Wheel running affects seasonal acclimatization of physiological and morphological traits in the Djungarian hamster (Phodopus sungorus)

Frank Scherbarth, Jan Rozman, Martin Klingenspor, Georg Brabant, and Stephan Steinlechner

1Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany; 2Faculty of Biology, Department of Animal Physiology, Philipps-University Marburg, Marburg, Germany; and 3Department of Endocrinology, Christie Hospital, Manchester, United Kingdom

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Wheel running affects seasonal acclimatization of physiological and morphological traits in the Djungarian hamster (Phodopus sungorus). Am J Physiol Regul Integr Comp Physiol 293: R1368–R1375, 2007. First published June 27, 2007; doi:10.1152/ajpregu.00106.2007.—Wheel running was previously shown to influence body mass and torpor in short-day-acclimatized Djungarian hamsters (Phodopus sungorus). To determine whether the exercise-induced effect on body mass depends on the annual phase, hamsters were exposed to the natural change in photoperiod and given access to a running wheel (RW), either before, in the middle of, or at the end of the descending body mass trajectory during seasonal acclimatization. Due to wheel running, the seasonal weight cycle was prevented or aborted by abruptly rising body mass, resulting in a weight appropriate for summer, despite exposure to short days. Torpor was inhibited, and testicular recrudescence was advanced, compared with controls. In contrast, the change into winter fur remained unaltered. Analysis of body composition and plasma leptin revealed a low body fat mass in RW hamsters, not only in winter but also in summer, suggesting a lack of seasonal adiposity. Chronic leptin infusion in winter only decreased body mass in RW individuals, although their relative body fat mass probably was even lower than in sedentary hamsters. A constantly low body fat mass is conceivably reflecting an exercise-dependent change in metabolism, consistent with increased bone mineral content and density in RW hamsters. Additionally, bone area was increased, again supported by elongated vertebral columns. Together, the results show a striking effect of wheel running on body composition and the seasonal pattern of body mass, and they suggest that the photoperiodic regulation of body mass is regulated differently than the reproductive and pelage responses.

body composition; torpor; testicular recrudescence; leptin

Address for reprint requests and other correspondence: F. Scherbarth, Institute of Zoology, Univ. of Veterinary Medicine Hannover, Buenteweg 17, D-30559 Hannover, Germany (e-mail: Frank.Scherbarth@tiho-hannover.de).

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Animals and Housing

Animal husbandry and all experiments were in accordance with the German Animal Welfare Act (ref. no. 05/1061). Hamsters were born and raised outdoors, thus exposed to the natural changes in photoperiod (52°N latitude) and ambient temperature. After weaning, they were housed singly with food (hamster breeding diet, Altromin 7014) and tap water available ad libitum, supplemented by a slice of apple once a week. Hamsters with access to a RW (14 cm inner diameter) were transferred into larger cages (Makrolon, type III, high), whereas control animals (sedentary) remained in standard cages (Makrolon, type II). In the RW cages, a wooden nest box was available throughout the experiment. Sedentary hamsters kept in standard cages were also provided with a wooden nest box (experiment 1) or soft paper tissues for nest building (experiments 2 and 3). Body mass data were used for calculation of group means only if all measurements were taken within 2 consecutive days.

Procedures

Experiment 1. Near the winter solstice, four female and four male Djungarian hamsters (6–7 mo old) were moved to RW cages. One female hamster avoided the wheel and was replaced after 9 days. Another female animal had to be removed from the experiment after 167 days. Four female and two male hamsters (6–7 mo old) remained in type II cages without a RW.

Experiment 2. Before the summer solstice, four male hamsters (5–8 wk old) were transferred to RW cages, whereas eight male individuals (6–8 wk old) were kept in standard cages without a wheel. The fur color index (for definition, see below) was determined once at the end of December and at the beginning of January.

Experiment 3. About 3 wk after fall equinox, during transition into the winter phenotype, eight male hamsters (5–7 mo old) were transferred into cages equipped with a RW. The control group also consisted of eight male hamsters (5–7 mo old) kept in small cages without a wheel. One RW individual died several weeks before the end of the experiment, thus reducing sample size for fat extraction to n = 7.

Fur Color Index

Melting from a grayish brown fur in summer to a white winter fur was determined according to the six stages defined by Figala et al. (11). The final stage was established in December.

Torpor

Events of daily torpor were determined by visual inspection and handling when animals were weighed. Since torpor bouts usually begin in the morning and may last for ~8 h, weighing was timed (usually 1:00 PM; range 12:00–3:00 PM Central European Time) to minimize the possibility of overlooked events. Determination is relatively easy due to lowered body temperature and breathing rate, typical posture, closed eyes (despite disturbance), and sluggishness of torpid hamsters.

Implantation and Leptin Treatment

Recombinant mouse leptin (R&D Systems, Germany) was dissolved in 15 mM HCl and adjusted to pH ~5.2 with 7.5 mM NaOH for administering 15 μg·day⁻¹·animal⁻¹ via osmotic minipumps (Alzet, model 1007D). Gelatine capsules of a similar size filled and coated with silicone served as dummies for sham treatment. In mid-December, minipumps and capsules were implanted subcutaneously in the scapular region under isoflurane anesthesia. They were replaced after 7 days. Thus the animals implanted with minipumps received leptin for ~14 days. During this period, all individuals were weighed every day. Minipumps and dummies were removed after ~6 wk.

Blood Samples

Blood samples were obtained under isoflurane anesthesia by retro-orbital sinus puncture with heparinized microhematocrit tubes, just before implantation of the osmotic minipumps and dummies. After centrifugation, plasma was stored at −20°C for later leptin analysis.

Leptin Assay

Bound leptin in plasma was measured by a specific radioimmunoassay, which was directed to human leptin. For details, see Lewandowski et al. (27) and Horn et al. (22). The antibody is directed toward a region of leptin, which is highly conserved between species (9, 33). Previous studies had confirmed that the antibody provides serum dilution curves with parallelism to the standard curve, suggesting the equivalence of leptin determinations in the hamster and thus confirming the suitability of the approach.

Testis Palpation

According to Hoffmann (20), four different testis sizes were distinguished: stage 0 (not palpable), stage 1 (small), stage 2 (medium size), and stage 3 (large). The initial palpation was carried out in the middle of December (14th/15th) when the first minipumps and dummies were implanted. From the beginning of January (6th) onwards, the testes were palpated weekly under slight isoflurane anesthesia.

Dual-Energy X-ray Absorptiometry

In February, body composition was analyzed under isoflurane anesthesia with dual-energy X-ray absorptiometry (DEXA) (PIXImus2 scanner, software version 1.46.007, GE Medical Systems, Madison, WI). The head of the animals was excluded from the measurement. Bone mass is not included in DEXA-provided values for total body mass (head excluded) and lean mass. Food was removed from the cages ~4–5 h before the procedure.

Lengths of the femora and the vertebral columns between head and pelvis were measured on radiographs of the animals’ dorsal side. The bodies were sprawled and the limbs were abducted. To measure the femora, a box was drawn and adjusted to the bones with the software CorelDRAW 12. The length of the box corresponded to the straight line between both ends of the femur, thus comparable to measurements with calipers. Values were averaged for each animal. For measurements of the vertebral columns, a plug-in (plotcalc) for CorelDRAW was used, providing the length of drawn curves.
Fat Extraction

In June, body composition was determined by fat extraction. About 3–6 h before analysis, food was removed from the cages. Under deep isoflurane anesthesia, the heart of the animals was excised. Subsequently, heart and testes were weighed, and the bladder was emptied. Body weight of the almost exsanguinous carcasses was determined again (basic value) before being stored at −20°C for later extraction. For this, the carcasses were minced and freeze-dried to a constant weight. After fat extraction with petroleum ether for 6 h in a Soxhlet apparatus, the solvent was removed, and the fat was weighed. In a second step, the dried material was heated together with hydrochloric acid. Remaining fat in the filtrate was analyzed as described above.

Statistical Analysis

The effect of wheel-running activity on body mass as well as the effect of leptin treatment on body weight were evaluated using repeated-measures (RM) ANOVA, with group (RW vs. control, or leptin vs. no leptin) and time elapsed (e.g., day of treatment) as factors. When interaction terms (group × day) were significant, the Tukey test for multiple comparison was applied. For comparison of two unpaired samples, the Mann-Whitney rank sum test was used. Paired samples were compared with the Wilcoxon signed-rank test. Analysis of covariance was used to compare linear regressions. The quality of relation between data is shown by correlation coefficients (Pearson). Differences were considered significant when P < 0.05. Data are given as means ± SE. Statistical procedures were made using Statistica 6 (StatSoft, Tulsa, OK).

RESULTS

Experiment 1

In late summer, all hamsters started to respond to the decreasing day length by reducing their body mass. Around the winter solstice when body weight reached the nadir, one group (RW) gained access to RWs. Thereupon the body mass abruptly increased and reached a high summer level within ~7 wk, i.e., at the beginning of February. Conversely, the control animals still retained their low short-day body weight for a further 6–7 wk before exhibiting the spontaneous gradual rise, which is generally completed in summer (Fig. 1A).

Experiment 2

RWs were available for one group of young hamsters from June onward. In the course of the following year, the sedentary group, i.e., without wheel, showed the normal annual cycle in body mass (Fig. 1B). The group with access to a RW failed to reduce the body mass. Instead, the individuals generally gained weight continuously until the following summer. There was no significant difference in the final stage of changed fur color between exercising (median 4, range 3–4) and sedentary hamsters (median 4, range 3–5).

Experiment 3

Access to a RW during the transition into the winter state inhibited a further decline in body mass (Fig. 1C). Instead of a continued reduction of body mass expected for the normal photoperiodic response of Djungarian hamsters, the individuals with wheels rapidly regained body mass, reaching a significant mass elevation within 12 days (RM ANOVA; F = 28.1; P < 0.001; Tukey). The sedentary hamsters, until May, had completed their normal seasonal rise in body mass, but did not attain the mean mass of the RW hamsters. Body mass data from the leptin experiment as well as the last seven measurements with reduced sample size in the RW group were excluded from the statistical analysis above.

Leptin Concentration

At the beginning of the leptin treatment, 1 wk before the winter solstice, body mass was significantly higher in the RW hamsters compared with control animals, unlike the plasma leptin concentration (6.9 ± 0.8 vs. 5.6 ± 0.6 ng/ml; P = 0.13; Mann-Whitney rank sum test; Fig. 2).

Fig. 1. Effect of wheel running on the seasonal body weight cycle. A: one group (n = 8 (°7)) had free access to running wheels (RW) from December 19th. The control group (n = 6 (°5)) was kept without wheels. B: RWs were available for one group (n = 4) from June 18th, whereas the second group (n = 8) had no access to wheels. C: from October 12th, one group (n = 8 (°7)) had access to RWs. Control animals (n = 8) were housed permanently without a wheel. Data are means ± SE. DEXA, dual-energy X-ray absorptiometry.
Leptin Treatment
Before leptin treatment, sedentary hamsters were at their nadir in body mass. They were significantly lighter than the RW group (28.7 ± 1.1 vs. 42.8 ± 1.6 g; n = 8; P < 0.001; Mann-Whitney rank sum test). Only hamsters with access to a RW responded to subcutaneous leptin infusion with a reduction in body weight (RM ANOVA; F = 3.3; P < 0.001; Tukey; Fig. 3).

Body Composition
Body composition was determined in February with DEXA when the body mass of the sedentary hamsters was already 6–7 g higher in relation to the nadir in December; these animals regained about one-half of the weight separating the distinctive winter phenotype from the summer hamster. Body mass, however, was still significantly different between the RW and sedentary group (46.4 ± 1.6 vs. 35.2 ± 1.6 g; n = 8; P < 0.001; RM ANOVA, see above). Despite this difference in body mass, DEXA (head and bone tissue excluded) revealed no significant difference in fat mass between RW and sedentary hamsters (P = 0.065; Table 1) as opposed to the lean mass, which was increased in the RW group (Table 1; Fig. 4, A and B). Bone mineral content, bone mineral density, and bone area were increased in hamsters with access to a RW (Table 2). Furthermore, on radiographs of RW hamsters, the vertebral columns between head and pelvis were significantly longer (7.6%; P < 0.05; Mann-Whitney rank sum test), unlike the femora (P = 0.38), compared with controls.

In June, body weights of the RW group (n = 7) were still higher compared with those of the controls (n = 8) (50.6 ± 1.6 vs. 43.4 ± 1.6 g; P < 0.05; Mann-Whitney rank sum test). This difference also applied to the heart weight (278 ± 11 vs. 234 ± 10 mg; P < 0.05), whereas relative heart weights (0.55 ± 0.01 vs. 0.54 ± 0.01%) were similar in both groups. Fat extraction revealed significantly increased fat mass in sedentary hamsters since February (Fig. 4, A and C). No further increased fat content was found in the RW individuals (Table 1).

Data of the two methods were compared directly, since DEXA reliably predicts body fat content in small-rodent species (10, 24, 32). Although it was shown that DEXA slightly overestimates total body fat (+1.1 ± 0.13 g) in P. sungorus (Ref. 24, in agreement with our own unpublished data), the present DEXA-derived fat values were not transformed due to potential confounding effects of season, age, and sex of the hamsters. Moreover, data transformation according to the published equation does not change any of the presented statistical comparisons.

Dry body mass was similar in both groups (RW vs. control: 19.3 ± 0.3 vs. 19.3 ± 0.7 g). Fat-free dry mass was elevated in RW individuals compared with controls (10.8 ± 0.4 vs. 9.6 ± 0.3 g; P < 0.05; Mann-Whitney rank sum test).

Fur Color
There was no difference between the groups concerning the final color stage of winter fur. Until the end of December, sedentary and RW hamsters molted on average to stage 4 (median), with a range of 3–5.

Torpor
Shallow daily torpor was observed in all sedentary animals. The torpor period ranged from mid-December to the end of January. During the 2-wk leptin treatment with daily weight determination, this winter trait was displayed at least once (median 3, range 1–6 events). In contrast, none of the RW group showed torpor.

Fig. 2. Difference in body mass (left) and plasma leptin concentration (right) between exercising (RW) and sedentary hamsters (n = 8 each) in December. Values are means ± SE.

Fig. 3. Effect of leptin treatment on body weight (December) in hamsters with and without access to a RW (n = 4/group). Values are means ± SE. Repeated-measures ANOVA revealed weight-reducing effects of leptin only in exercising hamsters (P < 0.001). *Significant differences on marked days (Tukey test).

Fig. 4. Changes in body mass (g) and relative body mass (g/kg) over time in hamsters with access to a RW (n = 7; bars) and without access to a RW (n = 5; open bars).
**Gonadal Development**

In mid-December, gonadal regression in all animals was progressed so far that testes were no longer palpable (stage 0). With respect to this starting point and the defined end point (stage 3), testicular recrudescence began and was finished earlier in hamsters with access to a RW compared with control animals without a wheel ($n/H110058; P/H110210.05; Mann-Whitney rank sum test; Fig. 5). In June, when body composition was analyzed for the second time, both RW and control group showed similar paired testis weights ($875/H1100678 vs. 829/H1100626 mg).

**DISCUSSION**

Short-day acclimatization allows Djungarian hamsters to survive in a strongly challenging habitat. Winter traits such as reduction in body weight and daily torpor contribute to saving energy in a cold environment where food availability is low (18, 19). Inhibition of both controlled hypothermia and reduction of body weight due to wheel running, as shown in the present study, would be disadvantageous under natural conditions. Therefore, one has to assume that this phenomenon is a laboratory artifact linked to the attractiveness of a RW. However, whether merely the activity level of a natural behavior is considerably increased or the wheel-running behavior itself is artificial remains open. Nevertheless, it might be a helpful tool for investigating the regulation of torpor as well as the seasonal body weight cycle.

In the present study, depending on the onset of RW availability, the typical weight change induced by short photoperiod was prevented or aborted by abruptly increasing body mass (Fig. 1). Determination of the body composition in February, when body composition was analyzed for the second time, revealed that the elevation of body mass was related to an increase in lean mass (Fig. 4, A and B). Fat mass in RW hamsters was not significantly higher than in sedentary animals (Table 1). Accordingly, the ratio of fat and body mass in the RW group indicates a leaner state compared with controls, because six out of eight values lie below the extrapolated regression line for sedentary hamsters (Fig. 4A). This difference in fatness is even more obvious in body composition data from June showing both higher fat values in sedentary hamsters and a lower proportion of lean body mass in RW hamsters.

Table 1. **Body composition of exercising (RW) and sedentary hamsters**

<table>
<thead>
<tr>
<th></th>
<th>Lean Mass, g</th>
<th>Fat Mass, g</th>
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<tbody>
<tr>
<td></td>
<td>Control</td>
<td>RW</td>
</tr>
<tr>
<td>February†</td>
<td>25.6±1.0</td>
<td>33.9±1.5‡</td>
</tr>
<tr>
<td>June</td>
<td>31.9±1.0</td>
<td>39.5±1.8§</td>
</tr>
</tbody>
</table>

Values are means ± SE; $n = 8$ (†$n = 7$). RW, running wheel (group). †The head was excluded from dual-energy X-ray absorptiometry measurement; therefore, lean mass was not tested for differences between measurements. ‡Significant difference compared with control group; §significant difference between measurements: $P < 0.01$.

Table 2. **Bone parameters from dual-energy X-ray absorptiometry measurement in February**

<table>
<thead>
<tr>
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<th>Area, cm²</th>
<th>BMC, g</th>
<th>BMD, g/cm²</th>
</tr>
</thead>
<tbody>
<tr>
<td>RW</td>
<td>10.28±0.44</td>
<td>0.635±0.031</td>
<td>0.062±0.001</td>
</tr>
<tr>
<td>Control</td>
<td>8.72±0.21*</td>
<td>0.470±0.013†</td>
<td>0.054±0.001†</td>
</tr>
</tbody>
</table>

Values are means ± SE; $n = 8$. BMC, bone mineral content; BMD, bone mineral density. *$P < 0.01$, †$P < 0.001$. 

Fig. 4. Relation between fat or lean mass and body mass in exercising and sedentary hamsters from February (A and B) and June (C and D). In DEXA-derived mass values (February), head and bones are excluded (see MATERIALS AND METHODS). Linear regressions were highly significant (ANOVA; $P < 0.01$), except for fat mass in the RW group in both February ($P = 0.5$) and June ($P = 0.4$). Comparison (analysis of covariance) of regression lines for lean mass (according to graphs) revealed a significant difference between both experimental groups in June ($F = 5.4; P < 0.05$).
mass (Fig. 4, C and D). Exercising individuals almost maintained their adipose tissue mass constant since February, while sedentary hamsters, as expected, significantly increased fat mass from winter to summer (Table 1). This reduced fat content in exercising hamsters was also supported by leptin analysis in December. Plasma leptin concentrations of the RW group were not significantly increased compared with the much lighter (~14 g) controls at their body weight trough (Fig. 2).

Since the amount of leptin in blood is positively correlated with body fat in Djungarian hamsters (25), one can assume that the fat mass was comparable in both experimental groups, despite the significant difference in body mass, i.e., a lower fat proportion in RW hamsters. Taken together, hamsters with access to a RW showed neither the annual cycle in body weight nor the pronounced seasonal fluctuation in fat mass; instead, body mass is increased but with decreased fatness compared with sedentary animals.

In Djungarian hamsters, the body weight is precisely regulated during the annual cycle, being continuously adjusted to the seasonally appropriate weight (31, 39). Thus, at first view, exercise-induced elevated body weight during winter could simply reflect the typical summer level. RW animals, however, differed clearly in plasma leptin from equiponderate summer hamsters, which show considerably higher concentrations (14) due to a high fat content (44). This indirect evidence for a summer-inadequate fat content in RW animals, underlined by later direct measurements, shows that the running-induced body mass in winter is not equivalent to the body mass in summer. Fat mass of exercising individuals, however, was more variable relative to body weight, both in February and June (Fig. 4, A and C). This lack of a definite correlation between fat and body mass indicates a varying effect of wheel running, presumably due to a different running quantity and/or evoked by individually unequal physiological responses.

Constantly low body fat of exercising hamsters could simply be a result of increased energy expenditure due to extensive locomotion. Consistent with this interpretation, the chemical carcass analysis showed a significantly higher proportion of body water in RW hamsters in June, maybe due to increased glycogen storage in liver and muscles. Moreover, bone mineral density and content were significantly increased in RW hamsters in February, probably reflecting a physiological/anatomical adaptation to the physical strain. However, a parameter for endurance performance, the relative heart weight, was not elevated in exercising animals compared with controls at the end of the experiment.

Controversial to the present results and our similar findings under a light-dark cycle of 16:8 h (unpublished observations), in a former study, P. sungorus showed no significant body weight increase when given access to a RW (~32 cm diameter) (3). This lack of any weight-inducing effect is possibly linked to the lower amount of activity. After 2 wk, revolutions per day (rev/day) declined and remained below 6,000 approximating a distance covered of <6 km. The present investigation revealed about 50% higher mean values at least during the first 3 mo of access to a RW (experiment 1: ~30,000 rev/day, experiment 2: ~20,000 rev/day, mean of the first 8 wk; experiment 3: ~20,000 rev/day, mean of 2 wk in February and March).

Simple comparison of the covered distances, however, has to be considered carefully because of unequal wheel sizes requiring different postures and torques. Indeed, in Syrian hamsters, it has been demonstrated that growth is only accelerated by more than 15,000 rev/day on an activity disk (5), indicating as precondition a minimum exercise level that is considerably higher than general activity.

Since the higher body mass of RW hamsters in the present study was not caused by fattening, stimulated growth could be a consequence of wheel running. Measurement of bones in DEXA radiographs taken in February revealed significantly lengthened vertebral columns (~7%) in exercising hamsters, which is well in accordance with the results for Syrian hamsters (8). Furthermore, significantly increased bone area in the RW group strongly supports the growth hypothesis. SD-induced decrease in body mass should be associated with a discontinuation of growth, which could well be prevented in hamsters with access to a RW. Supporting this interpretation, RW animals were still significantly heavier with increased fat-free dry mass when controls reached the summer plateau.

Annual cycles of adiposity and body mass have been associated with the adipose-derived hormone leptin, known for its anorectic effect (for review, see Ref. 1). A reduced leptin sensitivity in long-day animals compared with SD-acclimated individuals was shown for Djungarian hamsters (2, 25) and field voles (Microtus agrestis, Ref. 26), which was suggested to be regulated mainly by photoperiod (34). In the present study, however, sedentary SD hamsters showed no reduction in body mass during leptin treatment as opposed to the RW animals with higher initial body weights. In preceding investigations, leptin effects were tested already after 8 wk of SD when individuals were in the middle of transition. Absence of a reaction to leptin in this study could be due to the different state of acclimatization. Before leptin treatment, the sedentary hamsters had reached the nadir in body weight, which can be expected to be strongly defended. Another explanation for the lack of leptin sensitivity is provided by results concerning the underlying mechanisms. The suppressor of cytokine signaling 3 (SOCS3) has been shown to play a critical role in leptin sensitivity in mice (23) and Djungarian hamsters (43). This protein inhibits signal transduction distal of the leptin receptor, and an increase of arcuate nucleus SOCS3 gene expression was shown to precede the long photoperiod-induced increase of body weight in Djungarian hamsters by ~3 wk (42). Hence, in this present study, sedentary SD hamsters failed to respond to...
leptin administration, possibly due to an already raised SOCS3 level causing leptin resistance. Whether the leptin response in RW hamsters was related to the latter pathway, e.g., a low SOCS3 level, or merely to an increased potential for weight loss simply due to the higher body mass, or both, remains speculative.

For Syrian hamsters, exercise-induced increase in body weight has been reported as well as effects on testis development. Although testicular regression is incomplete in Syrian hamsters with access to a RW (17), neural integration of the shortened photoperiod is not prevented (29). Lack of perception of changing day length in exercising individuals can be excluded for *P. sungorus* as well, because of the present findings of complete gonadal regression and the change to winter fur. Since the course of testes involution has not been observed, it is not known whether the SD-induced testicular development on the whole was shifted forward or compressed. In any case, the recrudescence was advanced in Djungarian hamsters with access to a RW, indicating either an advanced termination of the winter state, i.e., refractoriness, or a testes-stimulating effect prevailing when suppressing signals become weaker or disappear. In the latter case, the testis regression should be decelerated in exercising hamsters. In this regard, it cannot be ruled out that a different pattern of entrainment and thus an altered photore sponsiveness is responsible for some of the effects in RW hamsters, as has been found in selectively bred photoperiodic nonresponsive hamsters that exhibited adjustments to SD only when given access to a RW (13). A prepinal influence of wheel running on the entrainment would explain the lack of weight-increasing effects in the study of Bartness and Wade (3). In this study, SD was mimicked by melatonin injections that potentially override upstream effects. More recent findings indicate that the thalamic intergeniculate leaflet is involved in the photoperiodic responsiveness and the activity feedback mechanism (12, 15).

Another typical SD trait, daily torpor, was not observed in RW individuals, confirming the results of Thomas et al. (41). The absence of torpor, however, was probably not due to an elevated leptin level, which was previously discussed to prevent hypothermia (14). First, there was no obvious difference in torpor frequency between the leptin-treated sedentary group and the untreated sedentary animals, thus corresponding to the results of Schmidt et al. (37), and second, in December, the plasma leptin concentration in the exercising hamsters with high body weights was only slightly increased (not significant) compared with sedentary animals. In this regard in *P. sungorus*, a negative correlation was found between the individual number of torpor episodes and the general intensity of nocturnal locomotor activity (35, 36). High torpor frequency was assumed to facilitate a constant low activity level, probably reflecting reduced foraging, which, in combination, yields an effective energy-saving strategy. In contrast, wheel running possibly shifts the hamsters to the other end of the behavioral range, characterized by a very low torpor frequency and a higher general activity level. Furthermore, physiological parameters related to hypothermia, such as metabolism and body temperature, which are influenced by wheel-running activity, may be responsible for inhibition of torpor.

In conclusion, wheel running strongly affected the typical seasonal acclimatization of Djungarian hamsters. As a consequence, testes recrudescence was advanced, and the reduction in body mass as well as daily torpor were inhibited. Elevation in body mass was due to significant increases in lean mass, and the fat content was reduced compared with sedentary hamsters. This alteration of body composition was accompanied by considerably increased mineral content and density in bones, reflecting the diversity of physiological responses due to wheel-running activity.

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