Living history: Elsworth R. Buskirk

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Tipton CM. Living history: Elsworth R. Buskirk. Adv Physiol Educ 33: 243−252, 2009; doi:10.1152/advan.00058.2009.—In 2005, the American Physiological Society (APS) initiated the Living History of Physiology Archival Program to recognize senior members who have made significant contributions during their career to the advancement of the discipline and the profession of physiology. Subsequently, the leadership of the APS Section of Environmental and Exercise Physiology selected Prof. Elsworth R. Buskirk of Pennsylvania State University to be profiled in Advances in Physiology Education.

American Physiological Society Living History

ELSWORTH R. BUSKIRK (Fig. 1) was born on August 11, 1925, in Beloit, WI, to Mr. and Mrs. Ellsworth F. Buskirk. He graduated from Beloit High School during the World War II year of 1943 and attended the University of Wisconsin with the intent of majoring in chemical engineering. However, his education was interrupted when he entered the Army later that year. After serving 3 yr in the infantry, which included combat in the European Theatre of Operation and an overseas commission, he returned in 1946 to enroll in St. Olaf College in Northfield, MN, with majors in biology and physical education. Four years later, he graduated with a BA degree while being accepted for graduate studies in Physical Education and Physiological Hygiene at the University of Minnesota in Minneapolis, MN. In 1951, he received the MA degree from the same institution and was accepted into the Physiological Hygiene PhD Program and appointed as a Laboratory and Teaching Assistant within the renowned Laboratory of Physiological Hygiene under the leadership of Dr. Ancel Keys.

Subsequently, E. R. Buskirk became a Research Fellow and a Research Associate while participating in multiple laboratory studies. It was a unique educational experience because, besides Keys, he was associated with and interacted with distinguished professors such as Joseph T. Anderson, Josef Brozek, Francisco Grande, Austin Henschel, Ernst Simonson, and Henry L. Taylor, who subsequently became his PhD Advisor. E. R. Buskirk made significant contributions to the important study conducted by Taylor et al. (53) on the determination of maximum O2 consumption (V\text{O}_{2max}) that was stimulated by the criterion uncertainties in previous investigations by A.V. Hill (34) and Sid Robinson (50). Hence, they systematically tested subjects and found that using a constant speed (11.3 km/h) while increasing the grade in 2.5% units was more precise than using a constant grade with changing speeds. In fact, a grade increase of this magnitude was ~300 ml/min. Therefore, they concluded that if the increase in V\text{O}_2 at two different grades was <150 ml/min, or 2.1 ml·kg\textsuperscript{-1}·min\textsuperscript{-1}, a plateau had been obtained and V\text{O}_{2max} had been achieved (Fig. 2). Although different methods have evolved with time, the assessment of plateau conditions, as determined by these investigators, continues to remain as the criterion measure for the determination of V\text{O}_{2max} values.

Although the Laboratory of Physiological Hygiene had completed and published the historic study on the biology of human starvation (40), many unresolved issues remained pertaining to restricted water and food intakes and their influences on performance capacity and body composition. Buskirk had important roles in these studies (12, 31, 52), which varied the carbohydrate caloric consumption from 580 kcal/day, 1,000 or 1,010 kcal/day, or 3,100 kcal/day with water intake being either 900 or 1,800 ml/day. They found that the low-carbohydrate diet was able to prevent the anticipated ketosis and liver damage but was unable to prevent the hypoglycemia that occurred with their standardized treadmill test. As the study progressed, V\text{O}_{2max} decreased, but it was not until 10% of body weight was lost that the reduction in V\text{O}_2 was manifested at the tissue level. When grip strength was measured, it followed the profile exhibited with V\text{O}_{2max}. They concluded that moderate energy output could be maintained when 10% of body weight was lost if the caloric intake and dietary supplements were able to prevent the ketosis, dehydration, and hypoglycemia associated with restriction.

Buskirk’s association with Keys, Brozek, Henschel, Mickelsen, and Taylor introduced him to their novel concepts and methodology associated with body composition, and, later, he became the first investigator (while a PhD candidate) to relate V\text{O}_{2max} to select body composition units (14). It is of interest 24 yr later that the Los Angles Rare Book Collectors, Zeitlin & Ver Brugge, designated his 1953 PhD dissertation as a rare book and publicized its addition to their inventory. Not published was that Drs. Claude Lenfant and Robert Joy of the National Institutes of Health (NIH) sent him congratulatory letters.

Using the methodology associated with his dissertation (14), Buskirk conducted and published, with Prof. Taylor as co-author, the first peer-reviewed study that measured maximal O2 intake (59 subjects) and related the findings to the body weight, fat-free body weight, active tissue, and cell mass of sedentary and athletic subjects (24). The highest correlation with V\text{O}_{2max} was fat-free mass (r = 0.85), whereas the lowest correlation was with cell mass (r = 0.45). Compared with sedentary subjects, athletic subjects had markedly higher V\text{O}_{2max} per unit of fat-free mass. After subjects were classified by percent body fat into three groups, there were no group differences when they were exposed to 46.1°C Dry Bulb (DB) and 27°C Wet Bulb (WB) temperatures (16). Subjects were assigned to three groups (sedentary, conditioned, conditioned and heat acclimated) with the experimental period lasting 3 wk. They became acclimated by exposure to temperatures ranging from 32.5°C DB and 27°C WB to 54.5°C DB and 30°C WB. Once dehydrated, subjects performed two work performance tests: a

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walk and a run. As anticipated, dehydration caused a decrement in $V_{\text{O}_2\text{max}}$ with the three groups but with the conditioned subjects having higher values than their sedentary counterparts when evaluated on a fat-free basis. They recommended for exhaustive work that $V_{\text{O}_2\text{max}}$ be expressed per kilogram of body weight, whereas to evaluate the performance of the cardiorespiratory system, the $O_2$ results should be presented as fat-free weight. Finally, they concluded that physical training by young men will affect $V_{\text{O}_2\text{max}}$ independently of the mass of active tissue (24).

Dr. Buskirk and the Quatermaster Research and Development Center

After receiving his PhD degree in 1954, Dr. Buskirk accepted an appointment as a Physiologist with the United States Army’s Quartermaster Research and Development Center in Natick, MA. Subsequently, he became Chief of the Environmental Physiology Section and remained in that position until 1957. As in Minnesota, he became associated with an outstanding group of scientists, which included David E. Bass, Ralph F. Goldman, Martin B. Kreider, P. Patrick Iampietro, and William E. Welch. At Natick, he became involved in a myriad of studies ($n = 17$) that related to nutritional, diurnal, environmental, climatic, and metabolic influences that related to physiological responses and work performance. In fact, he conducted the first study to address the single and combined effects of conditioning and heat acclimatization on performance and physiological responses (pulse rate, rectal temperature, and $V_{\text{O}_2\text{max}}$) of dehydrated subjects (5.5% loss in body weight) and their sedentary controls (Fig. 3) (16). An original finding was that conditioned dehydrated subjects had improved work performance results, whereas being conditioned and acclimatized did not enhance performance. Forty-two years later, in 2000, Buskirk and cohorts were honored by the Editor of *Wilderness and Environmental Medicine* for their authorship of this classic article (17).

Aware that the specific dynamic action (SDA) of food would increase metabolism, Buskirk, with Iampietro and Welch as co-authors (18, 37), investigated the single and combined effects of SDA, moderate exercise (marching 14–16 km/day), and climate (30 to 25°C) in three locations (Natick, MA; Yuma, AZ; and Ft. Churchill, MB, Canada) on basal $V_2O_2$ and resting $V_{\text{O}_2}$. They reported that the elevation in resting $V_{\text{O}_2}$ during the day was predominately the result of the SDA of foods. Because the SDA effect can be one- to twofold higher than basal values, the authors advised future investigators to be cognizant of meal schedules when scheduling metabolic measurements. Additionally, they reported moderate exercise alone did not alter resting $V_{\text{O}_2}$ values and that fasting would be associated with a “small diurnal” effect on resting $V_{\text{O}_2}$ that occurred with or without exercise. With one exception, they concluded that climate per se did not influence basal $V_{\text{O}_2}$ or the pattern of resting metabolism (18). In a related study (37), they demonstrated that climate did influence the diurnal pattern of rectal temperature (Fig. 4).

In cold exposure studies conducted by the institute, Buskirk had a supporting role in the investigations. They found that the elevated caloric intake with cold could be explained by the increased energy expenditure due to nondetectable shivering and to the shivering caused by activation of the nervous system. When the influence of dietary supplementation (600 or 1,200 kcal of a diet of 40% fat, 40% carbohydrate, and 20% protein) was investigated with individuals who had consumed three “normal meals per day” before sleeping in an arctic sleeping bag while being exposed to $-37^\circ\text{C}$, they
found that elevations occurred in \( V\dot{O}_2 \) and in rectal and toe temperatures but not in mean skin temperature (42). The supplement was also associated with a reduction in the incidence of wakefulness and in the degree of foot numbness when subjects rose in the morning. Otherwise, there were no additional advantages attributed to the 1,200-kcal supplement (42).

Iampietro, Bass, and Buskirk (36) exposed nude volunteers to various combinations of wind (1.6 and 16.0 km/h), temperature (10 and 15.5°C), and relative humidity (30% and 95%) and recorded \( V\dot{O}_2 \), skin and rectal temperatures, and sensations. Wind had the most influence on the responses with relative humidity having the least effect and importance (36). Kreider and associates, with Buskirk (43), had male subjects dressed in shorts and live in an environmental chamber for 14 days at 15.5°C before following the same outline at 26.7°C. \( V\dot{O}_2 \) and rectal temperatures were obtained at select times during the day to study the changes in diurnal rhythm and resting metabolism. With cold exposure, the resting metabolism was increased with every time period (8 AM, 12 PM, 4 PM, and 8 PM), although there was a progressive decline from 20% to 11% between 8 AM and 8 PM; there were no significant changes in the measurement of their basal metabolic rates. At 8 AM, rectal temperatures were significantly higher in the cold; thereafter, they were similar at the various chamber temperatures. The authors concluded that rectal temperatures were well maintained during cold exposure and that \( V\dot{O}_2 \) appeared to respond in such a fashion to “subserve this maintenance” (43).

Because African-Americans and Caucasians have different incidences of cold injury, Buskirk and colleagues exposed African-American and Caucasian subjects to 2 h of cold (10°C) or to 45 min of digital cooling at 0°C. Although the assessment of whole body cooling exhibited no significant differences among the groups, the Caucasian subjects had higher digital temperatures, faster “hunting” responses, and faster rewarming times than the African-American subjects, which supported the concept that ethnic physiological differences were contributing to their higher rates of cold injuries (38).

**Dr. Buskirk and NIH**

In 1957, Dr. Buskirk accepted a position as a Physiologist at the National Institute of Arthritis and Metabolic Diseases of NIH in Bethesda, MD. His responsibilities were to develop and to direct the Metabolic Chamber Facility and Program for the institute. As a result of his leadership, the facilities became recognized as being “state of the art” and the model for others to emulate. Seldom acknowledged has been his role in the development of templates for instruments and methodology associated with metabolic measurement that have been incorporated into “metabolic carts,” which serve as standard equipment in current research laboratories. While at the institute, he had the opportunity to interact and collaborate with prominent clinicians and scientists, which included Nathaniel Berlin, Eugene Braunwald, R. Moore, Daniel Steinberg, Ronald H. Thompson, and G. Donald Whedon.

With colleagues, he used the new metabolic chamber to conduct the first study on the SDA of foods when eaten at cold temperatures. After providing subjects with a 1,000-kcal meal, they measured \( V\dot{O}_2 \) at different temperatures. Unlike in the dogs used by Rubner (50a), they found a summation effect with the increment associated with food consumption as well as with the increment associated with cold air temperatures (26). The availability of the metabolic chamber made it possible to conduct the direct measurement of \( V\dot{O}_2 \) when subjects were sleeping. In the late 1950s, this was a major accomplishment. Although few subjects were studied, a direct relationship was observed between the level of \( V\dot{O}_2 \) for the night hours and the basal metabolic rate (26).

Buskirk and his NIH cohorts were the first to study the metabolic effects of exposing individuals with different body fat percentages (11–51%) to different air temperatures (10 and 26.7°C) (28). They found that with exposure to cold air, \( V\dot{O}_2 \) and CO2 production (11–51%) were significantly and inversely related to body fat percentages (Fig. 5). Moreover, they ob-
served that total body insulation with cold exposure was significantly and directly related to the percentage of body fat and inversely to the metabolic effect (28).

To learn whether patients with febrile episodes have abnormal thermoregulatory responses, Buskirk and colleagues measured changes in heat production, body temperatures, heat flow, and heat storage in normal and diseased subjects after intravenous injections of endotoxin (27). Subjects were classified as nonresponders, responders whose elevated heat production preceded an elevation in core temperature, and responders whose redistribution of heat resulted in an increase in core temperature before causing an increase in heat production. With normal subjects, endotoxin caused changes in heat distribution and heat production at independent rates, whereas subjects (patients) with fevers exhibited exaggerated metabolic responses that were caused either by an alteration in the vasomotor control of heat redistribution or by increased heat production per increment of core temperature. The authors were supportive of the latter possibility (27). Although in a supporting role in a 1971 cold experiment (10°C) with Thompson and Whedon, Buskirk conducted heat production and heat exchange responses (55) in normal subjects, an obese individual, normal subjects made hyperthyroid by triiodothyronine administration, and in a hypothyroid individual receiving l-thyroxine. They learned that heat exchange was greatly influenced by thyroid hormones or by thyroid analogs and that hypothyroidism appeared to be a result of an impaired regulation against the cold. However, they noted that “regulation may be restored by the administration of thyroid hormone or an analogue” (55).

Unknown to most American Physiological Society (APS) members, Dr. Buskirk was an effective “unpaid lobbyist” during his tenure at NIH for the establishment of a Study Section devoted to environmental and exercise physiology. His efforts were successful because, in 1963, NIH established an Advisory Committee on Applied Physiology that, in 1964, became an official Study Section with 8 members who evaluated 20 research proposals (56).

Dr. Buskirk and Pennsylvania State University

In 1963, Buskirk accepted a position as Professor of Applied Physiology at Pennsylvania State University with academic responsibilities in the College of Health and Physical Education and within the College of Medicine. He immediately became Director of the Laboratory for Human Performance Research, later known as the Noll Laboratory of Human Performance Research, and initiated a graduate program in Applied Physiology that rapidly became one of the premier graduate programs in exercise sciences in North America (56). His presence and program served as an instant magnet for graduate students, postdoctoral fellows, and individuals from other institutions, which came to his laboratory to learn methodology and techniques or to be exposed to his expertise on environmental or exercise matters (Table 1). In 1988, he became Marie Underhill Noll Professor of Human Performance in the College of Health and Human Development and, 4 yr later, was accorded emeritus status. As in previous positions, he was associated with creative and capable colleagues, which included Drs. James L. Hodgson, James Kolli, Jose R. Mendez, and W. Channing Nicholas. He was also associated with Mr. Joseph Loomis, a talented engineer, who for 36 yr was responsible for making the laboratory operational.

Not surprisingly, his research endeavors were extensive, productive, fundable, and publishable, with many being a continuation of previous interests. As space does not permit total coverage, only select topics will be emphasized.

Physiological effects of high altitude. Soon after accepting the position at Pennsylvania State University, Prof. Buskirk began investigations on the influences of altitude that included the Quechua Indians of Peru (4). These descendants from the ancient Inca empire live in an environment with an elevation of ~4,000 m and a barometric pressure of ~475 mmHg (15). It was from this and related investigations (19, 20, 22, 29, 41) that he emerged as an international authority on the effects of altitude on temperature regulation (in the cold, Quechua Indians exhibit higher heat production and heat loss capabilities than Caucasians) and on work (exercise) performance. For an insight of a 1978 perspective on the effects of altitude on work performance, readers should examine his scholarly chapter on the topic in The Biology of High-Altitude People (15).

Before the 1968 Olympics, which were to be held in Mexico City, Mexico, physiologists were uncertain as to the effects that competing at an altitude of 2,240 m with a barometric pressure of 585 mmHg would have on athletic performance. Thus, in the 1960s, Buskirk, colleagues, and track athletes from Pennsylvania State University investigated this subject while testing and training were in PA (300 m), Denver, CO (1,700 m), lower altitudes [athletic institute (19, 20)]. The sites involved in testing and training were in PA (300 m), Denver, CO (1,700 m), Alamosa, CO, Mount Evans, CO (4,600 m), and in Peru (4,000 m).

Select Pennsylvania State University runners were tested at sea level, immediately after arrival in Peru (Fig. 6), after 48 days of training at altitude level, and immediately after returning to sea level (19). Once in Peru, the runners experienced a 26% reduction in V\textsubscript{O}\textsubscript{2max}. When tested for bicycle riding, their times were reduced by 12%; however, after 20 days of training,
the times were similar to values obtained at sea level. Time trials were held for the 400-yd, 880-yd, 1-mile, and 2-mile runs and compared with sea level values, and the percent reductions were 91%, 82%, 77%, and 81%, respectively, of previously recorded values. Related time trials were conducted at lower altitudes in Colorado, and the results were comparable with those obtained at sea level. After returning to Pennsylvania, \( V_{O2max} \) tests were conducted, and no results were higher than their prealtitude values. Consequently, they concluded that there was no synergy between exercise training and a hypoxic environment at 4,000 m (19) and stated (20) that “training at high altitudes had no deleterious effect on subsequent performance at lower altitudes.”

To obtain more information on physiological and performance responses at different altitudes and the effect of prolonged training at low altitude, Buskirk participated in a collaborative study with Prof. John Faulkner (University of Michigan) and Prof. Bruno Balke (University of Wisconsin) (29). Subjects were essentially members from the track teams of Michigan and Pennsylvania State University and were assigned to groups of either low altitude (2,300 m), medium altitude (3,100 m), or high altitude (4,300 m) for testing and comparative purposes. \( V_{O2max} \) testing was performed and related to sea level (200–300 m) values; reductions of 13%, 20%, and 29% were noted for the respective groups. Run time trials were conducted at 2,300 m for distances between 1 and 3 miles, and the times were 2–13% slower than those previously recorded. After subjects had trained for 6 wk at 2,300 m and had been tested for \( V_{O2max} \), the results revealed no significant changes and were similar to those recorded at sea level. Although these results were too late to be of importance for the Mexico Olympics, they recommended that sport, military, and astronaut groups consider training at a low altitude (2,300 m) for high-altitude endeavors (29).

While the track athletes were in Peru, Kollias and Buskirk compared the athlete’s physiological responses after testing at 4,000 m with those of the Peruvian Indians, who performed manual labor, played soccer, rode bicycles, and walked long distances for fiestas. They classified the students as newcomers and the native workers as long-time residents (41). After the newcomers had resided between 50 and 64 days in Peru, both groups were subjected to submaximal and maximal testing for metabolic, respiratory, and cardiovascular responses. Aerobic capacity, as evaluated by various indexes, was similar for the newcomers and natives but was markedly lower for the nonathletic newcomers. Both athletic and nonathletic newcomers had higher maximal pulmonary ventilation values than the natives, whereas maximal heart rates exhibited no meaningful differences between the groups. The bicycle ergometer was used to evaluate work performance with the runners demonstrating the higher work rates and the natives lower work rates. However, at comparable exercise intensities, the natives had markedly higher \( V_O2 \) values than both groups of newcomers. From these collective results, they concluded that the Pennsylvania State University “fit newcomers” at altitude had an \( O_2 \) transport system that was relatively equivalent to the long-time resident native. On the other hand, the long-time resident native had an \( O_2 \) transport system that was superior to the nonathletic newcomer who arrives at altitude (41).

Several years later, with Ray Squires, Buskirk conducted an important study in an altitude chamber study to confirm his “field” \( V_{O2max} \) results obtained between 300 and 2,300 m. Using recreational distance runners from Pennsylvania State University, they confirmed that at ~1,200 m and thereafter (~1,500 and 2,300 m) \( V_{O2max} \) would be reduced by ~5.0%, 7.0%, and 12.0%, respectively (51).
Finally, Buskirk and Mendez (22) are to be commended for their article that critically evaluated the nutritional and environmental considerations required for optimal work performance at various altitudes. Using experimental results, they prepared detailed tables, charts, graphs, and figures that related food and water requirements to variables associated with climate and work performed.

**Physical activity intervention and coronary heart disease.** In the 1950s, the epidemiological research conducted by Morris and colleagues on the relationship between physical activity and coronary heart disease led to the “exercise hypothesis,” which indicated that physical activity would reduce the occurrence of coronary heart disease (49). It should be noted that Prof. Buskirk and his Laboratory for Human Performance Research on Physical Performance became one of the first in the United States to participate in a collaborative study (University of Minnesota, University of Michigan, and University of Wisconsin) on the feasibility of incorporating physical activity in a controlled trial on the prevention of coronary heart disease as sponsored by the Public Health Service (54).

In the study were 3,648 males between 40 and 59 yr of age, of which 209 subjects were assigned to treatment groups and 176 subjects to control groups (54). At Pennsylvania State University, 1,376 individuals were screened, and of the 171 subjects assigned to experimental groups, 85 subjects were assigned to the exercise group and 86 subjects to the control groups, respectively. Three exercise sessions were scheduled weekly and were considered to be of high intensity and consisted of jogging, swimming for distance, paddleball, and sports. The results after 18 mo showed that the trained group markedly improved in work capacity and psychosocial measures. However, they were surprised to learn that their adherence records, which had been at 75% at 3 mo, had progressively declined to ~50% at the 6-mo period, where it essentially remained until the end of the study. Measurements of resting blood pressure exhibited no significant benefits for the...
exercise program at any time period, whereas cholesterol levels were lower for the experimental group. However, the differences noted were not significantly different (54). Also, there were also no significant differences in mortality rates between the groups. The significance of the study for the Public Health Service was that it dramatically demonstrated that future controlled trials on coronary heart disease required more subjects (they recommended 12,000 individuals) and improved methods to maintain subject adherence (53).

Even so, 13 yr later, in 1979, Buskirk’s laboratory, led by MacKean, conducted a follow-up study with 51% of the potential subjects (46). Comparisons were made between the control and exercise groups on the prevalence of coronary heart disease, and no significant differences were found. Essentially 28% of the exercise group had continued their jogging activities. When the the groups were evaluated for differences in smoking, intake of dietary fat, alcohol consumption, cardiovascular fitness status, blood lipid concentrations, resting blood pressure, and percent body fat, again no significant differences were found. Positive results were found when they compared individuals within the exercise group that continued their physical activities with those who did not and found that the more active subjects had a lower percentage of body fat with higher aerobic capacities and HDL levels and zero smokers (46).

Body composition assessment. Recall that in his PhD dissertation, Buskirk was the first to advocate body composition to be expressed as fat mass, percentage of fat, or on a fat-free mass basis and to express energy expenditure data accordingly (13, 14). He continued to pursue this interest at Pennsylvania State University, and, under his leadership, the Laboratory for Human Performance Research became nationally recognized for its innovation and perfections of methods and techniques that enhanced the determination of body fatness and the assessment of cell mass (13, 23).

Since total body water information when coupled with body density will increase the accuracy of determining body fatness (13), Buskirk’s laboratory, with Mendez as the lead investigator, found that measuring D2O levels in saliva samples via gas chromatography was a “simple procedure” that could be effectively used for evaluating body composition and nutritional status (48). With Akers, they developed an electronic cube system that was capable of securing more accurate underwater weighing results (1). To improve the assessment of subcutaneous body fat, Haymes and colleagues perfected an ultrasonic technique and found a significant correlation (0.88) between the ultrasonic measurements and soft tissue roentgenograms recorded from the triceps. However, the relationship was lower (r = 0.78) when comparisons were made at the suprailliac site (32).

For years, urinary creatinine has been associated with muscle mass (11). Boileau and colleagues investigated its variability with sedentary Pennsylvania State University students with a wide range of fat weight. They found subject variability to be high and the relationship between urinary creatinine levels and fat-free weight to be low and reported that skin-fold caliper measurements would be just as precise for this purpose (11). Buskirk’s laboratory, under Mendez’s leadership, advanced the assessment of muscle mass by improving the biochemical measurement of endogenous 3-methylhistidine and reported that it was more closely associated with fat-free mass (0.93) than with VO2max (r = 0.78) (47). Additionally, they conducted a cooperative study with Brookhaven National Laboratory in which total body nitrogen and potassium levels were measured along with 3-methylhistidine in a carefully controlled dietary study. Neutron activation procedures were used to measure total body nitrogen along with careful dietary and metabolic measurements (44). They found that endogenous 3-methylhistidine was significantly correlated with mean muscle mass (r = 0.91), urinary creatinine levels (r = 0.87), and fat-free body mass (r = 0.81), whereas it had a low correlation (r = 0.33) with the nonmuscle component of fat-free body mass. If the dietary constraints they recommended were followed, the measurement of 3-methylhistidine would be an important inclusion to study in vivo total body muscle protein degradation (44).

Barlett, Puhl, Hodgson, and Buskirk examined the cross-sectional relationships between fat-free mass (determined densitometrically) and stature in 1,103 subjects aged 6–86 yr and reported a significant increase in the fat-free mass-to-height ratio that occurred during the pre- and postadolescent years. This spurt occurs for a longer period in males, causing significant gender difference starting at 16 yr and continuing throughout adulthood. Around 60 yr of age for males, the ratio begins to decline, whereas in females, the trend occurs at 50 yr of age (9).

Not unexpectedly, Buskirk’s laboratory examined the relationship between body composition and work capacity changes. They were evaluated in middle-aged women who participated in a 12-wk exercise program that required walking or jogging at 75% of their aerobic capacity (45). Sixty-four percent of the subjects had body fat percentages that were 30% or more. The program was successful as subjects improved their VO2max values and exhibited reductions in fat percentages. Eighteen months later, the laboratory conducted a followup study to assess the effectiveness of the program. Of the nonobese subjects, 40% continued their jogging programs but at lower intensities and durations. Thirty-three percent of the obese subjects followed the same practices. Both groups had aerobic capacity and body composition results that were similar to the ones obtained 18 mo earlier. The authors indicated that future exercise intervention programs that revert to exercise ad libitum programs were likely to have similar results (45).

Obesity and thermal considerations. Associated with Buskirk’s interest and expertise in body composition and thermal regulation was obesity. Soon after arriving at Pennsylvania State University, he initiated a heat acclimatization study in lean and obese men and women who were exposed to environmental conditions of 46°C DB and 27°C WB temperatures while walking on a treadmill at 4.8 km/m for 1 h (21). Buskirk and colleagues found, compared with lean individuals, that obese subjects, especially women, had higher skin temperatures, lower sweat production, and a poorer tolerance to a heat load. They concluded that physical condition appeared to be an important acclimatization consideration and suggested that individuals with large body surface areas had lower heat tolerance than leaner and smaller ones (21).

To gain more information on these differences, a study with Bar-Or was conducted on the distribution of heat-activated sweat glands in obese and lean men and women (6). Higher densities of heat-activated sweat glands were found in lean
men than in obese men. The same trend occurred in women. This difference in density was related to the number of sweat glands found on the trunk and limbs of men and to the trunk of men. Women were associated with an inverse relationship between density and percent body fat. In addition, the females with high body surface areas had lower densities than those with lower surface areas. In a related study with Bar-Or and Lundegren, the authors reinvestigated the heat tolerance of exercising obese and lean women (5). Subjects walked at 4.8 km/h in temperatures that ranged from 21.1 to 35°C (Fig. 7). An important finding was that when comparisons were made at a “critical effective temperature” or when the rectal temperature was 39.2°C, the women had responses similar to acclimatized men. In addition, obese women exhibited a higher heat strain than lean women ostensibly caused by higher heat loads from mechanisms associated with convection and radiation.

Buskirk’s laboratory investigated the heat tolerance of exercising lean and obese prepubertal boys between 9 and 12 yr of age using four environments ranging from 21.1 to 42.2°C and under standard conditions of 4.8 km/h at 5°C (33). They found that lean boys had lower rectal temperatures and heart rates than obese subjects at every test condition, with obese boys having markedly higher rectal temperatures at two of the four stages. Measurements of skin temperatures or sweat rates revealed no significant differences between the groups. When expressed on a kilogram body weight basis, obese subjects had lower V̇O₂ values even though they were exercising at a higher intensity. After comparing their results with earlier findings from prepubertal girls, the authors found that obese boys and heavy girls had similar responses except at 32.2°C, where the boys were more tolerant to the heat than the girls (33).

With Vronman and Hogdson (57), Buskirk measured cardiac output and skin blood flow in lean (body fat <20%) and obese (body fat ≥27%) individuals. Individuals exercised at 30%, 50%, and 70% of their maximal aerobic power in thermal-neutral conditions (22°C with a WB temperature of 14°C) and in a hot environment (38°C with a WB temperature of 20°C). They found that measurements of skin and esophageal temperatures revealed no significant differences between the groups in any of the conditions tested. Furthermore, when exercise intensity was normalized with regard to metabolic mass, cardiac output was not significantly different between the groups. However, forearm blood flow was lower in the obese subjects at the higher exercise intensities in the hot environment, as was the slope of the blood flow-esophageal temperature relationship. The slope was also less in the thermal-neutral condition. They concluded that differences in body composition had altered the relationships between the cutaneous vascular reflexes (thermal-induced vasodilation and baroreceptor-induced vasoconstriction), which, in turn, had reduced forearm blood flow in the obese subjects (57).

In a 1999 collaborative heat acclimation study with the Osaka International University for Women in Japan, Buskirk and colleagues studied the sweating responses of males classified into three groups by age and aerobic fitness levels (39). Subjects were exposed to conditions of 43°C for 8 days. Subsequent testing indicated that all groups had increased performance time, lower final rectal temperature and heart rates, and decreased sweat Na⁺ concentrations. Total body sweating rates tested during acclimation were highest in the young and old fit groups and lowest in old normal group but were not changed by the acclimation process. After subjects had been injected of methylcholine, sweat output per gland was measured at different sites. With acclimation, the sweat output per gland increased in all groups, but different sites had different responses, suggesting that fitness levels and age were involved. The authors concluded that heat tolerance and the improvement with acclimation were not significantly different in young and old fit groups when exercised at the same relative intensity. Moreover, the changes associated with acclimation were associated with a decrease in V̇O₂max. Finally, the sweat gland output results indicated that cholinergic sensitivity was related to age (39).

Energy expenditure, ventilation, and obesity. Buskirk’s experiences in Minnesota stimulated an interest in energy expenditure that increased with subsequent his appointments at Natick and Bethesda. When coupled with obesity, it was not surprising that his laboratory, with Blair, secured energy expenditure profiles and physical activity levels from lean and adult-onset obese women and in child-onset obese women (10). They found that mean daily energy expenditure was higher in obese women than in lean women because of the presence of additional body weight when performing sedentary and light physical activities. However, when performing moderate to strenuous exercise, the energy expenditure values between the lean and obese women were similar because the lean group was exercising at a higher intensity level. Since no differences were found in either daily energy expenditure or in habitual activity between the child- and adult-onset obesity groups, they concluded that daily energy expenditure is positively related to obesity and that obese women voluntarily perform exercise at reduced intensities (10).

With Barlett, Buskirk measured the expiratory reserve volume (ERV) in men and women who possessed fat percentages that ranged from 4% to 49% (7). When expressed as a per-
percentage of the vital capacity, significant negative correlations with percent fat were found (men = −0.70 and women = −0.78). Later, with Bartlett and Kenney, Buskirk measured the (ERV/vital capacity) × 100 ratio in prepubertal lean and obese boys and girls (8). Compared with the adults in the 1983 study, similar results were found for the boys, but not for the girls, as their values increased with increasing fatness. They postulated that the prepubertal obese girls had a history of limited physical activity and, as a result, had reduced upper muscle body development as they increased their fat mass (8). Babb, Buskirk, and Hodgson measured end-expiratory lung volumes in obese (35% fat) and lean (22% fat) women at rest and while exercising on a treadmill at 55% and 85% \( V_{\text{O}_2\text{max}} \), respectively (2). Obese subjects had significantly lower resting values than their leaner counterparts. The results from obese subjects were interesting in that when exercising at the two intensities, their results were similar to those obtained at rest. On the other hand, lean subjects exhibited significant decreases at 55% \( V_{\text{O}_2\text{max}} \), 65%, 75%, and 85% \( V_{\text{O}_2\text{max}} \), respectively.

In a collaborative study with Baylor College of Medicine in 1991 (3), the ventilatory responses of lean (22% fat) and obese (35% fat) women to submaximal exercise were assessed. Measurements were recorded at four submaximal stages, and the obese subjects had higher absolute and relative \( V_{\text{O}_2} \) values, ventilation volumes, and heart rates than the lean group. However, the obese subjects had findings that suggested that they had lower ventilatory thresholds. When the groups were evaluated at 55%, 65%, 75%, and 85% \( V_{\text{O}_2\text{max}} \), heart rates were similar between the two groups and ventilation was significantly elevated only at 85% \( V_{\text{O}_2\text{max}} \) whereas the breathing rate was significantly increased at three of the four intensity stages. Although no explanation was provided for the elevated breathing rates by the obese subjects, the authors postulated the overlying fat on the thorax had a restrictive effect (3).

**Professional Contributions and Service**

Including the citations mentioned previously, Prof. Buskirk is associated with >250 publications, chapters, and review articles. He was co-editor of *Science and Medicine of Exercise and Sport*, which was an early text suitable for graduate students in the exercise sciences. He is a member of >20 professional organizations, has served as a reviewer for >14 professional journals, not including those associated with APS, and has served on the editorial boards of 8 different journals, not including the *Journal of Applied Physiology* or the *American Journal of Physiology*. He has been a Section and Associate Editor for the *Journal of Applied Physiology* and has served two terms as Editor-In-Chief of *Medicine and Science in Sports and Exercise*.

In 1959, he first served as a consultant to the National Science Foundation, and his appointments have continued to the present day. They include, but are not limited to, study sections for NIH and committees for the President’s Council of Physical Fitness, National Research Council, National Academy of Science, National Academy of Engineering, United States Marine Corps, United States Air Force, National Institute of Occupational Safety and Health, National Aeronautics and Space Administration Space Shuttle Program, American Heart Association, and the Department of Health, Education, and Welfare.

Dr. Buskirk has served APS well as Chairman of the Temperature Regulation Group before Sections were established, Chairman of an APS Fall Meeting at Pennslyvania State University when such meetings were an integral component of APS, committee member of the Educational Materials Review Board, the Committee on Committees, the Daggs Award, and on the *News in Physiological Science* Joint Managing Board before the journal *Physiology* was established. Last but not least, he served as Chairman of the Exercise Group or as the Chairman of the Environmental and Exercise Section for a 10-yr period.

**Recognition and Honors**

He served as the 8th President of the American College of Sports Medicine (1963–1964) and was selected for Fellowship by the American Heart Association, American College of Sports Medicine, American Academy of Kinesiology and Physical Education (Honorary), American Society of Nutrition, and American Association for the Advancement of Science. Honor Awards have been bestowed by the American College of Sports Medicine, National Fitness Leaders Association, and by the APS Section on Environmental and Exercise Physiology. Not to be forgotten is that in 2002, he was selected by APS to receive their prestigious Daggs Award for service to the society.

**Conclusion**

Prof. Buskirk is an eminent environmental and exercise physiologist and a most deserving APS member to be recognized and included in the Living History Archival Program. His seminal contributions to the discipline and profession of physiology will be long remembered by those who follow him.

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Living History

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