhanced our

**Table 2. Slope and x-intercept of the sweating rate-temperature relation for rectal temperature during exercise in hot, dry conditions (32–34°C and 45–55% RH) at 50% \(V_{O2}^{\text{max}}\) on TD0, 28, and 56 of an 8-wk training regimen**

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>Slope (TD0)</th>
<th>Intercept (TD0)</th>
<th>Slope (TD28)</th>
<th>Intercept (TD28)</th>
<th>Slope (TD56)</th>
<th>Intercept (TD56)</th>
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<tbody>
<tr>
<td>1</td>
<td>6.7 ± 2.3</td>
<td>38.3</td>
<td>25.2 ± 3.8</td>
<td>37.3</td>
<td>24.9 ± 2.0</td>
<td>36.8</td>
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<tr>
<td>2</td>
<td>8.4 ± 1.6</td>
<td>36.7</td>
<td>10.5 ± 1.8</td>
<td>36.6</td>
<td>21.1 ± 1.8</td>
<td>35.5</td>
</tr>
<tr>
<td>3</td>
<td>19.9 ± 3.2</td>
<td>38.0</td>
<td>27.3 ± 4.1</td>
<td>37.2</td>
<td>25.8 ± 2.5</td>
<td>37.4</td>
</tr>
<tr>
<td>4</td>
<td>11.5 ± 2.5</td>
<td>37.2</td>
<td>16.9 ± 2.6</td>
<td>36.8</td>
<td>17.5 ± 4.8</td>
<td>37.1</td>
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<td>5</td>
<td>12.6 ± 2.0</td>
<td>36.3</td>
<td>32.7 ± 8.3</td>
<td>36.2</td>
<td>28.7 ± 3.4</td>
<td>36.3</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>11.8 ± 2.3</td>
<td>37.3 ± 0.4</td>
<td>22.5 ± 3.9*</td>
<td>36.8 ± 0.2</td>
<td>23.6 ± 1.9*</td>
<td>36.6 ± 0.3*</td>
</tr>
</tbody>
</table>

Values are means ± SE; \(n = 5\). Slope = ml·m\(^{-2}\)·min\(^{-1}\)·°C\(^{-1}\); intercept = estimated value of rectal temperature (°C) at sweating rate = 0. *Significantly different from TD0, \(P < 0.05\).

**Table 3. Slope and x-intercept of the sweating rate-temperature relation for pulmonary artery temperature during exercise in hot, dry conditions (32–34°C and 45–55% RH) at 50% \(V_{O2}^{\text{max}}\) on TD0, 28, and 56 of an 8-wk training regimen**

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>Slope (TD0)</th>
<th>Intercept (TD0)</th>
<th>Slope (TD28)</th>
<th>Intercept (TD28)</th>
<th>Slope (TD56)</th>
<th>Intercept (TD56)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>14.4 ± 2.7</td>
<td>38.5</td>
<td>20.7 ± 2.7</td>
<td>37.6</td>
<td>19.6 ± 0.9</td>
<td>36.7</td>
</tr>
<tr>
<td>2</td>
<td>11.1 ± 2.2</td>
<td>37.5</td>
<td>13.1 ± 1.8</td>
<td>36.9</td>
<td>21.7 ± 2.8</td>
<td>36.4</td>
</tr>
<tr>
<td>3</td>
<td>15.5 ± 5.3</td>
<td>37.6</td>
<td>29.6 ± 4.6</td>
<td>37.1</td>
<td>25.1 ± 5.1</td>
<td>37.0</td>
</tr>
<tr>
<td>4</td>
<td>8.0 ± 2.6</td>
<td>37.7</td>
<td>18.0 ± 2.6</td>
<td>37.0</td>
<td>18.9 ± 3.3</td>
<td>37.0</td>
</tr>
<tr>
<td>5</td>
<td>10.7 ± 1.8</td>
<td>36.8</td>
<td>16.1 ± 2.4</td>
<td>36.8</td>
<td>16.4 ± 1.0</td>
<td>36.6</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>12.0 ± 1.3</td>
<td>37.6 ± 0.3</td>
<td>19.5 ± 2.8*</td>
<td>37.1 ± 0.1</td>
<td>20.3 ± 1.5*</td>
<td>36.8 ± 0.1*</td>
</tr>
</tbody>
</table>

Values are means ± SE; \(n = 5\). Slope = ml·m\(^{-2}\)·min\(^{-1}\)·°C\(^{-1}\); intercept = estimated value of pulmonary artery temperature (°C) at sweating rate = 0. *Significantly different from TD0, \(P < 0.05\).
ability to investigate changes in the horses’ heat dissipatory mechanisms.

Whereas the RH of the laboratory was ~48%, the RH within the sealed pouch used for sweat collection was probably higher than that of the room. Consequently, it is possible that hidromeiosis (temporary local or general suppression of SR associated with saturation of the skin) may have altered SR. However, in this technique for collection and measurement of SR, sweat drains off the skin surface and into the ventral pouch, thereby minimizing the extent of skin saturation. Furthermore, in previous studies by our laboratory using this technique, SRs measured in hot, humid conditions (in which skin wetness inside and outside the pouch is similar) were comparable to those measured in hot, dry conditions at a similar exercise intensity (18).

SR. In this study, sweat production within an enclosed area on the lateral thorax was used to determine local SR and to collect sweat fluid for analysis of ion composition. This pouch technique provides a measurement of local SR comparable to that determined by dew-point hygrometry (20) and allows rapid and convenient collection of sweat fluid during treadmill exercise. The local SR, extrapolated to a whole body SR, indicated that there were early and significant alterations in SR during the training protocol. After 2 wk of training, initial and SRpeak during the SET increased in response to similar ambient conditions and an identical workload. By TD28, SRpeak had increased by

Fig. 2. Relation between local sweating rate, averaged for 5-min intervals during exercise in hot, dry conditions (32–34°C and 45–55% RH) at 50% V\textsubscript{O\textsubscript{2}}\text{max} and pulmonary artery (A) and rectal temperature (B) on TD0, 28, and 56 of an 8-wk training regimen (n = 5 horses).

Fig. 3. Concentrations of sodium ([Na\textsuperscript{+}]; A), chloride ([Cl\textsuperscript{-}]; B), and potassium ([K\textsuperscript{+}]; C) in sweat collected every 5 min from horses (n = 5) during exercise (50% V\textsubscript{O\textsubscript{2}}\text{max}) in hot, dry conditions (32–34°C and 45–55% RH) on TD0, 28, and 56 of an 8-wk training regimen. *TD28 and TD56 significantly different from TD0, P < 0.05; #TD56 significantly different from TD0, P < 0.05.
SR and body temperature. The sensitivity of the sweating response during exercise at 50% \(V_{\text{O2 max}}\) was examined before, during, and after training by using both \(T_{\text{pa}}\) and \(T_{\text{re}}\) as the regulated variables (Fig. 2). Several studies in humans have demonstrated that trained subjects are more capable of dissipating a thermal load imposed by exercise compared with untrained controls (6, 22, 23). A study by Nadel and colleagues (22) reported that human sweat glands develop an increased sensitivity during training with subsequent reductions in the sweating threshold after heat acclimation. However, Roberts et al. (24) showed that training reduced the threshold for sweating and also induced a small increase (0.12 ± 0.17 mg·cm\(^{-2}\)·min\(^{-1}\)·\(\degree C\)^{-1}) in the slope of the SR-core (esophageal) temperature relation posttraining, with further modification of both indexes during heat acclimation. In comparison, our findings indicate that significantly larger increases (−0.8–1.1 mg·cm\(^{-2}\)·min\(^{-1}\)·\(\degree C\)^{-1}) in the slope defining the SR-T\(_{\text{re}}\) or SR-T\(_{\text{pa}}\) relation are evident after 4 wk of moderate-intensity training in the horse. However, the extent of the change in slope of the regression line of the SR-T\(_{\text{re}}\) or SR-T\(_{\text{pa}}\) relation varied considerably among horses (Tables 2 and 3).

Similar variation existed for alterations in the sweating threshold, with a decrease in sweating threshold evident in some, but not all, horses in the study after 4 wk of training. Marlin et al. (14) reported sweating sensitivities in trained horses in hot, humid (30°C and 80% RH) conditions before and after 15 consecutive days of active (80 min of exercise) heat acclimation. Similar to findings in the present study, these measurements (based on SRs on the gluteal region and T\(_{\text{pa}}\))

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**Table 4. Mean losses of ions (Na\(^+\), K\(^+\), Cl\(^-\)) in sweat from 5 horses during exercise and recovery in a SET in hot, dry conditions (32–34°C and 45–55% RH) on TD0, 14, 28, 42, and 56 of an 8-wk exercise training regimen**

<table>
<thead>
<tr>
<th>TD</th>
<th>Ion</th>
<th>Total, mmol</th>
<th>Exercise, mmol</th>
<th>Recovery, mmol</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Na(^+)</td>
<td>1,075 ± 95</td>
<td>525 ± 33</td>
<td>551 ± 22</td>
</tr>
<tr>
<td></td>
<td>K(^+)</td>
<td>214 ± 35</td>
<td>98 ± 10</td>
<td>116 ± 9</td>
</tr>
<tr>
<td></td>
<td>Cl(^-)</td>
<td>1,196 ± 105</td>
<td>553 ± 29</td>
<td>642 ± 32</td>
</tr>
<tr>
<td>14</td>
<td>Na(^+)</td>
<td>1,254 ± 114</td>
<td>761 ± 35*</td>
<td>473 ± 24*</td>
</tr>
<tr>
<td></td>
<td>K(^+)</td>
<td>336 ± 28*</td>
<td>210 ± 15*</td>
<td>126 ± 9*</td>
</tr>
<tr>
<td></td>
<td>Cl(^-)</td>
<td>1,532 ± 118*</td>
<td>945 ± 38*</td>
<td>578 ± 28*</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3,113 ± 212*</td>
<td>1,916 ± 87*</td>
<td>1,177 ± 87*</td>
</tr>
<tr>
<td>28</td>
<td>Na(^+)</td>
<td>1,263 ± 104*</td>
<td>837 ± 34*</td>
<td>427 ± 19*</td>
</tr>
<tr>
<td></td>
<td>K(^+)</td>
<td>320 ± 37*</td>
<td>225 ± 17*</td>
<td>95 ± 6*</td>
</tr>
<tr>
<td></td>
<td>Cl(^-)</td>
<td>1,510 ± 109*</td>
<td>1,023 ± 58*</td>
<td>488 ± 22*</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3,093 ± 205*</td>
<td>2,080 ± 111*</td>
<td>1,015 ± 77*</td>
</tr>
<tr>
<td>42</td>
<td>Na(^+)</td>
<td>1,006 ± 89</td>
<td>663 ± 28*</td>
<td>343 ± 32*</td>
</tr>
<tr>
<td></td>
<td>K(^+)</td>
<td>232 ± 31</td>
<td>152 ± 13*</td>
<td>80 ± 9*</td>
</tr>
<tr>
<td></td>
<td>Cl(^-)</td>
<td>1,194 ± 97</td>
<td>763 ± 32*</td>
<td>431 ± 21*</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>2,435 ± 176</td>
<td>1,581 ± 87*</td>
<td>854 ± 51*</td>
</tr>
<tr>
<td>56</td>
<td>Na(^+)</td>
<td>910 ± 85</td>
<td>681 ± 26*</td>
<td>329 ± 14*</td>
</tr>
<tr>
<td></td>
<td>K(^+)</td>
<td>228 ± 33</td>
<td>147 ± 12*</td>
<td>80 ± 7*</td>
</tr>
<tr>
<td></td>
<td>Cl(^-)</td>
<td>1,122 ± 103</td>
<td>700 ± 28*</td>
<td>422 ± 22*</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>2,260 ± 133</td>
<td>1,428 ± 96*</td>
<td>831 ± 45*</td>
</tr>
</tbody>
</table>

Values are mean ± SE; \(n = 5\). *Significantly different from TD0, \(P < 0.05\).
or the temperature of the skin at the base of the tail) showed a large interindividual variation. In the horses studied by Marlin et al., postacclimation sweating sensitivity during exercise at 9.2 m/s (SR-Tpa relation: 6.6 ± 2.8 g·min⁻¹·m⁻²·°C⁻¹; SR-tail skin temperature: 10.8 ± 4.3 g·min⁻¹·m⁻²·°C⁻¹) was lower than the values calculated in the present study. Some of the variation in values among studies may relate to differences in the overall exercise protocol, in the region used to measure SR (lateral thorax vs. gluteal) and in the type of horses included in each study (Thoroughbreds vs. Thoroughbred crosses).

Sweat fluid losses. Sweat fluid losses calculated from changes in body mass, after fecal, urinary, and estimated respiratory water losses were taken into consideration, were consistent with sweat fluid losses calculated on the basis of mean whole body SR. In the estimation of sweat fluid losses, the contribution of respiratory heat loss was calculated as 15%, on the basis of estimates for such losses in the horse under various ambient conditions (8, 12, 20). As a result of higher SRs, exercise-associated sweat fluid losses increased after 2 wk of training but were unchanged during the remaining 6 wk. In contrast, there was a gradual decline in sweat fluid losses during recovery in the first 6 wk of training (from 4.7 liters on TD0 to 2.2 liters on TD56) that ultimately resulted in a decrease in total sweat fluid losses by the end of the study (Table 1). Marlin et al. (14) also reported a significant (~45%) reduction in the postexercise body weight loss after heat acclimation and attributed this decline, in part, to decreases in SR during recovery periods. Postacclimation decreases in SR and body weight loss during recovery in horses were also reported by Geor et al. (4) and McCutcheon et al. (17).

Sweat ion concentrations and sweat ion losses. During the initial 4 wk of the training protocol, increased ion losses in sweat during exercise resulted in significantly greater overall sweat ion losses compared with those on TD0 (Table 4). By TD56, despite a decrease in total sweat fluid losses of ~1.3 liters (Table 1), combined losses of Na⁺, Cl⁻, and K⁺ in sweat during the entire SET were not different from TD0 values (TD0: 2,485 ± 178 mmol; TD56: 2,260 ± 153 mmol). Similar overall ion losses with a reduction in sweat fluid losses reflect the alteration in the pattern of ion losses, with greater exercise-related sweat ion losses associated with higher SR during exercise and the decline in SR during recovery. Similar changes in the pattern of SR, as well as a reduction in sweat [Na⁺] and [Cl⁻], were also reported after active heat acclimation in horses (17). However, the mechanisms responsible for the adaptive responses in sweat ion concentrations are not known.

Whereas the pattern of change in sweat ion composition during exercise was similar for each SET, during the latter SETs, there was a significant increase in sweat [K⁺] and decrease in sweat [Na⁺] for a given time during exercise. In trained equine subjects, changes in sweat ion composition most typically reflect changes in SR in response to different ambient conditions and/or exercise intensities (2, 15, 16, 18, 19). In the present study, the increased sweating sensitivity in response to daily training also resulted in increased SR, despite consistent ambient conditions and workload during the five SETs. Whereas higher SRs could have contributed to the higher sweat [K⁺] measured on TD28, 42, and 56, there was a concurrent decrease in sweat [Na⁺], suggesting a tubular modification of the cation content of sweat fluid within the sweat gland. The high correlation between SR and sweat [Na⁺] for individual subjects (Fig. 5) may reflect an interrelationship between sweat gland water secretion and absorption rates and Na⁺ reabsorption rates (11). Although mineral corticoid action has been reported to influence the content of Na⁺ in sweat in human subjects (24, 25), Jansson (10) demonstrated that an acute increase in plasma aldosterone did not alter sweat [Na⁺] or [K⁺] in horses.

In a study by McConaghy et al. (15), no significant change in sweat ion composition was reported for five horses after 10 wk in either a low- or high-intensity training protocol compared with the untrained state, although a small decrease in sweat [Na⁺] and [Cl⁻] was evident between 5 and 10 wk of training. Although the nature of the training protocol was similar in both investigations, horses in the present study were training for 9–10 km/day at the end of 8 wk, compared with 3.6 km completed by the low-intensity training group in the study by McConaghy et al. Furthermore, although exercise duration and intensity for SETs in both studies were similar, the hotter conditions in the present study (32–34°C vs. 20.6–22.3°C) would have resulted in higher SRs during exercise and may have
REFERENCES


