Impact of Eccentric or Concentric Training on Body Composition and Energy Expenditure

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ABSTRACT

TOURON, J., H. PERRAULT, V. JULIAN, L. MAISONNAVE, P. DEAT, J. AUCLAIR-RONZAUD, J. SALLES, S. WALRAND, J. HERMET, J.-P. RIGAUDIERE, P. LEBECQUE, C. MALPUECH-BRUGERE, C. MONTAURIER, B. PEREIRA, V. COXAM, F. COSTES, and R. RICHARD. Impact of Eccentric or Concentric Training on Body Composition and Energy Expenditure. *Med. Sci. Sports Exerc.*, Vol. 51, No. 9, pp. 1944–1953, 2019. **Purpose:** To compare the effects of 8-wk eccentric (ECC) versus concentric (CON) training using downhill and uphill running in rats on whole body composition, bone mineral density (BMD), and energy expenditure. **Methods:** Animals were randomly assigned to one of the following groups: 1) control (CTRL), 2) +15% uphill-running slope (CON), 3) −15% downhill-running slope (ECC15), and 4) −30% downhill-running slope (ECC30). Those programs enabled to achieve conditions of isopower output for CON and ECC15 and of iso-oxygen uptake ($\dot{V}O_2$) for CON and ECC30. Trained rats ran 45 min at 15 $m \cdot min^{-1}$ five times per week. Total body mass, fat body mass, and lean body mass (LBM) measured through EchoMRI™, and 24-h energy expenditure including basal metabolic rate (BMR) assessed using PhenoMaster/LabMaster™ cage system were obtained before and after training. At sacrifice, the right femur was collected for bone parameters analysis. **Results:** Although total body mass increased in all groups over the 8-wk period, almost no change occurred for fat body mass in exercised groups (CON, −4.8 ± 6.18 g; ECC15, 0.6 ± 3.32 g; ECC30, 2.6 ± 6.01 g). The gain in LBM was mainly seen for ECC15 (88.9 ± 6.85 g) and ECC30 (101.6 ± 11.07 g). ECC was also seen to positively affect BMD. An increase in BMR from baseline was seen in exercise groups (CON, 13.9 ± 4.13 $kJ \cdot d^{-1}$; ECC15, 11.6 ± 5.10 $kJ \cdot d^{-1}$; ECC30, 18.3 ± 4.33 $kJ \cdot d^{-1}$) but not in CTRL one. This difference disappeared when BMR was normalized for LBM. **Conclusions:** Results indicate that for iso-$\dot{V}O_2$ training, the impact on LBM and BMD is enhanced with ECC as compared with CON, and that for isopower but lower $\dot{V}O_2$ ECC, an important stimulus for adaptation is still observed. This provides further insights for the use of ECC in populations with cardiorespiratory exercise limitations. **Key Words:** FAT MASS, LEAN MASS, DOWNHILL RUNNING, CALORIMETRIC CAGES, OSTEOGENIC RESPONSE

Eccentric (ECC) contraction is associated with active elongation as opposed to concentric (CON) contraction causing muscle fiber shortening. First studied by A. Fick, ECC exercise is receiving a renewed attention as a rehabilitation modality on account of its lower metabolic and cardiorespiratory demands for any given mechanical power output (1,2). For an ECC exercise of downhill running results typically show oxygen uptake ($\dot{V}O_2$) to be a third to one half that of uphill running (CON) at the same power output (3,4).

The ECC exercise is particularly known for inducing greater muscle micro tears and overall musculoskeletal constraint and muscle tension than CON (5,6). It is also associated with distinctive inflammation patterns and repair processes that are particularly effective in promoting adaptations, such as skeletal muscle fiber hypertrophy (6), positive osteogenesis (7), glycemic control, (8) or mitochondrial H_2O_2 production (9). The extent to which muscle damage, muscle tension output, or metabolic factors constitute the triggering adaptive factors remain unclear. The ECC knee extension training has also been seen to result in greater effects on insulin sensitivity and lipid profiles in elderly men (10), whereas similar results, as well as improvements in bone mineral density (BMD), were found following descending as compared with ascending stair

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Submitted for publication December 2018.
Accepted for publication March 2019.

0195-9131/19/5109-1944/0
MEDICINE & SCIENCE IN SPORTS & EXERCISE®

DOI: 10.1249/MSS.0000000000001992

walking in elderly obese women (11). Despite its lower energy and cardiorespiratory demands, Miles et al. (8) also found ECC exercise to be equally effective as CON in modulating glycemic control in a younger population.

The extrapolation of observed metabolic effects of dynamic ECC exercise to a more generalized effect on whole body remains poorly studied (12). Insights showing that, in addition to functional and structural muscle improvements, ECC training in elderly men and women also induced a significant loss of total body fat were first provided by Mueller et al. (13). The suggestion that dynamic ECC could more effectively impact whole body composition, substrate utilization or metabolism than CON is of particular interest for use in weight control management, because of its lower cardiorespiratory exercise demands. A caveat for exploring this issue remains the assurance that what is being compared is indeed comparable; namely that comparisons are made under conditions of both isopower outputs and iso-$\dot{V}O_2$, especially given the differences in oxygen cost per unit of power output (3).

In the present study, this was achieved using a rat model of downhill running previously developed in our laboratory, where variations in treadmill slope and speed are used to modulate exercise intensity and thus external power output (4). The study aimed at comparing the effects of ECC versus CON treadmill training on whole body composition including bone morphometry, bone mineral content (BMC) and BMD while also monitoring basal metabolic rate (BMR) and total energy expenditure (EE). In keeping with fundamental principles of bioenergetics, we hypothesized that after training at iso-$\dot{V}O_2$ changes in total body mass (TBM) and fat body mass (FBM) would be the same in ECC- and CON-trained animals. Conversely, downhill exercise training at the same mechanical power as uphill running (but half the $\dot{V}O_2$) would result in lesser changes in body composition but would have more of an osteogenic impact.

METHODS

Institutional Approvals

All procedures were approved by institutional and national regulating authorities for animal care and research ethics (Ethics Committee C2EA-02, Auvergne, France).

Experimental Protocol and Procedures

Animal population and testing conditions. Sixty 9-wk-old male Wistar rats (Janvier Labs, Le Genest-Saint-Isle, France) weighing between 300 and 360 g upon arrival were individually housed at 22°C ± 3°C in a light-controlled room (reverse cycle, 12:12 light–dark). Animals were given free access to water and to a mixture of 20.2% proteins, 75.9% carbohydrates, and 3.9% lipids (A04; Safe Diets, Augy, France) corresponding to a food quotient (FQ) (14) of 0.93.

Randomization and experimental conditions. Animals were randomly assigned to one of four groups of equal size (n = 15): 1) control (CTRL), 2) uphill-run training (CON), 3) downhill-run training at a slope of −15% (ECC15), 4) downhill-run training at a slope of −30% (ECC30). The CTRL animals did not undergo any particular intervention but were manipulated and placed on the stopped treadmill at the same frequency as the exercise-trained animals and were investigated in a similar fashion.

The study was completed over an 8-wk period as illustrated in Figure 1 with measurements obtained at baseline (T_0), after completion of 20 exercise sessions (T_1) and after 40 sessions (T_2). Exercise training duration was progressively increased from 5 to 45 min during the first week and maintained at 45 min per session for the remaining 7 wk. Training frequency was five times per week, on five consecutive days with two consecutive days of rest per week.

Animals assigned to an exercise group ran on a 10-lane treadmill (Quinton Instruments, Seattle, WA) at a speed of

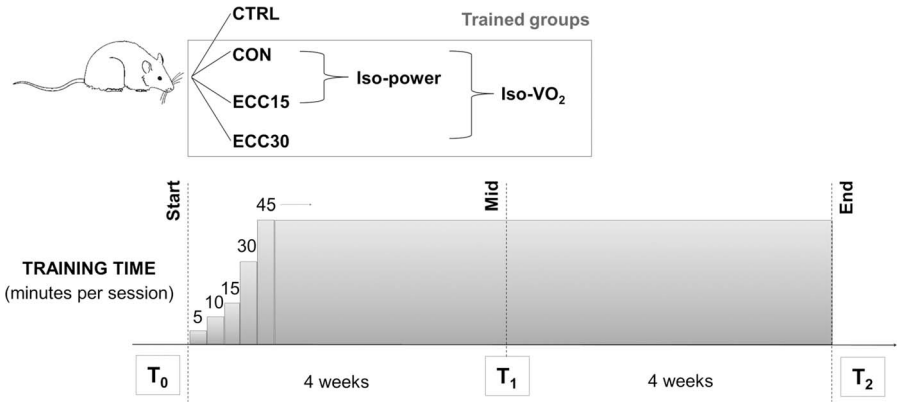


FIGURE 1—Study design and protocol. Training at the same mechanical power (isopower) was carried out by CON and ECC15; training at the same $\dot{V}O_2$ (iso-$\dot{V}O_2$) was carried out by CON and ECC30. Training duration was progressively increased over the five exercise sessions of the first week to reach 45 min by week 2. This duration was maintained throughout the rest of the experimental protocol. Baseline values were taken at T_0; T_1 reflects protocol midpoint at which time weight and body composition were reevaluated; T_2 was considered as the 8-wk completion time at which point animals were sacrificed and tissue samples were obtained.

15 m·min^{-1}. Rats in the CON group ran uphill at a treadmill slope of +15%, whereas those in the ECC15 and ECC30 groups ran at a downward slope of −15% and −30%, respectively. These treadmill settings were selected based on our prior results showing similar mechanical power output resulting from uphill running at +15% slope (CON) and downhill running at −15% slope (ECC15) thus enabling isopower comparisons (4,9). Briefly, external power output was determined by design, using mean initial animal body mass (kg) in each group × positive or negative slope and treadmill speed (m·s^{-1}) to obtain vertical displacement (m) × gravitational acceleration. Given that mean animal body mass was not different between groups, the computed external power for same treadmill settings of slope and speed resulted in similar external power outputs. Conversely, the oxygen cost of running uphill at +15% slope (CON) is similar to that of downhill running at −30% slope (ECC30) thus enabling iso-$\dot{V}O_2$ group comparisons. It also follows that the oxygen cost of ECC30 is twice that of ECC15.

Rats were sacrificed after completing a 48-h stay in the metabolic cage. To control for animal age at the time of sacrifice, rats were introduced into the experimental protocol in a progressive fashion. Following the baseline metabolic cage exposure, pairs of animals of the same age were included daily over a period of 6 wk to reach the desired numbers per group.

After completion of the 8-wk protocol, an isotope-based incorporation procedure was achieved after an overnight fast. Animals were then anesthetized by inhalation of 3% isoflurane and 1 L·min^{-1} O_2 in an induction box, removed from the box and maintained under anesthesia using a face mask (1.5% isoflurane, 1 L·min^{-1} O_2) while exsanguination at the abdominal aorta level was carried out. The right vastus intermedius muscles were collected and cut into 50-mg portions that were immediately frozen at −80°C. The right femurs were also collected promptly after the animal's cardiorespiratory arrest, cleaned of adjacent tissues, and stored at +4°C in a standard saline solution (9 g NaCl·L^{-1}) until analysis.

Analyses and Measurements

Body composition. Total body mass was recorded at T_0, T_1, and T_2. An EchoMRI™ device (Echo Medical Systems, Houston, TX) was used to assess body compartments at each time point. The quantitative magnetic resonance (QMR) body analysis, validated for use in rodents, enables measurements of fat and lean tissue masses, as well as total body water and free (unbound) water (15,16). The device is highly suited for repeated assessments of animals as it provides highly accurate measurements, is easy to use with scan times of less than 90 s, does not require sedation or anesthesia, and does not expose animals to radiation or invasive procedures (15,17).

EE and motor activity. At T_0 and at T_2, 24 h after the last exercise session for running groups and simultaneously for CTRL, animals were placed in a PhenoMaster/LabMaster home cages system (TSE Systems, Bad Homburg, Germany). A standard cage environment of 22°C temperature, 8:00 PM to 8:00 AM lights-on cycle, with free access to food and water, was maintained for a period of 48 h for determination of BMR and total EE.

$\dot{V}O_2$ (mL·min^{-1}) and carbon dioxide production (VCO_2 mL·min^{-1}) were obtained for computation of the $VCO_2/\dot{V}O_2$ or respiratory quotient (RQ). Food (g) and water intakes (mL) were obtained from variations in weight and volume of rations, and spontaneous motor activity (m) through detection of movements by infrared sensors.

Muscle mass and protein turnover. To study the impact of the exercise training on muscle protein synthesis, the rate of incorporation of L-[1-^{13}C] valine into muscle proteins was measured at T_2 using the flooding dose method (18). After an overnight fast, rats were injected subcutaneously with a large dose of a stable isotope, that is a labeled amino acid (L-[1-^{13}C] valine, Eurisotop Saint-Aubin, France), to flood the precursor pool of protein synthesis (300 μM per 100 g body weight). Tracer incorporation time was 50 min in all groups.

Total protein isolation and hydrolysis were obtained from the vastus intermedius. Amino acids were derivatized in N-acetylpropyl for analysis using gas chromatography-combustion-isotope ratio mass spectrometry (Gas System; Fisons Instruments, VG Isotech, Middlewich, UK). L-[1-^{13}C] valine enrichments in tissue fluid was assessed using gas chromatography–mass spectrometry (Hewlett-Packard 5971A; Hewlett-Packard Co., Palo Alto, California) and used as precursor pool enrichment to obtain fractional synthesis rate (FSR) and absolute synthesis rate (ASR).

Bone morphometry, absorptiometry, and biomechanical testing. Right femoral length and mean diaphyseal diameter were measured using a precision caliper (Mitutoyo, Shropshire, UK). Total femoral, epiphyseal and diaphyseal BMD were assessed through dual-energy x-ray absorptiometry using a Hologic QDR-4500 A x-ray bone densitometer (Hologic, Massy, France) with scans taken at the upper and lower quarters of the bone for proximal and distal trabecular assessments. Diaphyseal BMD was taken in the central portion of the femur (19). Bone stress and strain were assessed through standard approaches (20). Femoral failure load (N) was determined using a 3-point bending test (Instron 4501; Instron, Canton, MA), the two lower supports being separated by a 20-mm distance, and an upper crosshead roller being applied to the middle of the bone at a speed of 0.5 mm·min^{-1} until failure. Femoral stiffness (N·mm^{-1}) was determined from the slope of the linear portion of the load-deformation curve.

Treatment of Data and Computations

Body composition, BMC, and femoral diameter. A QMR digital report of raw values was generated for each animal at each evaluation time and values of FBM, lean body mass (LBM), total body water, and free water (g) were recorded and served to determine groups' mean at T_0, T_1 and T_2. BMC (g) was estimated from the standard QMR algorithm (21). Mean femoral diameter diaphysis was taken as the mean of the greatest and the smallest femoral diaphysis diameters to account for its irregular shape.

Energy expenditure. Energy expenditure (kJ) was computed from gas exchange according to Weir (22), taking into account that 20.2% of diet energy was provided by proteins. For each animal, total EE was calculated as the sum of the two hundred eighty-eight 5-min sampling measurements over the 24-h period. Mean values for animals of a given group were calculated. Basal metabolic rate was computed from a series of the four lowest values of 5-min EE values over the 24-h monitored period. Minimal EE was taken as the average of these values and reported as kilojoules per day.

Vastus intermedius protein turnover. Fractional synthesis rate of proteins (%·h^{-1}) was calculated as: FSR = $100E_i/E_{prec}t$, where E_i was the enrichment as atom percent excess of L-[1-^{13}C] valine derived from decarboxylation of valine from proteins at time t (minus basal enrichment), E_{prec} was the mean enrichment in the precursor pool (tissue fluid L-[1-^{13}C]valine) and t was incorporation time in hours. Absolute synthesis rate of proteins (mg·h^{-1}) was calculated as: ASR = Q_{prot}FSR/100, where Q_{prot} was the amount of protein per muscle.

Statistics

Sample size. The sample size estimation was determined based on: 1) the CONSORT 2010 statement (23), 2) the Cohen's-J recommendations (24), and 3) the preliminary results achieved by our team. The number of 15 animals per group was selected to highlight an effect size around 1.5 for a two-sided type I error at 0.008 (correction for multiple comparisons) and a statistical power at 90%.

Statistical Analyses

Statistical analyses were performed using Stata software (version 13; Stata Corp, College Station, TX). Values were expressed as mean ± SEM. Statistical significance for two-sided comparisons was set for a type-I error of 0.05. Random-effects models for correlated data were performed for consideration of between- and within-animal variability due to repeated measurements on a same animal. Timepoint evaluations, groups and their interactions were considered as fixed effects whereas subject (animal) was random effect (slope and intercept). A Sidak's *post hoc* test for multiple comparisons was applied. The normality of residuals from these models was studied using the Shapiro–Wilk test. When appropriate, the data were log-transformed to achieve normality of the dependent endpoint. Concerning non–repeated-measures, quantitative variables were compared between groups by ANOVA or Kruskal–Wallis tests when assumptions required for the ANOVA were not met (normality and homoscedasticity analyzed using the Bartlett test). When appropriate (omnibus $P < 0.05$), a *post hoc* test to take into account multiple comparisons was performed: Tukey–Kramer post-ANOVA and Dunn after Kruskal–Wallis test.

RESULTS

Body Composition

TBM, FBM, and LBM. Figure 2 shows changes in TBM, FBM, and LBM at baseline, after 4 and 8 wk of intervention in all groups. For those parameters, baseline values were not different between groups. As seen in panel A, no differences were seen between groups whatever the measurement time point, and a similar increase in TBM was seen in all groups from T_0 to T_2. The table, inserted as Figure 2B, shows FBM and LBM expressed in grams, whereas panels C and D represent the relative contribution of FBM and LBM as percent of TBM. Results in CTRL indicate a significant increase in FBM from baseline when expressed in absolute (panel B) or in relative terms (panel C), with FBM at T_2 (in grams or percent) being significantly higher in CTRL compared with running groups. Consistent with a continuous growth model, significant increases in LBM (g) were seen at T_2 from T_0 in all groups (panel B). However, at T_2 results show significantly higher LBM in ECC15 and ECC30 compared with CTRL. This is also reflected by the significant decrease of LBM (%) in CTRL and its significant increase in all running groups from T_0 (panel D). Figures 2E and F show the absolute changes in FBM and LBM at T_2 from T_0 in all groups. A significant group difference from CTRL is seen at T_2 in exercise groups (panel E) and greater changes in LBM are seen for ECC15 and ECC 30 (panel F).

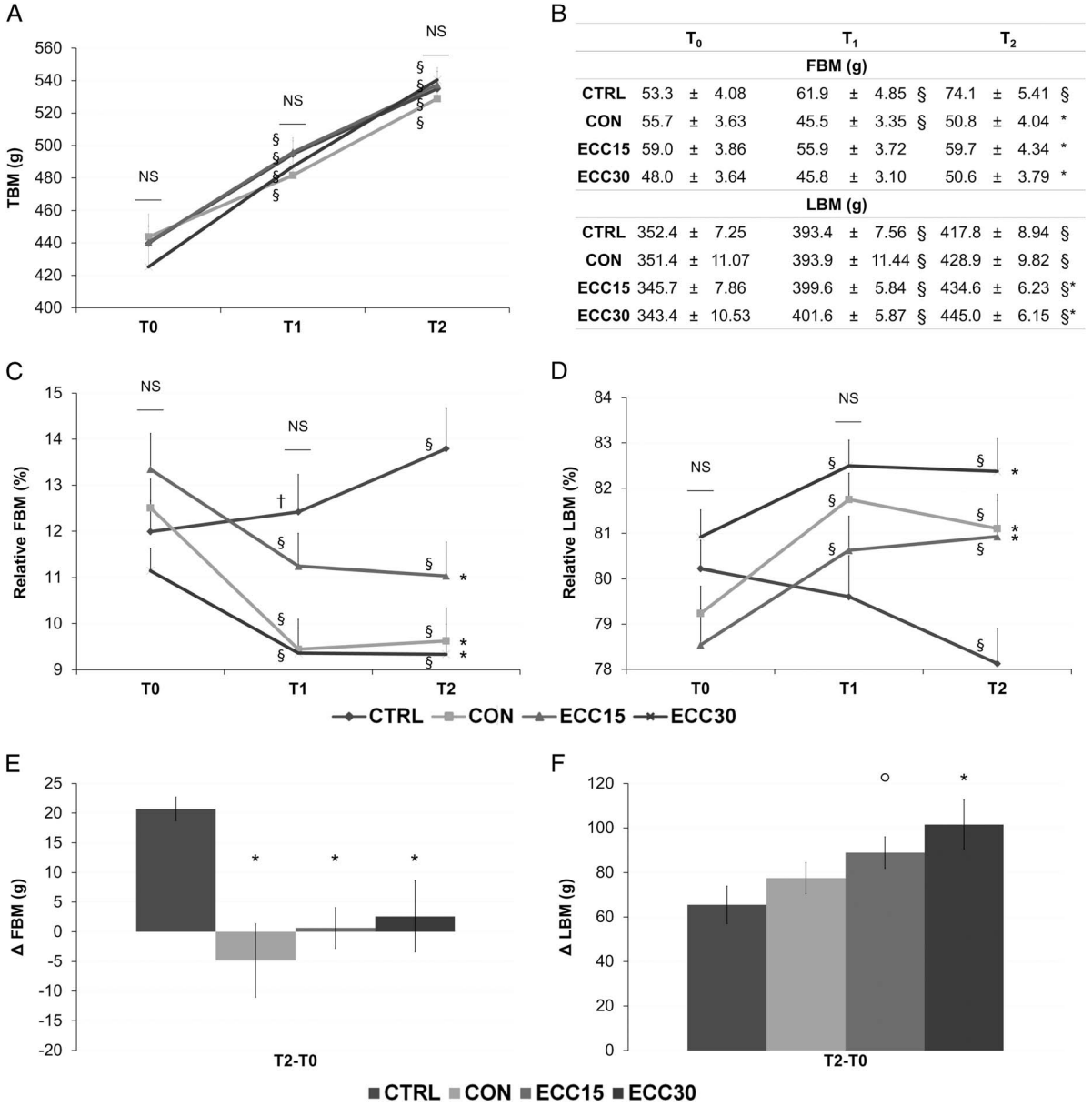
Bone mineral content. Mean ± SEM values of BMC (g), calculated from QMR, were not different between groups either at T_0 (CTRL, 32.95 ± 0.74; CON, 35.36 ± 1.04; ECC15, 34.69 ± 0.61; ECC30, 32.96 ± 1.63), T_1 (CTRL, 38.03 ± 1.34; CON, 41.23 ± 2.97; ECC15, 39.35 ± 1.06; ECC30, 38.50 ± 1.27) or at T_2 (CTRL, 41.84 ± 0.90; CON, 47.93 ± 5.64; ECC15, 41.95 ± 1.17; ECC30, 43.19 ± 1.54) but a significant increase from T_0 was found in all groups at T_2.

BMD, Morphometry, and Biomechanical Properties

Results for BMD obtained at T_2 are shown in Figure 3A. As can be seen, the CON condition was associated with a significantly higher proximal BMD, as compared with the CTRL group. Regarding ECC15, the elicited effect is higher at both total and proximal level. Finally, all the BMD measurements were found to be significantly higher in ECC30 compared with CTRL, whether they were performed on cortical bone or on trabecular bone. Figures 3B and C, showing femoral length and diaphyseal diameter, reveal no significant differences between groups. Measured failure loads (N) were not significantly different between groups (CTRL, 152.44 ± 5.96; CON, 162.43 ± 5.97; ECC15, 154.23 ± 3.88; ECC30, 159.16 ± 4.23) nor were stiffness values (N·mm^{-1}) (CTRL, 221.78 ± 12.24; CON, 244.73 ± 12.12; ECC15, 233.75 ± 10.29; ECC30, 255.51 ± 7.71).

Energy Balance

Food and water intake. Twenty-four–hour food and water intakes at T_0 and T_2, are shown in Table 1. Results indicate a significant decrease in water intake at T_2 in CTRL. No other significant differences were seen in food or water intakes at T_2 compared with T_0. There was no significant difference in food intake between groups either at T_0 or at T_2. There was no



	T_0	T_1	T_2
FBM (g)			
CTRL	53.3 ± 4.08	61.9 ± 4.85 §	74.1 ± 5.41 §
CON	55.7 ± 3.63	45.5 ± 3.35 §	50.8 ± 4.04 *
ECC15	59.0 ± 3.86	55.9 ± 3.72	59.7 ± 4.34 *
ECC30	48.0 ± 3.64	45.8 ± 3.10	50.6 ± 3.79 *
LBM (g)			
CTRL	352.4 ± 7.25	393.4 ± 7.56 §	417.8 ± 8.94 §
CON	351.4 ± 11.07	393.9 ± 11.44 §	428.9 ± 9.82 §
ECC15	345.7 ± 7.86	399.6 ± 5.84 §	434.6 ± 6.23 §*
ECC30	343.4 ± 10.53	401.6 ± 5.87 §	445.0 ± 6.15 §*

FIGURE 2—QMR data. (A) TBM (g). (B) Absolute FBM and LBM compartments (g). (C) FBM relative to TBM (%). (D) LBM relative to TBM (%). (E) Δ FBM (g). (F) Δ LBM (g). Values are mean ± SEM (for sake of clarity only positive SEM are presented in panels A, B and C). §$P < 0.05$ from T_0; †$P < 0.10$ from T_0; *$P < 0.05$ from CTRL; ○$P < 0.10$ from CTRL; NS, nonsignificant difference between groups.

difference in water intake between groups at T_0, but exercised groups had higher values at T_2 compared to CTRL.

Energy expenditure. Total EE and BMR expressed in kilojoules per day at T_0 and T_2 are, respectively, shown in Figures 4A and B. Results indicate no significant difference in mean values between groups in either total EE or BMR at T_0. In ECC groups, total EE was found to be higher at T_2 compared to T_0. At T_2, BMR was statistically different from CTRL for all trained groups. Analysis of pretraining to posttraining BMR indicate significantly higher values at T_2 compared with T_0 in CON, ECC15, and ECC30 but not in CTRL. Figures 4C and D show changes in total EE and BMR at T_2 from T_0. Results provide evidence for an increase in total EE in all trained groups, but statistical significance was only reached for ECC30. Similarly positive changes ($P < 0.05$: CON and ECC30, $P < 0.1$: ECC15) in BMR were seen in all exercised groups but not in CTRL. When corrected for LBM, results for total EE and BMR were lower at T_2 compared with both T_0 in all groups; however, there was no difference between groups at either measurement time (Figs. 4E and F).

Spontaneous activity. Mean ± SEM values of activity ($m \cdot d^{-1}$) were not different between groups, either at T_0 (CTRL, 347.93 ± 24.77; CON, 326.96 ± 20.69; ECC15, 313.88 ± 20.07; ECC30, 317.96 ± 23.47) or at T_2 (CTRL, 270.60 ± 14.89; CON, 267.94 ± 14.95; ECC15, 255.88 ± 9.86; ECC30, 247.61 ± 18.17). The decrease found between T_2 and T_0 was significant in all groups.

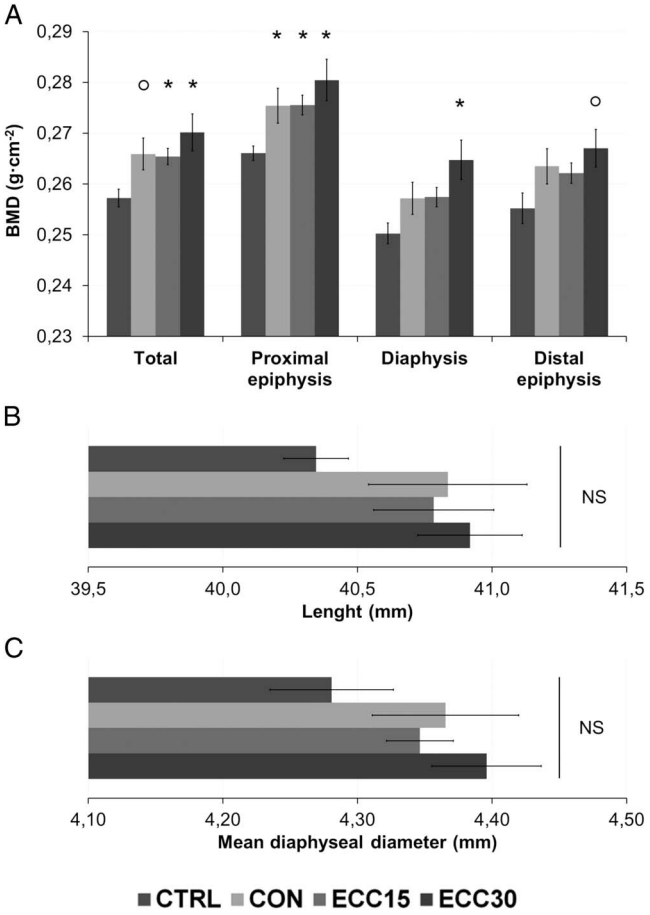


FIGURE 3—BMD and morphometry. (A) Total, proximal epiphysis, diaphysis and distal epiphysis femoral BMD (g·cm^{-2}). (B) Femoral length (mm). (C) Mean diaphyseal diameter (mm). Values are mean ± SEM. *$P < 0.05$ from CTRL; ○$P < 0.10$ from CTRL; NS, nonsignificant difference between groups.

24-h RQ. Mean ± SEM values of 24-h RQ were not different between groups, either at T_0 (CTRL, 1.02 ± 0.01; CON, 1.01 ± 0.01; ECC15, 1.02 ± 0.01; ECC30, 1.00 ± 0.01) or at T_2 (CTRL, 0.99 ± 0.01; CON, 1.00 ± 0.01; ECC15, 1.01 ± 0.01; ECC30, 1.00 ± 0.01). A decrease from T_0 was found in CTRL, CON, and ECC15 ($P < 0.05$) at T_2 but not in ECC30. As can be seen, in all groups, RQ exceeds the FQ of 0.93 at both T_0 and T_2.

Muscle Mass and Protein Turnover

As shown in Table 2, there was no statistical difference in total vastus intermedius muscle mass measured at T_2 between CTRL and exercise-trained groups. Similarly, no significant differences between groups were found for measurements of FSR and ASR.

DISCUSSION

Main findings. General findings indicate an increase in TBM in all groups but compartment differentiation with exercise training serving to limit gains in FBM, irrespective of contraction modality. As per the working hypothesis, conditions of iso-$\dot{V}O_2$ training (ECC30 and CON) resulted in effects of similar magnitudes on FBM as compared to the isopower lower $\dot{V}O_2$ condition (ECC15). Lean body mass and bone density increased in all exercise-trained animals compared to CTRL with greater effects in ECC30 but a positive effect seen even in the ECC15 group, with no changes in bone length or biomechanical characteristics. Basal metabolic rate and total EE increased after training, which can be explained by an increase in LBM in running groups.

General physiological response to dynamic ECC exercise training. Explanation of adaptations to ECC type exercise is beyond the scope of this article, and recent review articles report on the current understanding of findings from studies in humans and in animals (25–27). Briefly, findings show that ECC is effective for inducing muscle adaptations that may translate into enhanced strength and endurance functional abilities. There is, however, no clear evidence of an increase in aerobic parameters. This could be related to the difficulty of comparing training programs of similar metabolic overload using CON and ECC, because it would require imposing a CON power load in cycling or running two or three times that of ECC. The fact that the metabolic and cardiorespiratory requirements of dynamic ECC exercise are one third to one half those of CON is nonetheless of a particular interest for use in populations in whom the level of metabolic overload is limited by the cardiorespiratory exercise ability. It is, therefore, not surprising that much of the dynamic ECC exercise literature stems from studies conducted in patients with chronic heart, respiratory, metabolic or muscle disease or obesity (1,2,12). In animals, there are little data on the dynamic ECC versus CON repeated cardiorespiratory and metabolic exercise responses or their impact.

TBM and body mass compartments. To our knowledge, the present study is the first to report on the effects of dynamic CON and ECC exercise training on body composition compartments in rats. The study was conducted in rodents to enable comparisons of modalities for metabolic demands of similar magnitudes.

As expected from the continuous growth pattern of rodents, an increase in TBM was observed over the 8-wk period in all animals. The increase seen in CTRL is of a similar magnitude as the aging-related increase usually reported in Wistar rats of

TABLE 1. Food and water intakes at T_0 and at T_2.

	T_0	T_2
Food intake (g·d^{-1})		
CTRL	27.2 ± 1.19	26.3 ± 1.13
CON	26.5 ± 0.58	27.7 ± 1.42
ECC15	27.4 ± 0.82	27.7 ± 0.67
ECC30	26.4 ± 0.90	27.8 ± 0.94
Water intake (mL·d^{-1})		
CTRL	31.2 ± 2.97	26.0 ± 2.34*
CON	28.4 ± 1.45	26.8 ± 1.23**
ECC15	27.9 ± 1.48	27.4 ± 1.49***
ECC30	27.3 ± 1.72	31.2 ± 2.07***

Values are mean ± SEM.
*$P < 0.05$ from T0.
**$P < 0.10$ from CTRL.
***$P < 0.05$ from CTRL.

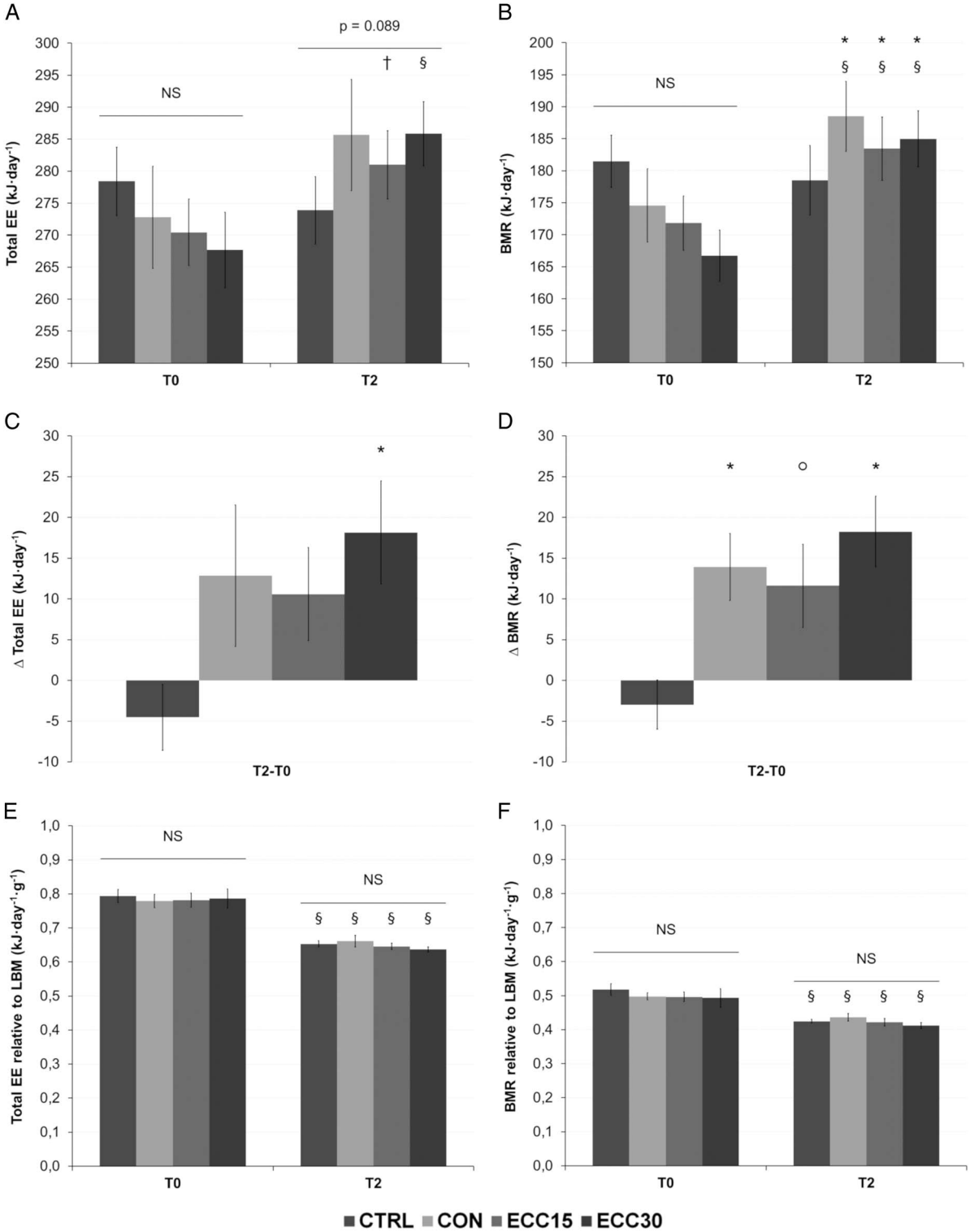


FIGURE 4—Total EE and BMR. (A) Total EE (kJ·d^{-1}). (B) BMR (kJ·d^{-1}). (C) Δ total EE (kJ·d^{-1}). (D) Δ BMR (kJ·d^{-1}). (E) Total EE (kJ·d^{-1}) relative to LBM. (F) BMR (kJ·d^{-1}) relative to LBM. Values are mean ± SEM. §$P < 0.05$ from T_0; †$P < 0.10$ from T_0; *$P < 0.05$ from CTRL; ○$P < 0.10$ from CTRL; NS: nonsignificant difference between groups.

a similar age, over the same period (28) and the magnitude of increase in trained animals is in keeping with that after downhill running in rats (7). Our results, however, also show that the exercise-induced impact on whole body composition may be training-overload dependent and specific to the exercise modality. In fact, measurements made at study mid-point show that exercise-induced changes in body compartments occur primarily over the first 4 wk of training.

TABLE 2. Muscle mass and protein turnover of vastus intermedius.

	Muscle Mass (g)	FSR (%·h^{-1})	ASR (mg·h^{-1})
CTRL	0.38 ± 0.058	0.36 ± 0.012	0.22 ± 0.060
CON	0.43 ± 0.051	0.35 ± 0.011	0.20 ± 0.014
ECC15	0.38 ± 0.037	0.35 ± 0.010	0.24 ± 0.032
ECC30	0.42 ± 0.107	0.36 ± 0.013	0.21 ± 0.052

Values are mean ± SEM.

As opposed to the average FBM increase of 20 g over the 8-wk period in the CTRL group, none of the three groups of exercise-trained animals exhibited a significant increase in FBM over the same period. Present results also show animals submitted to downhill running (ECC) to exhibit more important increases in LBM that those in the CON group. The magnitude of change is also consistent with the standard overload principles such that higher gains in LBM are seen with higher metabolic overload (ECC30 > ECC15). Thus, a significant increase in FBM (g) was seen in CTRL but not in exercised groups confirming the effect of exercise training to limit fat mass gain but also showing significant increases in lean mass which appeared enhanced with the ECC modality.

In a landmark study, Lynn and Morgan (29) used rats of similar age range as ours to examine at iso-power (16° incline and decline) the effects on vastus intermedius remodeling after 1 wk of consecutive days of treadmill running at a speed similar to the one used in the present study (14 m·min^{-1} vs 15 m·min^{-1}). Results showed sedentary rats to have a similar sarcomere count as rats submitted to incline (CON) running. However, in decline (ECC) running rats, an average difference of +11% was seen in the number of sarcomeres compared to incline running animals. Such effects were further summarized in a recent review by Hedayatpour and Falla (25).

Aerobic exercise training using standard CON-type exercise has been widely used for body weight management (30,31). Results from these studies commonly show training-induced reductions in body fat and increases in LBM if the exercise-training stimulus was of sufficient intensity. Reports on segmental body composition evaluation using dual-energy x-ray absorptiometry scanning after dynamic ECC training have recently become available (13,32,33), showing an increase in lean tissue mass of trained muscle groups. A few studies also report decreases in whole-body total fat mass (13,33), which is of a particular interest considering that cardiorespiratory and metabolic demands of ECC are generally lower than those of CON type exercise (3).

Body composition and bone tissue. Exercise training-induced changes in bone tissue may also contribute to the observed variations in body composition. Compressive and tensile strains resulting from the muscle contractions of weight bearing exercise can induce an osteogenic and bone remodeling through mechanotransduction (34,35). To trigger the osteogenic cascade leading to morphological and mechanical adaptation of bony structures, stresses and strains must be of a sufficient impact, dynamic and variable (34,36,37). In humans, a remodeling cycle of bone resorption, formation, and mineralization is estimated to extend over a period of up to 4 months (38). The timeframe in adult rats is significantly less with histomorphometric measurements establishing the cycle to be completed over 36 to 38 d for trabecular bone (39).

The particular osteogenic potential of flat or uphill running including high-intensity intermittent training has been well described and has been ascribed to the action of the repeated high impact ground reaction forces (40). The impact of downhill running or ECC on bony structures remains incompletely documented. In rats, the comparison of peak and rate of rise of ground reaction forces exerted on forelimbs and hindlimbs during uphill or downhill treadmill walking showed that even without additional body loading, downhill walking resulted in higher bone strain (41).

The present results show a significant increase in femoral BMD in ECC-trained groups as compared with CTRL, irrespective of slope, which was not the case in rats trained using uphill running. These findings are consistent with previous reports in rats showing increased in BMD after downhill but not uphill treadmill activity (7,41). Similar to the present observations, results from measurements of bone morphometry or biomechanical characteristics do not show significant changes after ECC training despite significant impact on BMD.

Energy balance and changes in body composition. Our results show no significant differences in food intake or spontaneous activity between groups whether before or after training, despite a decrease in activity from T_0 to T_2 seen in all groups probably as a result of aging and habituation to the metabolic cage environment. Rats were fed a mixture containing 20.2% protein, 75.9% carbohydrate and 3.9% lipids leading to an FQ calculated to be 0.93. The 24-h RQ values were higher than the FQ in all groups, both before and after the training period, consistent with the presence of *de novo* lipogenesis required to convert ingested carbohydrates to lipids (42). This lipogenesis may be seen as a natural phenomenon which contributes to the continuous age-related growth in rodents and the accumulated fat mass seen in CTRL animals.

This is not observed in exercise-trained animal groups suggesting a contribution of the added exercise-related EE because neither food intake nor spontaneous activity were different from CTRL. Using the average O_2 cost of +15% uphill running and −15% and −30% downhill running (4) and applying an oxygen energy equivalent of 5 kcal·L^{-1}, an additional EE of 3.4 kcal per running session for CON and ECC30 groups and of 1.7 kcal per session for the ECC15 group may be calculated. Totaling these extra oxygen costs over the entire 8-wk training volume results in an additional EE of 120 kcal for CON and ECC30 and of 60 kcal for the ECC15 group. Differences in FBM gains in exercised groups despite the presence of *de novo* lipogenesis could thus be explained by the increased EE to offset fat accumulation. The observed increase in EE is also reflected in BMR as shown in Figure 4. In turn, the observed posttraining increase in BMR may be explained by the concomitant increase in LBM given its predominant contribution to BMR and as may be seen by the disappearance of differences when BMR is expressed relative to LBM.

In humans, an increase in resting metabolic rate lasting up to 48 h after ECC exercise has been reported (43,44) with a suggested explanation of an increase in protein turnover, presumably resulting from the high rate of muscle microlesions associated with the ECC contraction modality.

In the present study, no differences in protein turnover between groups were observed. It is commonly accepted that exercise-induced physiological responses result from repair processes of muscle damage incurred in exercising muscles and that more extensive muscle micro tears and inflammation is seen after ECC type contractions, which also explains the more extensive muscle soreness reported in humans after ECC (5). For this reason, a period of progressive increase in ECC loading is commonly included in ECC training programs, as it was done in the present study for duration. However, because loading was not continuously increased over the 8-wk period, it is likely that the stimulus for an enhanced protein turnover was not maintained, resulting in no difference in ^{13}C-labeled valine incorporation between trained groups and CTRL at the time of sacrifice. It is also possible that any exercise-induced increase in protein turnover could have been missed on account of the 24-h time lapse from the last exercise training bout.

Study limitation. In the present study, a progressive overload across the interventional period was not applied to reflect as much as possible the approach more commonly used in weight reduction exercise programs. This however may represent a limitation in the interpretation of findings. For example, it cannot be excluded that a significant effect of ECC over CON on protein turnover and incorporation or that a continued increase in LBM between T_1 and T_2 might have been seen if a progressive overload had been used.

CONCLUSIONS

The present study was specifically designed to allow comparisons of the impact of CON and ECC modalities at same power output (isopower) or same EE (iso-$\dot{V}O_2$) on body composition in rats. Results indicate regular exercise, irrespective of modality, to favorably modulate body composition in a way to limit the increase in whole body fat mass and conversely to enhance lean mass. The latter observation is of a particular significance for the use of dynamic ECC exercise as an adjunct to the clinical management of individuals with limited functional capacities or suffering from chronic health conditions, knowing its characteristics of lower metabolic and cardiorespiratory demands. In practice, the feasibility of dynamic ECC exercise training in individuals with chronic disorders has been demonstrated in patients with chronic obstructive pulmonary disease and chronic heart failure (1,2). Recent results obtained in clinically obese individuals showing a greater FBM reduction with ECC-trained adolescent compared to CON also confirm its interest for weight control (33). It is well acknowledged that one of the factors acting to limit the benefits of exercise training in humans is the capacity for the individual to sustain sufficient metabolic overload.

The practical implication of present finding that effects of ECC training on body composition are seen even at lower intensity and constant overload training may open new avenues for designing weight reduction exercise programs. In particular, with the increase availability of ECC cycle ergometers on the market, overweight/obese individuals may benefit from gains in LBM through exercise that would not require extensive metabolic and cardiorespiratory requirements. The extent to which regular ECC cycling or descending treadmill walking can also be an adjunct for clinical management of osteoporosis remains to be clearly determined.

The authors thank the staff from the Experimental Animal Facility of the Human Nutrition Unit (INRA of Clermont-Ferrand) for their assistance throughout the animal protocol, and the staff from the metabolism exploration platform for their expertise in protein enrichment analysis. The authors also acknowledge the members of the ASMS team and the staff from the CRNH who participated closely into the success of this project.

The authors certify that the results of the study are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. The results of the present study do not constitute endorsement by the American College of Sports Medicine.

The authors declare no conflict of interest.

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