



Preference for Western diet coadapts in High Runner mice and affects voluntary exercise and spontaneous physical activity in a genotype-dependent manner



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ABSTRACT

Do animals evolve (coadapt) to choose diets that positively affect their performance abilities? We addressed this question from a microevolutionary perspective by examining preference for Western diet (WD: high in fat and sugar, but lower in protein) versus standard rodent chow in adults of both sexes from 4 lines of mice selectively bred for high levels of voluntary wheel running (High Runner or HR lines) and 4 non-selected control (C) lines. We also assessed whether food preference or substitution affects physical activity (wheel running and/or spontaneous physical activity [SPA] in the attached home cages). In experiment 1 (generation 56), mice were given 6 days of wheel acclimation (as is used routinely to pick breeders in the selection experiment) prior to a 2-day food choice trial. In experiment 2 (generation 56), 17 days of wheel acclimation allowed mice to reach a stable level of daily running, followed by a 7-day food-choice trial. In experiment 3 (generation 58), mice had 6 days of wheel acclimation with standard chow, after which half were switched to WD for two days. In experiment 1, WD was highly preferred by all mice, with somewhat greater preference in male C mice. In experiment 2, wheel running increased and SPA decreased continuously for the first 14 days of adult wheel testing, followed by 3-day plateaus in both. During the subsequent 7-day food choice trial, HR mice of both sexes preferred WD significantly more than did C mice; moreover, wheel running increased in all groups except males from C lines, with the increase being significantly greater in HR than C, while SPA declined further in all groups. In experiment 3, the effect of being switched to WD depended on both linetype and sex. On standard chow, only HR females showed a significant change in wheel running during nights 7 + 8, increasing by 10%. In contrast, when switched to WD, C females (+28%), HR females (+33%), and HR males (+10%) all significantly increased their daily wheel-running distances. Our results show for the first time that dietary preferences can coadapt in response to selection on activity levels.

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1. Introduction

Evolution occurs via more-or-less coordinated genetic and phenotypic changes at multiple levels of biological organization. Even within a level, such as behaviour, coadaptation is expected (e.g.,

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see Brashares and Arcese, 2000; Jarman, 1974). Two aspects of behaviour that seem likely to exhibit coadaptation are diet and physical activity. For example, the classic (but oversimplified) dichotomy between active and sit-and-wait foragers entails variation in both activity patterns and diet (as well as life-history traits, locomotor abilities, the predation regime experienced, social behaviour, and mating systems (Huey et al., 2001; Perry et al., 1990; Verwajen and Van Damme, 2008).

In addition to an expectation of correlated evolutionary changes, dietary choices and physical activity can influence each other during an individual's ontogeny, both acutely and chronically. Effects of physical activity on appetite have been studied extensively (Blundell and King, 1998; Hopkins et al., 2014; Westerterp, 2010). Generally, food or energy intake increases as physical activity

increases (Koteja et al., 1999; Melzer et al., 2005; Stevenson, 1967; Westerterp, 2010). In a few cases, physical activity has been shown to affect dietary choice. For example, Tour de France cyclists voluntarily consumed more carbohydrates as their primary fuel source during their training than when not training (Saris et al., 1989). The underpinnings of these bidirectional, within-individual effects may themselves have evolved in response to past correlational selection, as part of the homeostatic mechanisms underlying both physiology and behaviour. From the perspective of coadaptation, we would expect that animals may generally evolve to choose diets that enhance their ability to perform various functions, such as particular types of locomotion or reproductive activities.

Studies of laboratory rodents show that diet choice and composition can affect both physical activity and whole-animal performance capacities. For example, 3 months of high-fat diet increased maximal aerobic capacity ($VO_2\max$) by 15 percent in sedentary rats, whereas endurance training for 3 months increased $VO_2\max$ by 20 percent (Simi et al., 1991), and the effects were additive. A different study of rats compared effects of a high-fat versus a high-carbohydrate diet fed for 2 months on exercise endurance and body composition. Half of the rats had their diets switched for 3 days prior to endurance testing. Rats that received the high-fat diet first, followed by the high-carbohydrate diet, fatigued later than the rats fed a high-carbohydrate or high-fat diet only (Lapachet et al., 1996). In another study of rats fed one of three diets (high in saturated fat, high in n-3 fatty acids, or high in n-6 fatty acids), those fed the high n-6 diet increased treadmill endurance-running performance compared to the other groups (Ayre and Hulbert, 1997). Increased consumption of polyunsaturated fatty acids (PUFAs) has also increased treadmill endurance-running performance in rats (Ayre and Hulbert, 1997). A large and often conflicting literature also concerns effects of dietary supplements and carbohydrate loading on human athletic performance (e.g., Bucci, 2000).

Diet choice and composition can also affect physical activity and performance ability in wild animals. A field study demonstrated that just prior to their long-distance migration from Canada to South America, sandpipers consumed a diet rich in amphipod crustaceans, which have greater polyunsaturated fatty acids (PUFA) content than other crustaceans (Weber, 2009). Unsaturated fatty acids have increased fluidity, accelerating peroxidation rates and influx into cells more than saturated fatty acids (Maillet and Weber, 2006). Enhanced fuel accessibility may be the reason sandpipers consume certain crustaceans prior to migration. Similarly, migratory red-eyed vireos prefer long-chain unsaturated fatty acids over long-chain saturated fatty acids (Pierce et al., 2004). In a different experiment, vireos had improved aerobic performance (mass-specific peak metabolic rate during forced exercise) with a diet containing lower unsaturated fatty acids as compared with a diet containing more unsaturated fatty acid (Pierce et al., 2005). These and other studies (e.g., Frank et al., 1998; Weber, 2009) support the general hypothesis that dietary preferences should coadapt with other aspects of behavioural and physiological ecology in ways that facilitate organismal performance abilities (Angilletta et al., 2006; Bauwens et al., 1995).

Selection experiments and experimental evolution can provide powerful tools for elucidating the coadaptation of behavioural and other traits (Garland et al., 2016; Garland and Rose, 2009; Rhodes and Kawecki, 2009). The purpose of the present study was to test the coadaptation hypothesis by examination of preference for “Western diet” (relatively high in fat and sugar, but low in protein) and the effects of Western diet on physical activity in a unique rodent model: four replicate lines of High Runner (HR) mice that have experienced long-term selective breeding for voluntary exercise on wheels, as compared with four non-selected control (C) lines (Acosta et al., 2015; Careau et al., 2013; Copes et al., 2015; Swallow et al., 2009, 1998). In addition to running voluntarily 2.5–

3-fold more revolutions per day, HR mice have increased endurance capacity (Meek et al., 2009) and $VO_2\max$ (Dlugosz et al., 2013; Kolb et al., 2010; and references therein), reduced body fat (Girard et al., 2007; Swallow et al., 2001), lower circulating leptin levels that are not explained solely by their lower body fat (Acosta et al., 2015; Girard et al., 2007), alterations in the brain reward system (Belke and Garland, 2007; Caetano-Anollés et al., 2016; Claghorn et al., 2016; Kolb et al., 2013; Rhodes et al., 2005; Saul et al., 2016), and may experience withdrawal symptoms when wheel access is removed (Kolb et al., 2013) (review in Wallace and Garland, 2016).

Previous studies found that Western diet can positively affect wheel running in male HR mice but not in C mice (Meek et al., 2014, 2010). This unusual response of HR mice could be related to constraints that their hyper-lean phenotype places on sustained endurance exercise (given that they have inherently high motivation for voluntary exercise) and/or an effect on the reward they receive from running, alternatives that have yet to be discriminated. Here, we report on three separate experiments, all that used both sexes, designed to address several hypotheses and predictions about the HR mice. Most generally, we hypothesized that HR mice would have elevated preference for Western diet compared to C mice (Experiments 1 and 2), and that this difference might depend on context, e.g., whether they were fully acclimated to wheels when tested (6 vs. 17 days in Experiment 1 vs. 2). In addition, we expected that HR mice might respond differently from C mice, in terms of wheel running and/or home-cage activity, when Western diet was substituted (Experiment 3) for standard chow (Meek et al., 2014, 2012, 2010). Finally, we expected males and females might differ in food preferences (Experiments 1 and 2) and responses (Experiment 3) to Western diet (Asarian and Geary, 2013; Bender, 1976; Fukushima et al., 2015) in a manner that depends on genetic background (Svenson et al., 2007; C vs. HR lines in the present study) (C vs. HR lines: all three experiments).

2. Materials and procedures

2.1. Experimental animals

Mice were from generations 56 and 58 of an ongoing artificial selection experiment that breeds for high voluntary wheel running activity (for more details on the selection process, see (Careau et al., 2013; Swallow et al., 1998). The base population consisted of 224 outbred, genetically variable Hsd:ICR house mice (*Mus musculus*). Ten pairs of mice were used to create eight closed lines, four of which were randomly designated and bred for high running (HR) on wheels and the other four were non-selected control (C) lines, bred without regard to wheel running. In each generation, mice are weaned at 21 days of age and housed in same-sex groups of four until approximately 6–8 weeks of age, when they are individually housed in standard cages attached to a Wahman-type activity wheel (1.12 m circumference, 35.7 cm diameter, 10 cm wide running surface). Wheels are interfaced to a computer that records revolutions in 1-min intervals continuously for 6 days of wheel testing. In the HR lines, breeders for the next generation are chosen based on their wheel running for days 5 and 6. For the HR lines, the highest-running males and females within each family are chosen as breeders, whereas random males and females are chosen from within families in the C lines (sibling mating is disallowed in all lines).

Room temperature was maintained at approximately 22°C. Lights were on at 0700 with a photoperiod of 12:12 h. Water and food (Harlan Teklad Laboratory Rodent Diet [W]-8604 or Harlan Teklad Custom Research Western Diet TD.88137) were available *ad libitum*. Many different “Western” and “high-fat” diets are used in research with rodents, including several that are commercially

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