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L. J. McCutcheon and R. J. Geor
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Heat acclimation improves regulation of plasma volume and plasma Na⁺ content during exercise in horses

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Equine sweating responses to submaximal exercise during 21 days of heat acclimation

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McCutcheon, Laura Jill, Raymond J. Geor, Gayle L. Ecker, and Michael I. Lindinger. Equine sweating responses to submaximal exercise during 21 days of heat acclimation. *J. Appl. Physiol.* 87(5): 1843–1851, 1999.—This study examined sweating responses in six exercise-trained horses during 21 consecutive days (4 h/day) of exposure to, and daily exercise in, hot humid conditions (32–34°C, 80–85% relative humidity). On *days 0, 3, 7, 14, and 21*, horses completed a standardized exercise test on a treadmill (6° incline) at a speed eliciting 50% of maximal O₂ uptake until a pulmonary artery temperature of 41.5°C was attained. Sweat was collected at rest, every 5 min during exercise, and during 1 h of standing recovery for measurement of ion composition (Na⁺, K⁺, and Cl⁻) and sweating rate (SR). There was no change in the mean time to reach a pulmonary artery temperature of 41.5°C (range 19.09 ± 1.41 min on *day 0* to 20.92 ± 1.98 min on *day 3*). Peak SR during exercise (ml·m⁻²·min⁻¹) increased on *day 7* (57.5 ± 5.0) but was not different on *day 21* (48.0 ± 4.7) compared with *day 0* (52.0 ± 3.4). Heat acclimation resulted in a 17% decline in SR during recovery and decreases in body mass and sweat fluid losses during the standardized exercise test of 25 and 22%, respectively, by *day 21*. By *day 21*, there was also a 10% decrease in mean sweat Na⁺ concentration for a given SR during exercise and recovery; this contributed to an ~26% decrease in calculated total sweat ion losses (3,112 ± 114 mmol on *day 0* vs. 2,295 ± 107 mmol on *day 21*). By *day 21*, there was a decrease in sweating threshold (~1°C) but no change in sweat sensitivity. It is concluded that horses responded to 21 days of acclimation to, and exercise in, hot humid conditions with a reduction in sweat ion losses attributed to decreases in sweat Na⁺ concentration and SR during recovery.

incompensable heat stress; thermoregulation; sweat; sodium; potassium; chloride

PHYSIOLOGICAL ADAPTATIONS associated with exposure to and exercise in hot conditions have been extensively investigated in human subjects. Studies of acclimation to exercise in the heat have demonstrated changes in sweating responses that occur after a few days of daily heat exposure (3, 9, 13, 20, 21, 39). Increases in sweating rate (SR) and sweat sensitivity (grams of sweat per °C increase in core body temperature) are the most consistently reported thermoregulatory adaptations associated with sweat gland function after heat exposure (2, 37, 39). In human subjects, heat acclima-

tion results in augmentation of sweating capacity reflected as increases in peak SR (SR_{peak}) from ~1.5 l/h in healthy, unacclimated individuals to as much as 2–3 l/h in those well acclimated to heat (38). Although increased sweating capacity is considered a peripheral adaptation related, in part, to enlargement of eccrine sweat glands (6, 8–10, 38), reductions in core temperature threshold for onset of sweating have been interpreted as a central nervous system alteration in the thermoregulatory set point (31). A further adaptation that has not been reported in all studies of heat acclimation is an alteration in sweat composition that results in more dilute sweat in acclimated subjects (31, 35, 38). Insufficient knowledge of the dietary (in particular, Na⁺) status of individuals before or during a study has sometimes confounded interpretation of findings related to sweat composition.

The horse is one of the few mammals that, like humans, relies on sweating as the primary thermoregulatory mechanism. However, the greater muscle mass and higher metabolic rate of the horse than of humans results in greater heat production during exercise. Coupled with the horse's smaller surface area-to-mass ratio for cutaneous dissipation of heat, the potential for more extensive heat production can be exercise limiting for this species (14, 15). Thus the capacity to maximize cutaneous heat loss is extremely important to the horse's ability to compete in hot conditions.

Equine athletes, like their human counterparts, are frequently required to exercise and compete in hot humid conditions. Increasingly, competitions that require sustained, strenuous effort are being held in locations and during seasons with ambient conditions that have the potential to result in severe, exercise-related heat stress. Despite the need to prepare equine athletes for competition in such adverse climatic conditions, remarkably little is known about the capacity of the horse to adapt to exercise in the heat. In the present study we were interested in determining whether horses were capable of altering their sweating responses as a result of a period of heat acclimation. Specifically, we hypothesized that daily exposure (4 h) to, and exercise in, hot humid conditions for 21 days would result in increases in SR and sweating sensitivity during exercise and recovery in the heat. On the basis of findings in studies of human heat acclimation in which sweat Na⁺ concentration ([Na⁺]) was decreased after acclimation (1), we also hypothesized that acclimation to exercise in the heat would decrease sweat [Na⁺] at a given SR, resulting in a reduction in total sweat ion losses. Thus the objectives of the present study were 1) to determine

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the rate and composition of sweat produced during exercise and recovery in trained horses during 21 consecutive days of daily exposure to, and exercise in, ambient conditions of high temperature and relative humidity and 2) to determine whether repeated exposure to, and exercise in, humid heat would result in alterations in sweating responses and fluid balance during exercise and recovery.

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, Canada). 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. All experiments were conducted during the fall and winter, and the horses received no other controlled exercise during the entire study.

Animals. Six Thoroughbred horses ranging in age from 3 to 6 yr and weighing 414–505 kg [455 ± 12 (SE) kg] were maintained on a diet consisting of grass hay and a mixed-grain ration (Professional Horse Mix, Ralston Purina). In addition, the horses were provided with 150 g/day of a salt supplement (40 g Na⁺, 26 g K⁺, and 84 g Cl⁻) and had free access to a trace mineral block. Throughout the study the horses were housed individually indoors at an ambient temperature of 16–19°C with free access to 36 liters of water provided in 2 × 18 liter buckets; the contents of the buckets were measured and the buckets were refilled at 0700 and 1700.

Before the study the horses were conditioned for 10 wk with a 5 day/wk program of walking, trotting, cantering, and galloping on a high-speed treadmill (Sato) set on a 3° incline. The duration and intensity of exercise were gradually increased until the horses were exercising for 40 min at 4 m/s, 4 min at 7 m/s, and ≥2–3 min at 9 m/s by the 10th wk of training. All training was conducted under cool dry conditions [20°C room temperature (RT), 45–50% relative humidity (rh)]. The maximal O₂ uptake ($\dot{V}O_{2,max}$) of each horse was determined (11) during the 8th and 10th wk of training.

Experimental protocol. After the initial 10 wk of training, each horse completed a standardized exercise test (SET) that evaluated sweating responses under hot humid conditions (33–35°C RT, 80–85% rh). For each horse, 10 wk of training in cool dry conditions and the initial SET (*day 0*) were followed by 21 consecutive days during which each animal was exposed to, and exercised in, the hot humid conditions for 4 h between 0700 and 1100. This daily exercise training protocol was undertaken in a treadmill room in which the stated temperature and relative humidity for hot humid conditions were maintained throughout the 4 h of acclimation. The daily exercise training protocol consisted of an initial 1 h in which animals stood on the treadmill, 1 h of submaximal treadmill exercise on a 3° incline, and 2 h at rest. Exercise consisted of a 5-min warm-up (1.75 m/s), 10 min of trotting (4.2 m/s), 5 min of cantering (6.5 m/s), a further 10 min of trotting (4.2 m/s), and 30 min of walking (1.75 m/s) for a total distance of ~10,600 m.

In addition to the initial SET completed on *day 0* (before the 21 days of heat training), on *days 3, 7, 14, and 21* of heat acclimation the horses completed the SET instead of the usual daily exercise protocol.

SET. Food was withheld overnight (12 h). Water was withheld for 3 h before, and for the duration of, each experiment. Body mass was measured on a large-animal scale (± 0.5 kg; KSL Scales, Kitchener, ON, Canada) immedi-

ately before the animals were walked onto the treadmill for the exercise protocol and at 60 min of recovery after exercise.

All exercise was conducted on a treadmill set on a 6° incline. Resting measurements were obtained during 15 min before exercise, during which the horses remained stationary on the treadmill. The exercise test consisted of 5 min of walking (1.5 m/s) followed by exercise at a speed calculated by regression analysis to elicit 50% of each animal's $\dot{V}O_{2,max}$ (range 3.8–4.3 m/s). Exercise was continued until a pulmonary artery blood temperature (T_{pa}) of 41.5°C was attained. On cessation of exercise, the horses stood for 5 min, then completed a 25-min walking recovery (1.5 m/s) and a further 30-min standing recovery on the treadmill. During and after exercise, a high-speed fan, mounted above and in front of the treadmill, was used to maintain an air velocity of 3.5–4.0 m/s over the anterior and dorsal aspects of the horses. 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. Fecal and urinary losses within the period of exercise and recovery were also measured (unpublished data).

Collection of sweat and measurement of SR. Sweat was collected from an area of skin on the lateral thorax by a method previously described for use in the horse (28). The area designated for sweat collection consisted of a 500-cm² area of skin overlying the thorax between the 9th and the 16th rib, 30 cm ventral to the spine. This area was chosen after determination of SR at several sites (midcervical, lateral thorax, and gluteal region of hindquarters). Although there are regional variations in SR in the horse, previous studies have demonstrated that the SR measured on the lateral thorax is not significantly different from the mean whole body SR estimated from changes in total body water after correction for respiratory water losses (18, 26). The area was clipped and shaved, washed, and then rinsed with distilled water. A sealed polyethylene pouch enclosing a 150-cm² area of skin was attached to the skin on all edges with an 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 removal of collected sweat through polyethylene tubing (1.67 mm ID; Intramedic, Becton-Dickinson, Parsippany, NJ) incorporated into the lateral margin of the pouch. During each SET, sweat was collected at rest, every 5 min after the onset of exercise, on cessation of exercise, and every 5 min during walking and standing recovery. For successive SETs, placement of the pouch was alternated between left and right lateral thorax.

Local SR ($\text{ml} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$) was calculated on the basis of the volume of sweat collected from the measured skin area within the pouch at the end of each time interval. 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 using the formula

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

(15). SR_{peak} was used to describe the highest rate of sweat production attained during each SET. Total sweat fluid loss for the duration of exercise and recovery was estimated from the total body water losses after correction for estimated respiratory water losses; this was assumed to represent a constant percentage (~15%) of the overall water losses (14). The effect of heat acclimation on the SR-internal temperature relationship was evaluated by determining the slope ($\text{ml} \cdot \text{m}^{-2} \cdot \text{min}^{-1} \cdot ^\circ\text{C}^{-1}$) and the *x*-intercept of the regression

line representing the individual mean SR and core temperature [rectal temperature (T_{re}) and T_{pa}] for each 5-min interval during exercise; mean of temperatures (T_{re} and T_{pa}) measured at the start and end of each interval was used to represent mean core temperatures (29). The x -intercept (the temperature at which the regression line of the SR-temperature relationship extends to a zero value on the x -axis) was used as an estimate of the sweating threshold (33).

Measurement of T_{re} and T_{pa} . T_{pa} was measured by inserting a thermocouple into the pulmonary artery within an 8-Fr polyethylene catheter. The catheter was introduced via a jugular vein, and its position within the pulmonary artery was verified by pressure wave recordings. Catheterization was performed after aseptic preparation and local analgesia of the skin. Temperature in the lumen of the rectum (T_{re}) was measured with a thermocouple inserted 20–30 cm proximal to the anal sphincter. Thermocouples were connected to a thermometer (BAT-10, Physitemp Instruments, Clifton, NJ). Temperature was measured at rest, after 0, 2, and 5 min, and every 5 min of exercise thereafter, at the end of exercise, and at 2, 5, 15, 30, and 60 min of recovery at both sites with use of copper-constantan thermocouples (Physitemp Instruments). Both thermocouples had response times of $\sim 1^\circ\text{C/s}$ and were calibrated in a heated water bath.

Measurement of sweat ion concentrations and sweat ion losses. $[\text{Na}^+]$, K^+ concentration ($[\text{K}^+]$), and Cl^- concentration ($[\text{Cl}^-]$) in sweat were determined with an ion-selective analyzer (Statprofile 9 Plus, Nova Biomedical, Mississauga, ON, Canada). All analyses were performed in duplicate. Total sweat ion losses of Na^+ , K^+ , and Cl^- were calculated on the basis of 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 relationship between SR and sweat $[\text{Na}^+]$ for every 5-min interval during exercise.

Statistical analysis. Data were analyzed by two-way ANOVA in which repeated measures were used to compare measures over time and among trials. Post hoc multiple comparisons were made by the Bonferroni method when an F ratio was significant. Significance was determined as $P < 0.05$. Values are means \pm SE.

RESULTS

Exercise duration. Mean exercise duration for the SETs completed on days 0, 3, 7, 14, and 21, on the basis of the time at which a T_{pa} of 41.5°C was attained after the commencement of exercise at 50% $\dot{V}O_{2\max}$ (after warm-up at a walk), ranged from 19.09 ± 1.41 (day 0) to 20.92 ± 1.98 min (day 3). Mean exercise duration was not significantly different for any SET ($P = 0.645$, power of test with $\alpha = 0.05$: 0.049; Table 1).

Changes in body mass. Calculated sweat fluid losses were comparable to measured changes in body mass after subtraction of estimated respiratory water losses from the total decrease in body mass (14, 18). Mean change in body mass during exercise and recovery was 11.7 ± 1.0 kg for day 0 but had decreased significantly by day 14 to 10.1 ± 1.3 (Table 1). By day 21 the mean decreases in body mass ($P = 0.0206$) and in calculated sweat fluid losses ($P = 0.0183$) were 23–25% less than the losses measured on day 0 (Tables 1 and 2).

SR. During each SET, SR increased during the first 15 min of exercise at 50% $\dot{V}O_{2\max}$. In one animal, SR_{peak} was achieved by 15 min of exercise and was sustained until the end of exercise. In all other animals, SR

Table 1. Run time, preexercise body mass, and change in body mass on days 0, 3, 7, 14, and 21 of heat acclimation

	Run Time, min	Preexercise Body Mass, kg	Change in Body Mass Associated With SET, kg
Day 0	19.09 ± 1.41	454.1 ± 11.7	11.67 ± 1.23
Day 3	20.92 ± 1.98	452.0 ± 12.0	12.00 ± 0.86
Day 7	19.59 ± 1.70	449.5 ± 11.5	11.50 ± 0.99
Day 14	20.42 ± 1.78	449.7 ± 10.1	10.08 ± 1.31
Day 21	19.61 ± 1.86	445.7 ± 8.7	$8.67 \pm 0.71^*$

Values are means \pm SE for 6 horses. Run time represents duration of exercise at 50% of maximal O_2 uptake ($\dot{V}O_{2\max}$) to attainment of pulmonary artery blood temperature of 41.5°C . Change in body mass includes exercise and 1 h of recovery. SET, standardized exercise test. *Significantly less than day 0, $P < 0.05$.

continued to increase throughout exercise. Although mean SR_{peak} increased on days 3 and 7 compared with days 14 and 21, these changes were only significant for day 7 compared with day 21. By day 21, there was a more rapid decline in SR during recovery, such that SR was lower ($P < 0.05$) after 5 min of recovery. Whereas the calculated total volume of sweat produced during exercise and the 1-h recovery had decreased by $\sim 25\%$ by day 21, the volume of sweat fluid produced during exercise at 50% $\dot{V}O_{2\max}$, as a percentage of the total sweat production, increased by $\sim 17\%$ (Table 2). By day 21, sweat fluid losses during recovery decreased from 66 to 49% of total sweat losses ($P = 0.003$, power of test with $\alpha = 0.05$: 0.88) compared with day 0 (Table 2).

Table 3 presents the slopes and x -intercepts of the SR-core temperature relationship during exercise for days 0, 14, and 21, and Fig. 1, A and B, depicts representative responses from two animals for days 0, 14, and 21. The relationship between SR and T_{re} and T_{pa} for all animals (exercise values) on days 0 and 14 is illustrated in Fig. 1C. Whereas SR at a given value of T_{re} and T_{pa} was increased by days 14 and 21 for some individual animals (Fig. 1), this relationship was not significantly different for the group of six animals for T_{re} ($P = 0.509$) or T_{pa} ($P = 0.544$; power of the test with $\alpha = 0.050$: 0.0495; Table 1). Individual correlations between SR and T_{re} for day 0 ranged from $r = 0.936$ to $r = 0.998$ (mean $r = 0.972$) and for SR and T_{pa} from $r = 0.965$ to $r = 0.998$ (mean $r = 0.986$). For day 14, individual correlations between SR and T_{re} ranged from $r = 0.610$ to $r = 0.998$ (mean $r = 0.835$) and, for SR and T_{pa} , ranged from $r = 0.814$ to $r = 0.990$ (mean $r = 0.945$); for day 21 these values ranged from $r = 0.814$ to $r = 0.992$ (mean $r = 0.958$) and from $r = 0.909$ and $r = 0.993$ (mean $r = 0.961$) for SR vs. T_{re} and SR vs. T_{pa} , respectively. The value of the x -intercept of the regression line of the SR-temperature (T_{re} and T_{pa}) relationship was decreased by day 21 compared with day 0 (Table 3).

Sweat ion composition and sweat ion losses. Mean $[\text{Na}^+]$, $[\text{Cl}^-]$, and $[\text{K}^+]$ measured in sweat fluid produced during exercise and recovery on days 0, 14, and 21 are presented in Fig. 2. On day 0, there was a significant increase in sweat $[\text{Na}^+]$ during exercise from 104 ± 8 mmol/l in the first 5 min of exercise to 134 ± 4 mmol/l at

Table 2. Estimated volume of sweat fluid losses during exercise and recovery on days 0, 3, 7, 14, and 21 of heat acclimation

	Total Sweat Fluid Loss, ml	Sweat Loss During Exercise, ml	% of Total Loss (Exercise)	Sweat Loss During Recovery, ml	% of Total Loss (Recovery)
Day 0	11,374 ± 990	3,844 ± 380	33.8 ± 2	7,413 ± 953	66.2 ± 2
Day 3	11,015 ± 1,132	4,179 ± 645	38.0 ± 4	6,452 ± 818	62.1 ± 4
Day 7	10,759 ± 1,235	4,324 ± 756	39.8 ± 3	5,772 ± 875	59.8 ± 3
Day 14	10,608 ± 910	4,451 ± 577	41.7 ± 3*	5,323 ± 444	58.0 ± 3*
Day 21	8,766 ± 808	4,452 ± 490	50.7 ± 3*	4,193 ± 435*	49.1 ± 3*

Values are means ± SE for 6 horses. Total sweat fluid loss includes exercise at 50% $\dot{V}_{O_{2max}}$ to attainment of pulmonary artery blood temperature (T_{pa}) of 41.5°C and 1 h of recovery. Sweat loss during exercise includes exercise at 50% $\dot{V}_{O_{2max}}$ only. Sweat loss during recovery includes 1 h of recovery only. *Significantly different from day 0, $P < 0.05$.

the end of exercise. Sweat $[Na^+]$ subsequently declined during recovery to values not significantly different from those at the onset of exercise. This pattern of change in sweat $[Na^+]$ during exercise and recovery was similar during each SET. By day 14, sweat $[Na^+]$ was significantly lower than day 0 data at each sampling point throughout exercise and recovery, with values of 72 ± 6 and 122 ± 3 mmol/l at the onset and end of exercise, respectively. Sweat $[Cl^-]$ did not change significantly throughout exercise and recovery on day 0. On days 14 and 21, the $[Cl^-]$ in sweat produced during the first 10 min of exercise was significantly lower than that during the initial 10 min of exercise on day 0. Sweat $[Cl^-]$ increased by ~20 mmol/l during exercise and remained unchanged during recovery, such that sweat $[Cl^-]$ on days 14 and 21 was not significantly different from that at day 0 for the remainder of exercise. On day 21, sweat $[Cl^-]$ was lower at 60 min of recovery than in previous SETs. In contrast to the increases in sweat $[Na^+]$ and $[Cl^-]$ during exercise, there was a gradual but significant decline in sweat $[K^+]$ throughout exercise and the first 5 min of recovery ($P < 0.05$) during each SET. During the remaining 55 min of recovery, the $[K^+]$ increased ($P < 0.05$), such that at 1 h after exercise, sweat $[K^+]$ was greater than in samples collected at the onset of exercise. There was a similar pattern of change in sweat $[K^+]$ during exercise and recovery on days 0, 3, and 7, but there were no significant between-day differences. Although the pattern of change in sweat $[K^+]$ during exercise and recovery was unchanged on days 14 and 21, values were higher ($P < 0.05$) at each sampling interval than at day 0.

Table 3. Slope and x-intercept of sweating rate-temperature relations during exercise at 50% $\dot{V}_{O_{2max}}$ on days 0, 14, and 21 of heat acclimation

	Sweating Rate- T_{re}		Sweating Rate- T_{pa}	
	Slope, ml·m ⁻² ·min ⁻¹ ·°C ⁻¹	Intercept	Slope, ml·m ⁻² ·min ⁻¹ ·°C ⁻¹	Intercept
Day 0	15.80 ± 1.8	37.64 ± 0.5	11.85 ± 1.8	38.07 ± 0.2
Day 14	17.66 ± 2.5	36.06 ± 0.4*	12.86 ± 1.3	37.41 ± 0.3
Day 21	18.33 ± 2.6	36.36 ± 0.2*	12.94 ± 1.7	36.92 ± 0.3*

Values are means ± SE for 6 horses. Intercepts are estimated values (°C) at sweating rate = 0. T_{re} , rectal temperature. *Significantly less than day 0, $P < 0.05$.

Calculated total sweat ion losses of Na^+ , K^+ , and Cl^- during exercise and recovery on days 0, 3, 7, 14, and 21 are presented in Fig. 3. Total sweat Na^+ and Cl^- losses declined by ~36 and 25%, respectively, by day 21. There was no change in calculated K^+ losses for all SETs.

Figure 4 illustrates individual and group data for alterations in the effects of SR on sweat $[Na^+]$ during the 21 days of heat exposure. By day 21 of heat acclimation, $[Na^+]$ in sweat was lower at a given SR than on day 0. Regression analyses performed to determine the relationship for each individual and for all animals indicated that sweat $[Na^+]$ was highly correlated to SR during the 21 days of active heat acclimation. Individual correlations between SR and $[Na^+]$ ranged from $r = 0.729$ to $r = 0.992$ on day 0, from $r = 0.833$ to $r = 0.982$ on day 14, and from $r = 0.905$ to $r = 0.995$ on day 21. Whereas the range of SR and sweat $[Na^+]$ for individual animals varied considerably, a similar relationship existed between SR and sweat $[Na^+]$ for all animals (Fig. 4C).

DISCUSSION

This study provides initial information in horses pertaining to the alterations in sweating responses during a period of heat acclimation. The most important findings by 14–21 days of active heat acclimation were as follows: 1) the rate of sweat fluid loss during recovery decreased in hot humid conditions, 2) sweat $[Na^+]$ at a given SR decreased during exercise and recovery, and 3) the decrease in sweat fluid loss and sweat $[Na^+]$, in combination, resulted in a decrease in total (primarily Na^+ and Cl^-) ion losses. These results are consistent with improved maintenance of plasma volume and Na^+ content in these horses (unpublished observations). It therefore appears that heat acclimation in horses results in increased conservation of water and ions during exercise and recovery.

SR. Although the area used for measurement of local SR was enclosed within a pouch, collection of sweat fluid within a ventral reservoir minimized the quantity of sweat that remained on the skin surface and could have interfered with the rate of sweat production. Furthermore, in a previous study, this method of direct sweat collection provided similar estimates of local SR in horses during moderate-intensity exercise compared with measurements determined using dew-point hygrometry (19). By measuring sweat production over a

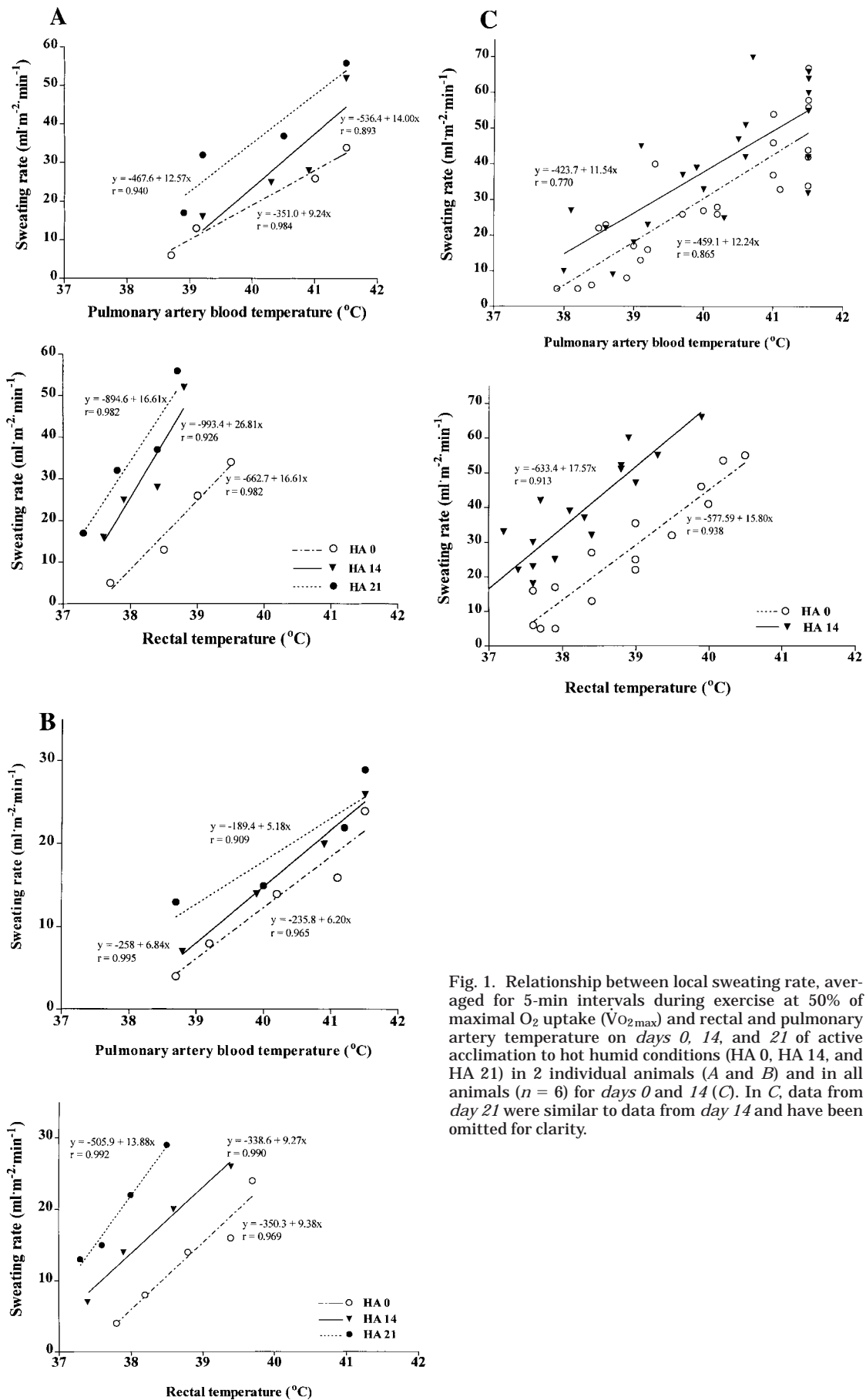


Fig. 1. Relationship between local sweating rate, averaged for 5-min intervals during exercise at 50% of maximal O_2 uptake ($\dot{V}\text{O}_{2\text{max}}$) and rectal and pulmonary artery temperature on days 0, 14, and 21 of active acclimation to hot humid conditions (HA 0, HA 14, and HA 21) in 2 individual animals (A and B) and in all animals ($n = 6$) for days 0 and 14 (C). In C, data from day 21 were similar to data from day 14 and have been omitted for clarity.

specific area of the lateral thorax during each SET, we were able to determine alterations in SR. Specifically, a more rapid reduction in SR early in recovery contributed to a reduction in total sweat losses. Although these findings were based on a local SR, it is likely that interregional variations in SR were small (18, 26) and would not significantly affect interpretation of the whole body responses. However, with the assumption of no change in the rate of respiratory evaporative losses, the similar rate of decline in whole body fluid losses

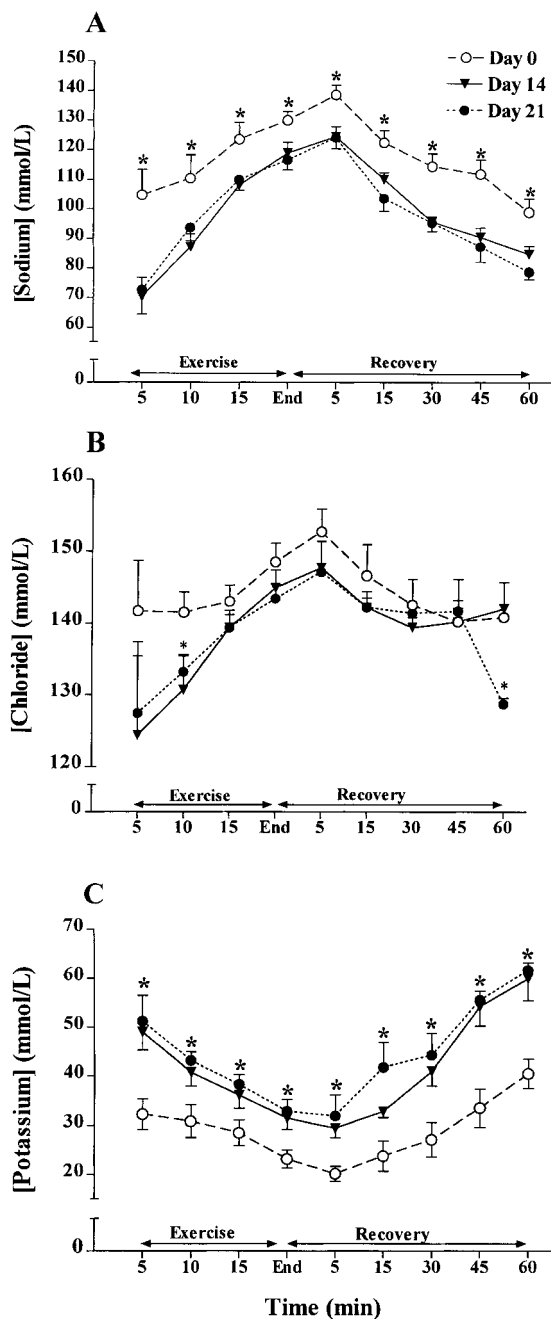


Fig. 2. Concentrations of Na^+ (A), Cl^- (B), and K^+ (C) in sweat collected every 5 min in horses during exercise ($50\% \dot{V}\text{O}_{2\text{max}}$) and recovery in hot humid conditions on days 0, 14, and 21 of active heat acclimation. Values are means \pm SE; $n = 6$. *Significantly different from days 14 and 21 (A), $P < 0.05$, and significantly different from day 0 (B and C), $P < 0.05$.

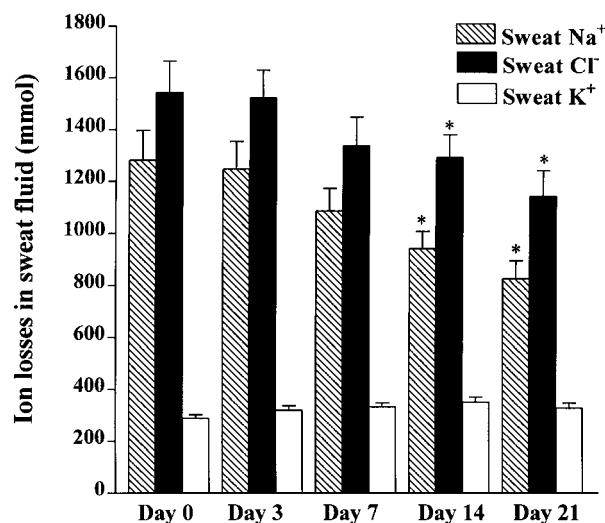


Fig. 3. Calculated losses of Na^+ , Cl^- , and K^+ in sweat fluid from horses during exercise ($50\% \dot{V}\text{O}_{2\text{max}}$) and 1 h of recovery in hot humid conditions on days 0, 3, 7, 14, and 21 of active heat acclimation. Values are means \pm SE; $n = 6$. *Significantly different from day 0, $P < 0.05$.

measured during each SET substantiates the belief that sweat losses declined by day 21 of heat acclimation. The SR measured in the present study are similar to those measured in Thoroughbred horses in hot dry conditions ($32\text{--}34^\circ\text{C}$ RT, $45\text{--}55\%$ rh) with use of the same methodology (24, 25). Importantly, SR in hot conditions are $\sim 30\text{--}40\%$ higher than those measured in cool dry conditions ($20\text{--}25^\circ\text{C}$ RT, $45\text{--}55\%$ rh) for horses exercising at a comparable work intensity (15, 26, 27, 32, 36).

In humans, it has been hypothesized that acclimation to humid heat is accompanied by selective increases in regional SR (9, 21, 39), thereby making more efficient use of the potential for evaporative cooling while minimizing sweat drizzle (38). Simultaneously, the core temperature threshold for the onset of sweating may be decreased, with enhancement of the sensitivity of the sweating response (39). However, some studies of heat acclimation/acclimatization in human subjects have shown little or no change in whole body sweating (12, 34), and others have reported a decline in mean SR after 3 days of continuous heat exposure (20). This variability in reported responses appears to reflect differences in duration of acclimation, the ambient conditions to which the subjects were acclimated, and differences in the fitness of individuals.

In the present study the decline in the volume of sweat produced during the entire SET largely reflected alterations in thermoregulatory responses after exercise (Tables 2 and 3). Because of substantial variation in the SR of individual animals, no significant change in the mean SR response or sweat volume produced during exercise was detected over the 21 days of humid heat acclimation. Recently, Marlin and co-workers (23) also reported no change in the SR-core temperature (T_{pa}) relationship in a group of five horses after 15 days of active humid heat acclimation. In contrast to exer-

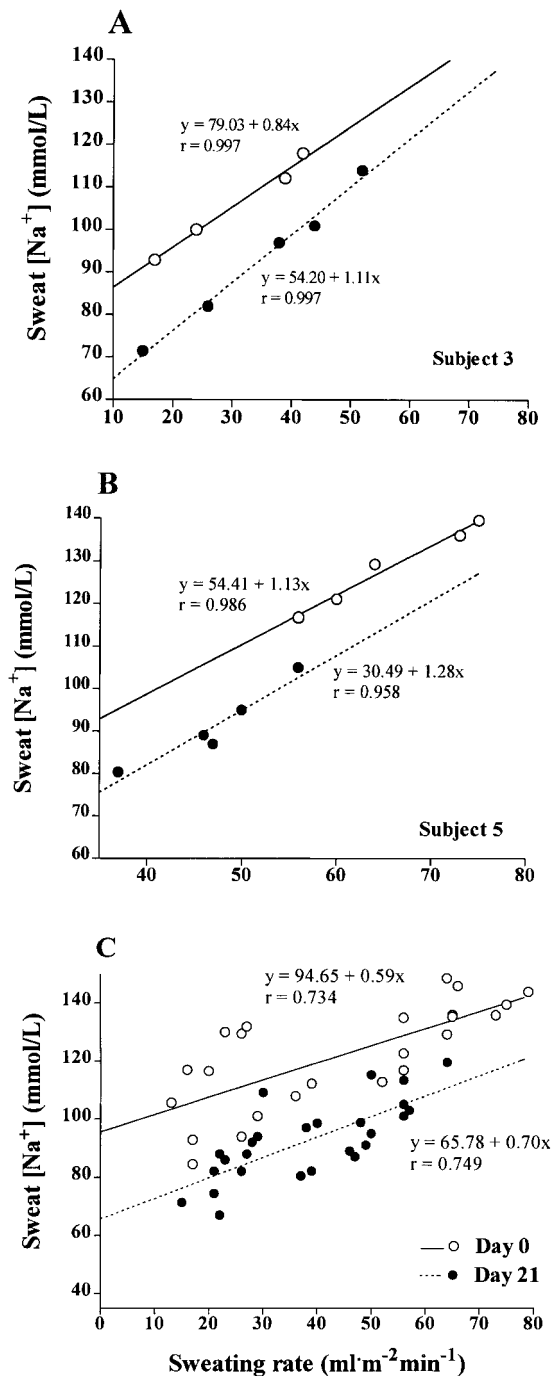


Fig. 4. Relationship between sweat $[\text{Na}^+]$ and local sweating rate, averaged for 5-min period during exercise at $50\% \dot{V}_{\text{O}_{2\text{max}}}$, in 2 individual animals (A and B) and in all animals ($n = 6$; C) on days 0 and 21 of active acclimation to hot humid conditions.

cise, during the 1-h recovery in the present study, there was a decrease in mean SR by *day 7* compared with *day 0* in a seeming attempt to conserve some of the large quantity of water and ions lost in the nonacclimated state. Our measures could not be used to determine how the changes in SR were achieved; however, a redistribution of sweat gland activity or changes to regional variations in SR are possible. Normally, an increase in SR to maximal levels results in an initial

recruitment of sweat glands, followed by increased sweat secretion per gland (38), and presumably the reverse could occur to reduce SR. However, in the latter case, areas with higher SR still secreted sweat at a rate superfluous to that of evaporative loss, resulting in considerable dripping of sweat from the skin surface. The decline in SR during recovery measured on the lateral thorax could represent a reduction in sweat production in areas in which SR was well in excess of that evaporated from the skin surface. In addition, the decline in recovery SR could reflect greater reliance on heat loss achieved by increased skin blood flow and/or enhanced respiratory heat loss. In the group of horses used in this investigation, at least eight consecutive weeks of training were undertaken before commencement of the period of heat acclimation. As a result of their extensive working muscle mass, elevations in the horses' core temperature to $41.5\text{--}42.0^\circ\text{C}$ were rapidly attained during moderate-intensity exercise in cool dry conditions (25). We speculate that much of the stimulus for increases in SR resulting from elevations in core temperature that might normally be associated with heat acclimatization was achieved during this initial period of exercise training.

SR and core body temperature. We used T_{pa} and T_{re} as the regulated variable to examine the sensitivity of the sweating response during exercise at $50\% \dot{V}_{\text{O}_{2\text{max}}}$ (Fig. 1). Studies of heat acclimation in human subjects have reported increases in the sensitivity of SR to changes in core temperature, with subjects starting to sweat at a lower core temperature after acclimation (31, 37, 39). By *day 14* of this study, all animals showed visible signs of sweating within 15 min of entering the treadmill room. When the relationship of SR to T_{re} or T_{pa} is plotted (Fig. 1C), the results indicate a leftward shift of $\sim 0.75\text{--}1.0^\circ\text{C}$ in the curve defining this relationship with the progression of heat acclimation. This is consistent with human studies in which a greater sweating response was elicited by a standard thermal stress after acclimation (38, 39). Although a more sensitive sweating response was evident in several animals, we were not able to detect a significant change in slope of the regression line of the SR-core temperature relationship for the group of six horses (Table 3). We attribute the inability to detect a change in this response to widely variable individual SR given the small group of animals and to the limited number of SR measurements (3–5) obtained during exercise.

In some studies of human heat acclimation, the slope of the SR-core temperature relationship (sweating sensitivity) has been shown to increase, with a plateau for this relationship occurring at a higher SR after heat acclimation (7, 10, 13, 39). In the present study, there was little alteration in the slope of the line defining this relationship. This lack of change in slope is consistent with the findings of Nadel and co-workers (31), who reported that exercise training increases the slope of this relationship, whereas heat acclimation lowered the threshold for the onset of sweating. As a result of the relatively short duration of exercise, no definitive plateau in SR was reached for the six horses. Although SR

exceeded $55 \text{ ml} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$ ($\sim 16 \text{ l/h}$) in several animals, SR had not reached a plateau at the end of exercise. Thus the short duration of exercise and the high SR attained precluded a comparison of this aspect of the SR-core temperature relationship.

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 in agreement with sweat fluid losses calculated on the basis of mean whole body SR. Estimates of the contribution of respiratory heat loss in the horse vary between 15 and 30% (14, 30), and, given the high relative humidity in this study, the more conservative estimate of 15% was used in the calculation of sweat fluid losses. An SR comparable to that measured at 10–15 min of exercise on *day 21* would have resulted in sweat fluid losses of $\sim 14 \text{ l/h}$, a rate of fluid loss comparable to previous estimates (10–15 l/h) based on changes in body mass obtained during endurance exercise in hot dry conditions (4, 17). The significant reduction in sweat fluid losses measured during the SETs on *days 14* and *21* was the result of the more rapid reduction in SR in early recovery. Even with this reduction in SR, as a result of the high relative humidity, much of sweat loss still constituted drippage and did not contribute to evaporative heat loss.

Sweat ion concentrations. The sweat $[\text{Na}^+]$, $[\text{K}^+]$, and $[\text{Cl}^-]$ measured during the 21-day protocol are, to our knowledge, the first reported measurements of equine sweat ion composition during a period of heat acclimation. To minimize any reduction in sweat ion concentrations based on diet, the horses in this study received a salt supplement in their grain during the period of training and acclimation.

Previous studies have demonstrated the isotonic-to-slightly hypertonic nature of equine sweat, as well as changes in sweat ion concentrations that largely reflect alterations in SR due to different ambient conditions or exercise intensities (5, 24, 26–28). As SR increases, the rate at which sweat glands reabsorb Na^+ does not increase proportionately, resulting in an elevation in sweat $[\text{Na}^+]$. In addition to individual variation in SR and sweat $[\text{Na}^+]$, factors such as the type of acclimatization (passive vs. active, hot dry vs. hot humid) and mineralocorticoid action may influence the content of Na^+ in sweat (35, 38).

In the present study the ambient conditions and workload remained constant during the five SETs, making it possible to assess changes in sweat ion composition during acclimation. The reduction in total sweat Na^+ losses on *days 14* and *21* compared with *day 0* partially reflects the decrease in SR during recovery but also a decline in sweat $[\text{Na}^+]$ at any given SR during exercise and recovery (Fig. 4). These changes are consistent with the production of a more dilute sweat during human heat acclimation (2, 38). The high correlation between SR and sweat $[\text{Na}^+]$ for individual animals (Fig. 4, *A* and *B*), although not as strong for the group of six horses (Fig. 4*C*), may reflect an interrelationship between sweat gland water secretion/absorption rates and Na^+ reabsorption rates (16). A reverse

pattern of change in sweat $[\text{K}^+]$ compared with changes in sweat $[\text{Na}^+]$ was evident during exercise and recovery in the SETs. $[\text{K}^+]$ is considerably higher in equine than in human sweat and characteristically declines, independent of SR, from onset of sweating in hot conditions (26) or during exercise (18). In horses completing 45 km of treadmill exercise in cool dry conditions, sweat $[\text{K}^+]$ declined by a similar amount (from initial values of ~ 39 to $\sim 29 \text{ mmol/l}$), whereas SR was maintained at a constant rate ($\sim 26 \text{ ml} \cdot \text{m}^{-2} \cdot \text{min}^{-1}$) (18, 19). Lower sweat $[\text{K}^+]$ measured at the onset of exercise on *days 14* and *21* may, in part, reflect the earlier onset of sweating before exercise in the latter 7 days of heat acclimation. Additionally, however, the altered cation composition of equine sweat after acclimation (specifically, higher $[\text{K}^+]$ and lower $[\text{Na}^+]$) may represent tubular modification of cation content of sweat fluid within the sweat gland. It remains to be determined whether the latter process is dependent or independent of SR.

Sweat ion losses. The combined ion losses of Na^+ , Cl^- , and K^+ in sweat during exercise and recovery were $>2,200 \text{ mmol}$ (*day 21*) to $3,100 \text{ mmol}$ (*day 0*). The decrease in ion losses during the period of acclimation was due to a decrease in SR during recovery and reductions in sweat $[\text{Na}^+]$ and $[\text{Cl}^-]$. The reduction in sweat $[\text{Na}^+]$ measured by *day 14* of the protocol is consistent with a concurrent increase in resting plasma volume. This increase in plasma volume was directly and linearly related to increases in total plasma protein content and total Na^+ and Cl^- content (unpublished observations). In contrast to Na^+ and Cl^- , sweat $[\text{K}^+]$ losses during each SET were unchanged. The mechanisms responsible for the adaptive responses in sweat ion concentrations are not known and require study. In practical terms, these rates of ion loss underline the necessity for dietary ion supplementation for horses training and competing in hot ambient conditions. Furthermore, they point to the fact that the proportion of Na^+ , Cl^- , and K^+ provided as oral electrolyte supplements during exercise in hot conditions may change over the course of time with, particularly, an increasing requirement for K^+ .

In conclusion, this study examined sweating responses in horses during 21 days of humid heat acclimation chosen to reflect adverse environmental conditions in which horses may be required to train or compete. Despite the uncompensable heat stress associated with these conditions, adaptive changes in sweating responses were evident by *day 14* of active heat acclimation. Adaptations included a lowering of the thermal set point for the onset of sweating, a reduction in overall sweat fluid losses attributed to a decline in SR during recovery, and a reduction in sweat ion losses as a consequence of the decrease in SR during recovery and in sweat $[\text{Na}^+]$ at all SR.

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