Food wasting by house mice: variation among individuals, families, and genetic lines

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Abstract

Under ad libitum conditions, laboratory house mice (*Mus domesticus*) fragment considerable amounts of pelleted food and leave it scattered in their cages. The proportion of food thus wasted (in relation to food eaten) varies remarkably among individuals, from 2% to 40%, but is highly consistent in consecutive trials, even when the mice were moved from 22 to -10 °C and food consumption doubled. Food wasting did not differ either between the sexes or between genetic lines that had been selected (10 generations) for high voluntary wheel-running behavior ($n = 4$) and their unselected control lines ($n = 4$). However, it varied significantly among replicate lines within the selection groups and among families within the lines (coefficient of intraclass correlation for full sibs, $\rho_f = 0.41$ in room temperature trials and $\rho_f = 0.34$ in cold trials). Moreover, the percent of food wasted was negatively correlated with food consumption in the cold trials (males: $r = -.36$, females: $r = -.20$) and with total litter mass at weaning (the litters into which they were born; $r = -.24$), two traits that may affect Darwinian fitness. We conclude that food wastage should not be ignored without justification in calculations of food consumption. In addition, "table manners" can convey reliable information about family origin of an individual and its quality, and therefore could potentially play a role in establishment of social status.
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1. Introduction

Captive animals often fragment some amount of food and leave it scattered in their cages, even when given a high-quality, fairly homogenized food [1–4]. This sort of food wasting is a nuisance in measurements of food consumption [3,5] and has the potential to compromise studies with animal models that aim to elucidate human eating disorders and the regulation of food intake and body weight (e.g., Refs. [6–8]).

From a behavioral perspective, fragmentation of food could be regarded as a stereotypic or compulsive behavior. Alternatively, it could be suggested that laboratory animals, such as mice, fragment food pellets to create nesting material, and differences in food fragmentation might reflect differences in nest-building propensity. Food wastage is also common in some wild animals. Herbivorous rodents cut and leave uneaten large amounts of grass and herbs [9]. Some foods, such as seeds, require dissection to avoid unpalatable or toxic components, which may lead to discarding even 95% of the mass of food processed [10]. From an ecological perspective, leftovers are important because the impact of herbivores on populations of plants, or of predators on populations of prey, depends not on how much has been eaten but on how much has been damaged or killed [9]. Moreover, uneaten food may become a resource for other individuals or species, possibly including humans [11,12]. On the other hand, spillage from human meals might have contributed to domestication of dogs [13]. Thus, food-wasting behavior of one species may affect populations of several other species.

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Common knowledge among pet owners, animal breeders, and researchers working with laboratory animals indicates that individual animals vary in food wasting, just as human beings vary in "table manners" (some are neat, others messy). Thus, it is reasonable to hypothesize that this aspect of feeding behavior may be determined by neurophysiological mechanisms common to humans and to animals used as models for human behavior.

The abovementioned ideas are, at present, pure speculations, because it appears that no attempts to quantify and explain sources of individual variation in this aspect of behavior have been undertaken. The purpose of this study was to analyze sources of variation in the food-wasting behavior of laboratory house mice, quantified as the amount of food fragmented (broken into small pieces, sometimes nearly a powder). We asked whether food wasting was consistent across trials repeated on the same individuals and whether it changed in response to increased energy demand caused by cold exposure. We also tested whether it differed between the sexes, among genetically closed lines that had been selectively bred for high wheel-running behavior and among families within the lines. Other questions addressed were whether individual values of the trait correlated with body size, food intake, efficiency of food digestion, nest-building and wheel-running behaviors, and aspects of reproductive performance.

2. Methods

2.1. Animals and experimental protocol

The results presented here were obtained as part of an experiment designed to study the effects of selective breeding for increased wheel running on food consumption and energy budgets in laboratory house mice (*Mus domesticus*) [14–16]. We used 143 mice from second litters of generation 10 of the selection experiment, in which four replicate lines have been selected (within family) for high wheel running, while four other lines have been maintained as controls by random mating [17,18]. In generation 10, mice from the selected lines ran 70% more wheel revolutions per day than the control mice (the difference is statistically significant) [14]. The original progenitors were outbred, genetically variable Hsd:ICR mice [19–22]. Sib mating was disallowed in all lines. In each of the eight lines, we tested mice from 9 to 11 full-sib families. In most families, we had one male and one female, but in some, only one individual was available.

After weaning at 21 days of age, mice were housed individually in cages equipped with a running wheel (Wahman type, circumference 112 cm, Lafayette Instruments, Lafayette, IN). When the mice were 37–53 days old, nesting behavior was scored by measuring the amount of nesting material used over a 4-day trial, as reported earlier

[23]. At the age of 64–80 days, a series of consecutive (usually 3 days) feeding trials was performed (a total of 56 days) simultaneously on all individuals, as follows:

- Trial 1: 3 days at 22 °C, in cages with attached wheels. Further trials were performed without wheels;
- Trials 2–4: three 3-day trials at 22 °C;
- Trial 5: 3 days at − 5 °C, without prior cold acclimation;
- Trials 6–9: 16 days at 5 °C, to allow cold acclimation;
- Trials 10–12: 12 days at − 5 °C (Trial 11 had 6 days);
- Trials 13–16: 14 days at − 10 °C (Trial 15 had 4 days);
- Trial 17: at − 15 °C, interrupted after 2 days, because most of our mice were unable to maintain energy balance; all individuals were then euthanized.

Details and rationale of the protocol were presented in our earlier work [14–16].

During the entire experiment, the photoperiod was 12 light/12 dark. Mice were maintained in standard clear polycarbonate cages ($27 \times 17 \times 12.5$ cm, metal tops), equipped with a perforated (diameter of holes: 3.15 mm) polypropylene plate suspended over the floor to allow collection of feces and uneaten food. No nesting material was provided. Paper towel was placed below the perforated plate to absorb urine.

At the beginning of each trial, mice were given a known amount (to ± 0.01 g) of pelleted food (Harlan Teklad Laboratory Rodent Diet [W] 8604), about the same for all individuals (± 2 g), placed directly on the perforated plate (typical metal feeders could not be used at subzero temperatures). After 3 days, animals were transferred to clean cages (during light phase, between 14:30 and 18:00 h) and remaining food and feces were manually segregated, dried to constant mass, and weighed. The data were used to calculate the rate of food consumption (C; g/day)

$$C = [(\text{food given} \times \text{dry mass content})$$
$$- (\text{dry food uneaten})]/(\text{time in days})$$

and the apparent digestibility of dry mass (d; %)

$$d = 100 \times (\text{food consumed} - \text{feces mass})$$
$$/(\text{food consumed})$$

reported in our earlier work [14–16].

Here we report results only from the four trials at room temperature (Trials 1–4) and four trials at cold temperature (Trial 12 at − 5 °C and Trials 13, 14, 16 at − 10 °C; Fig. 1), for which we separately weighed the food remaining as intact pellets and that fragmented into small particles (we did not do this for all trials because it required excessive labor). In every case, some amount of food remained as intact pellets. Although the fragmented particles varied in size from tiny dust up to pieces of about 3 mm in diameter, they could always be easily distinguished from the remaining pellets (by shape and teeth
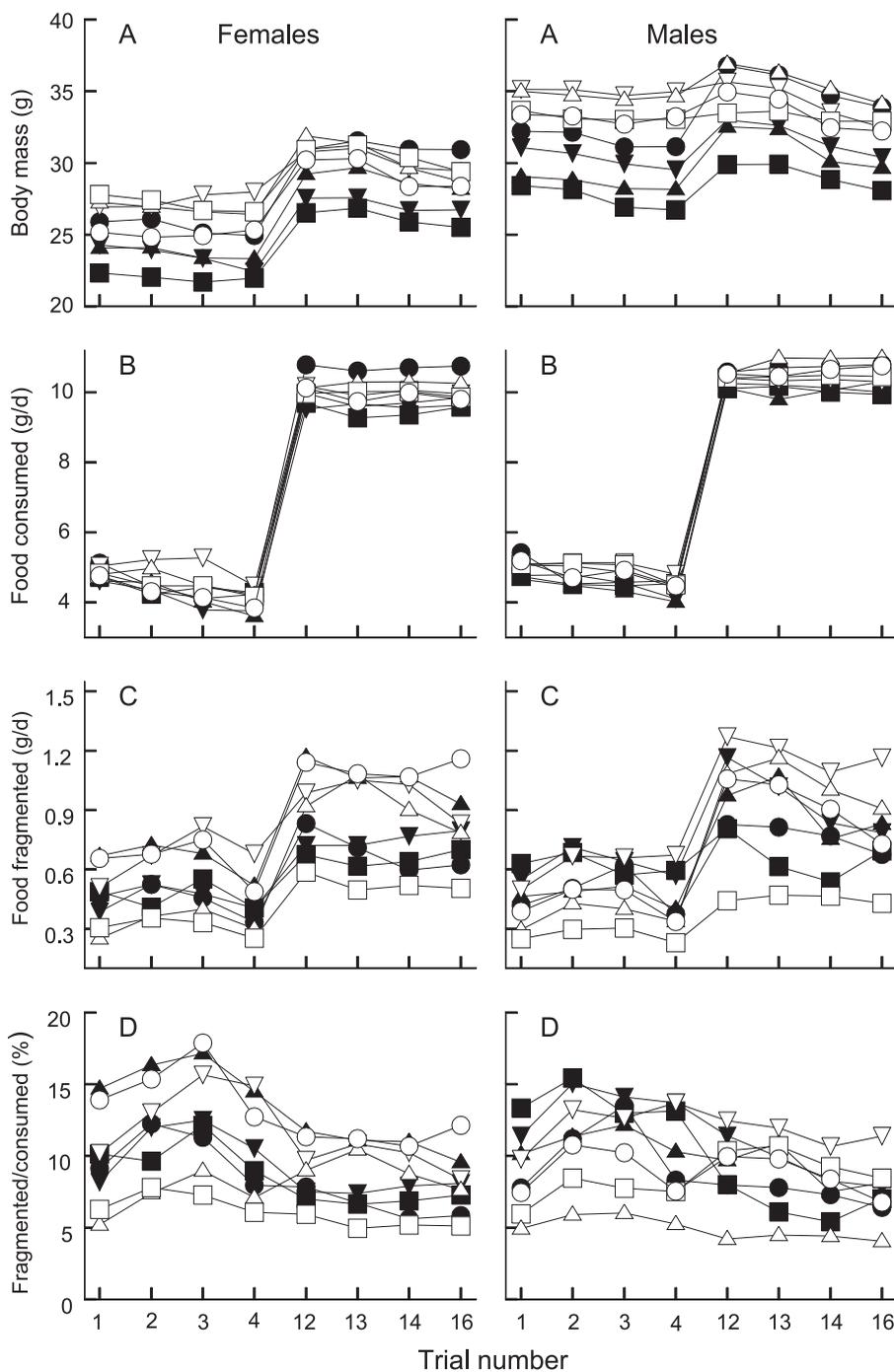
Fig. 1. Average body mass (A), food consumption (B), amount of food fragmented (C), and percent of food fragmented (D) measured in four 3-day trials at room temperature (Trials 1–4; Trial 1 with access to wheels) and four trials in cold (Trial 12 at $-5\ °C$ and Trials 13–16 at $-10\ °C$) in laboratory house mice from eight lines (distinguished by different symbols): four selected for high wheel-running activity (closed symbols) and four control lines (open symbols).

marks), even if the pellets had been largely eaten. The results were used to calculate the amount of food fragmented per day (FF; g/day) and percent of food fragmented, PF = 100 (food fragmented)/(food consumed), reported in this study.

The protocol was approved by the Institutional Animal Care and Use Committee of the College of Letters and Science, University of Wisconsin-Madison.

2.2. Statistical analyses

We used nested ANCOVA to test significance of the effect of selection groups (G; fixed effect), variation among replicate lines nested within selection groups ($L(G)$; random effect), families nested within lines ($F(L)$; random), individuals nested within families ($I(F)$; random), and sex (S; fixed), on the amount and percent of food fragmented. As

the distributions of the variables were right skewed, the statistical analyses were performed on log-transformed values. Log-transformed food consumption and/or body mass were used as covariates (COV). Because we had no more than one male and one female per family, the $I(F)$ effect accounts for the same source of variation as $S \times F(L)$ interaction. Therefore, we tested two types of ANCOVA models. In models for results from separate trials and for values averaged across trials, in which variation among individuals is equivalent to the error term, sex was included as a cross-factor (i.e., the model was cross-nested):

$$Y_i = \mu + G + L(G) + F(L) + S + G \times S$$
$$+ L(G) \times S + COV + e_i$$

where Y_i is a dependent variable, i is a mean, and e_i is a random error term for individual i.

In models with replicate measurements on the same individuals, which included "individual within family" effect, sex was not included:

$$Y_{ij} = i + G + L(G) + F(L) + I(F) + COV + e_{ij}$$

where e_{ij} is a random error term of measurement j on individual i. Because the first models showed that sexes did not differ in the proportion of food fragmented, ignoring sex in the latter models probably had no bearing on the results. F statistics were calculated with denominator mean squares (MS) appropriate for particular fixed and random effects [24,25].

MS from the models were used to calculate coefficients of intraclass correlation (ρ) and their standard errors [26,27]. Variation among replicate trials (MS_e) was used as an error term for correlation within individuals (ρ_i), whereas variation among siblings ($MS_{ID(F)}$) was used as the error for calculating correlation within families (ρ_f).

In addition to calculating intraclass correlations, the correlation between trials performed at the same or at different temperature was assessed by calculating partial correlations (r, Pearson's coefficients between residuals [28]), i.e., correlations between values adjusted for the effects of food consumption and differences among lines. For these analyses, the models with family effect would be not appropriate, because residuals from such models amount to deviations of siblings from family means. Therefore, for this purpose, we made the analyses separately for males and females. Because we had no more than one male and one female per family, in these ANCOVA models, each individual represented an independent observation within a line:

$$Y_i = i + G + L(G) + COV + e_i$$

A similar procedure was applied to test for the correlation between the proportion of food fragmented and other traits: coefficient of digestibility, the amount of wheel running, nest-building score, and reproductive performance. Finally, we also used a repeated measures ANOVA to test for differences among subsequent trials on the same individuals.

The mice used in this study were sacrificed at the conclusion of the experiment, so we could not study their reproductive performance. However, we had the data on litter size, total litter mass, and average individual mass at weaning (day 21 from parturition) of the entire litters our mice came from, and also of first litters born by the same dams. These values represent reproductive performance of mothers of the mice. We checked whether the reproductive performance (averaged across two litters) was correlated with the percent of food fragmented averaged across two siblings (in some families only one individual was available) and all the feeding trials.

All the significance levels (P values) are given for two-tailed tests. The analyses were performed with SYSTAT 6.0 (SPSS).

3. Results

3.1. Overview

Details of the results concerning food consumption and body mass changes were presented elsewhere [14–16]. Shortly, food consumption was slightly higher in the first 3-day trial (with wheels) than in the next three trials without wheels, and increased to about 10 g/day at cold temperatures (Trials 13–17; Fig. 1B). Body mass of the mice increased when they were exposed to moderately low temperatures (Trials 5–11, not shown here), but at -10 °C, most of the mice could not maintain body mass (Fig. 1A).

In the four trials at room temperature, the average amount of food fragmented was about 0.5 g/day, and it increased to about 0.9 g/day in the cold (Fig. 1C; $P < .001$). In room temperature, the amount of food fragmented varied proportionally to consumption, so that the percent of food fragmented did not depend significantly on food consumption (Fig. 2A,C; Table 1a). The results presented hereafter are for the percent of food fragmented (PF; log-transformed). However, in all the analyses food consumption was included as a covariate to assure that the trait analyzed is indeed statistically independent from variation in food consumption. PF did not depend on body mass (all trials: $P \geq .29$, except Trial 1 on males: $P = .12$) and did not differ between sexes (in all trials: $P \geq .2$; Fig. 1D). Hence, these variables were not included in the analyses presented below.

3.2. Sources of variation and repeatability of food-fragmenting behavior

The percent of food fragmented increased in Trial 2 (i.e., after removing wheels; $P = .01$), then decreased in Trial 4 (difference between Trials 3 and 4: $P = .02$), but the variation
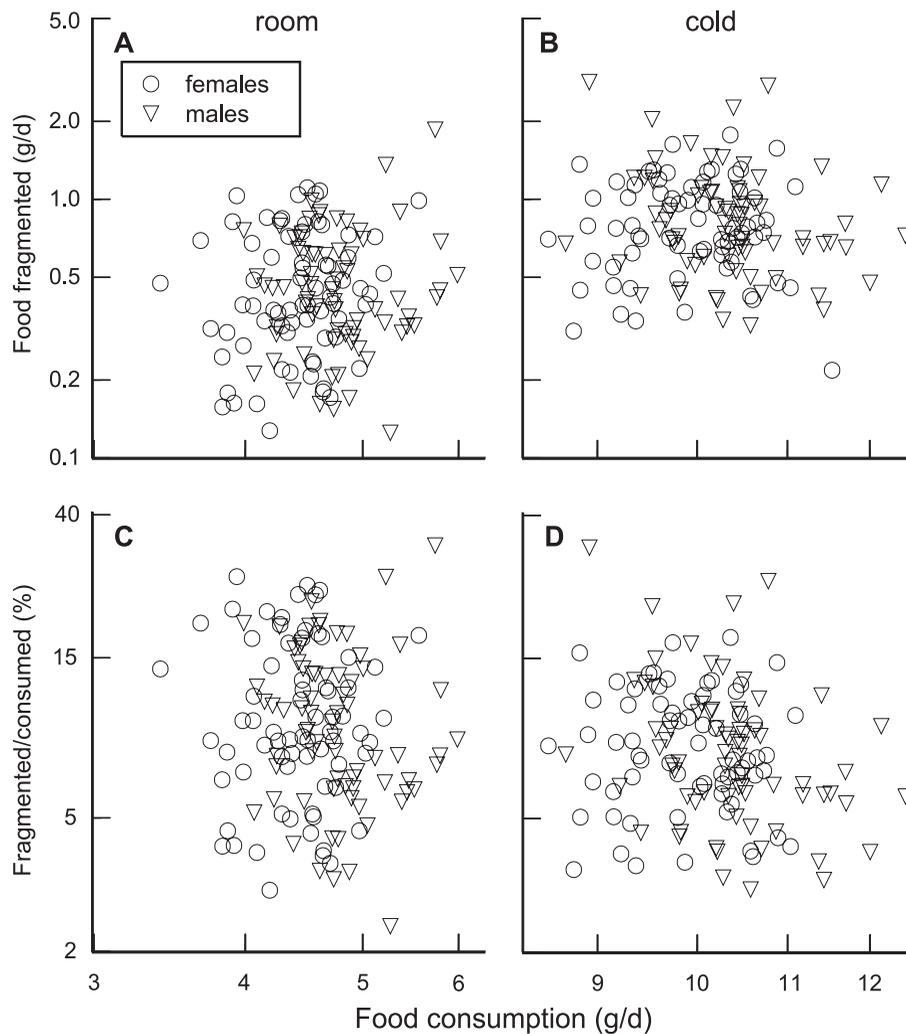
Fig. 2. Individuals' average (from replicate trials) amount of food fragmented (A, B) and percent food fragmented (C, D) plotted against food consumption at room temperature (left) and in the cold (right). Note log–log scale.

in PF among trials was generally small (Fig. 1D). Within each trial, PF varied immensely among individuals, from about 2% to 40% (Fig. 2C,D). PF did not differ significantly between mice from the selected and control lines (Fig. 1C,D; Table 1), but the differences among replicate lines, among families within the lines, and between the two individuals within families were all highly significant, both in the trials at room temperature and in the cold (Table 1).

Repeatability of PF was very high (Table 1). The coefficient of intraclass correlation, ρ_i, was 0.62 ± 0.04 ($\pm$ S.E.) for the four trials at room temperature and 0.69 ± 0.04 for the four trials at cold temperatures. Moreover, individuals' average PF at room temperature was also highly correlated with that in the cold (males: $r=.61$, $P < .001$; females: $r=.65$, $P < .001$).

The proportion of food fragmented was highly correlated between siblings (Table 1). The coefficient of intraclass correlation for the full-sib families (ρ_f) was 0.41 ± 0.11 for room temperature and 0.34 ± 0.13 for cold-exposure trials. Note that these results are from ANCOVA with food

consumption and lines as cofactors, which means that the correlations between trials or between siblings could neither be explained by consistent differences in food intake nor by differences among lines.

3.3. Correlates of food-fragmenting behavior

As noted above, in the trials at room temperature PF was not correlated with food consumption (Fig. 2C; Table 1). However, in the four cold-exposure tests the mice achieved higher rates of food consumption in the trials in which they fragmented less food, as indicated by a significant negative effect of the covariate in the ANCOVA model ($P=.02$; Table 1B). In addition, individuals that fragmented less food tended to achieve higher consumption in cold-exposure tests, although the relation was significant only in males (males: $r=-.36$, $P=.003$; females: $r=-.20$, $P=.1$; Fig. 2D). Similarly, males that fragmented more food loose more body mass in the cold-exposure tests (males: $r=.48$, $P < .001$; females: $r=.06$, $P=.6$). PF was not correlated with

Table 1

Analysis of the sources of variation in log-transformed proportion of food fragmented by house mice, measured in four 3-day trials in (A) 116 individuals (58 full-sib families) at room temperature and (B) 92 individuals (46 full-sib families) at cold temperatures

Source	SS	df	MS	F	P	ρ *	S.E.$_\rho$
(A) At room temperature (R^2=.842)							
Food consumption rate (a covariate)	0.032	1	0.032	2.33	.127		
Selected vs. control lines	1.540	1	1.540	1.63	.248		
Lines within selection groups	5.652	6	0.942	3.88	.003		
Families within lines	12.153	50	0.243	2.39	.001	0.41	0.11
Individuals within families	5.910	58	0.102	7.49	<.001	0.62	0.04
Replicate trials on an individual (error)	4.719	347	0.014				
(B) At cold temperature (R^2=.858)							
Food consumption rate (a covariate)	0.042	1	0.042	5.47	.020		
Selected vs. control lines	0.016	1	0.016	0.04	.855		
Lines within selection groups	2.694	6	0.449	2.85	.021		
Families within lines	5.981	38	0.157	2.07	.009	0.35	0.13
Individuals within families	3.494	46	0.076	9.98	<.001	0.69	0.04
Replicate trials on an individual (error)	2.093	275	0.008				

*ρ—coefficient of intraclass correlation with its standard error, S.E.$_\rho$.

the coefficient of digestibility, either in room temperature or in cold-exposure trials ($P>.4$).

Although PF did not differ significantly between the lines selected for high wheel running and the control lines (Table 1), in the trial with wheel access, PF tended to be positively correlated with total number of revolutions run per day (males: $r=.25$, $P=.07$; females: $r=.30$, $P=.02$) and with average running speed (revolutions per minute interval; males: $r=.25$, $P=.05$; females: $r=.24$, $P=.06$). The correlation between PF and the amount of time spent running was not significant (males: $r=.11$, $P=.37$; females: $r=.21$, $P=.11$).

Mice from the selected lines built smaller nests in trials with access to wheels [23]. This result held for the subset of these mice that also experienced the feeding trials, although the difference was significant only in females (females: $P=.03$, $n=59$; males: $P=.08$, $n=65$). Individual scores of nesting behavior were not correlated with PF measured in the trials at room temperature, with or without wheels ($P>.3$). However, in females, PF measured in cold-exposure trials appeared negatively correlated with the nesting scores (female: $r=-.38$, $P=.007$; males: $r=.02$, $P=.3$).

In this experiment, we used individuals born as second litters to 79 dams. At weaning (21 days after parturition), litter size ranged from 4 to 18 (mean ± S.D.: 13.0 ± 2.7), litter mass ranged from 47.4 to 195.5 g (138.4 ± 22.7), and body mass of the dams was 38.4 ± 3.5 g. Not surprisingly, when weaning the first litters (used in the main selection protocol) the dams were smaller (36.4 ± 3.7 g), and both litter size (10.4 ± 2.2) and mass (103.5 ± 21.9 g) were smaller than in the second litters (the figures did not differ from values observed in other generations of our mice; [29]). Litter size and mass increased with body mass of females also among families ($P=.002$ and .008, respectively). Therefore, in the following analyses, the reproductive traits were adjusted by ANCOVA to remove effects of body

mass of dam. The percent of food fragmented, adjusted for food consumption and lines, and averaged within families across siblings and all the feeding trials, was negatively correlated with total mass at weaning, averaged across both litters (partial correlation $r=-.24$, $P=.043$). Thus, mice born and reared in smaller litters tended to fragment a larger percentage of their food.

4. Discussion

4.1. Overview

Results of this study showed that (a) the percent of food fragmented (PF) in house mice is, at least in some individuals, substantial; (b) individual variation in PF is large, and differences among individuals are highly consistent across replicate trials, even when important environmental conditions, such as ambient temperature or access to wheels, are changed; (c) PF does not differ between the sexes and is not correlated with body mass or efficiency of digestion; (d) PF is not correlated with food consumption when energy requirement is low, but when the consumption approaches its maximum level, a negative correlation appears; (e) at the level of individual variation, PF is positively correlated with wheel-running activity, specifically with average running speed, but does not differ significantly between the four replicate lines that had been selectively bred for high wheel running and their unselected control lines; (f) PF measured at room temperature is not correlated with nesting-behavior score; PF measured at low ambient temperatures is negatively correlated with the nesting score in females, but not in males; (g) PF is negatively correlated with total litter mass at weaning; and (h) perhaps most interesting, PF is highly correlated between siblings.

4.2. Consequences for measurements of food consumption

The amount of food fragmented and potentially lost in feeding experiments performed in standard cages rather than in specialized metabolic cages [3,5] is in some individuals substantial. Food thus "fragmented" is not necessarily wasted, as it is possible for mice to eat very small pieces of food, and fragmented food may be more likely to be consumed if food availability is limited in an experiment. However, we have no data on whether mice ever go back and eat food that has been previously fragmented.

The variation in PF among individuals is high and the trait is quite repeatable, even when important environmental factors, such as access to running wheels or ambient temperature, are changed. Similar patterns can be found in other species of small rodents, including wild ones, and in tests performed with food provided in feeders rather than on the cage floor (P. Koteja, unpublished data). Thus, food-fragmenting behavior is not peculiar to laboratory mice or to the specific protocols applied in this study.

The consistency of food fragmenting suggests that it may be correlated with other behavioral and physiological traits. Indeed, in males, PF was negatively correlated with the maximum food consumption, and estimation of the latter would be biased if the measurements were performed without collecting leftovers. Similarly, food spillage in rats depended on thiamin level in the diet [1]. Thus, researchers should not ignore leftovers without justification (see also Ref. [3]). In many studies, however, "food consumption" is measured as a simple difference between the amount of food provided and that left in a feeder, and the possible error of neglecting food fragmented and mixed with bedding is rarely discussed [3,4,30,31]. Commendably, some workers label such measurements as "apparent food consumption" (e.g., Ref. [3]).

A remarkable example of the problem comes from a long-term artificial selection experiment, in which laboratory mice were selected for either high or low apparent food intake [3]. After 14 generations of selection, the apparent food consumption was 30% higher in the high-selected lines compared to the low-selected lines. However, 23% of the difference resulted from a difference in food spillage (proportion of food spillage relative to apparent consumption was 7.6% in the high-lines and 3% in the low lines) [3]. This effect jeopardized to some extent further studies of correlated responses to the selection, e.g., in emotionality, hunger drive, or nest building [32], because it is difficult to know whether responses in the traits would result from different food consumption per se or a behavioral profile manifested, in part, as food spillage.

4.3. Inheritance and biological significance of table manners

In quantitative-genetic terms, the coefficient of intraclass correlation for full sibs (ρ_f) is a joint estimator of narrow-sense heritability (h^2) and common environment effects (c^2; with some simplifying assumptions, e.g., of no genetic dominance effects [26]):

$$\rho_f = h^2/2 + c^2.$$

In other words, the coefficient represents a joined effect of additive genetic and "family-culture" (or maternal [33]) sources of variation in the trait. The high intraclass correlations for the proportion of food fragmented (.41 at room temperature and .35 in the cold-exposure trials; Table 1) indicate that the "table manners" in mice appear to be largely determined by genetic factors and/or environmental conditions that individuals experience before weaning from their mothers.

Although we could not decompose the ρ_f coefficient into pure values of additive genetic and other sources of variation, such a high value of correlation between siblings would be very unusual if the heritable component were not substantial (cf. Fig. 7.9 in [34]). As well, significant differences among replicate lines (Fig. 1; Table 1), after as few as 10 generations following their separation, suggest that the variation in food fragmenting is in part genetically based. Finally, results of Hastings et al. [3], who have found differences in food spillage between lines of mice selected for high or low apparent food intake, also provide strong evidence that the trait is heritable in the narrow sense.

Irrespective of its proximate causes, the high within-family correlation in food fragmenting indicates that this aspect of behavior conveys reliable information about the family origin of an individual. Moreover, "table manners" in mice seem to provide information about the quality of the individuals and families. At least among males, mice that fragmented more food achieved lower levels of the maximum food consumption (Fig. 2D), and lost more mass during cold-exposure trials. Thus, "messy eating" indicates a lower physiological performance in some traits that are possibly related to reproductive success (Darwinian fitness) [15,35,36], even if we do not yet know the functional link between the traits. Similarly, food fragmenting was negatively correlated with total litter mass at weaning. Thus, "messy eaters" come from families that exhibited lower reproductive performance, and, if the trait is heritable, may themselves be unattractive partners for reproduction.

If similar correlation of "table manners" with fitness-related traits was present in primates and in early humans, then it would not be surprising if table manners evolved as an important component of establishing social status in human populations. Some sociobiologists would, on principle, root nearly all cultural norms, beliefs, and taboos in animal behaviors (e.g., Ref. [37]). Although we and many others [38] would not advocate such an extreme paradigm, evidence of inheritance (genetic or cultural) of "table manners" in animals, or at least of a component of the table manners, and of their association with fitness related

traits, should not be ignored by those who wish to understand this aspect of human culture.

Clearly, it would be premature to suggest that food-fragmenting behavior of mice is an adequate model for making inferences about human table manners. We do not know what biological phenomenon the proportion of food fragmented represents, and we have found no counsel in the literature. Nevertheless, our results provide some clues.

The first clues are of a negative sort. The percent of food fragmented is independent of body mass and sex. Many other aspects of behavior are strongly correlated with body size and/or differ between the sexes, so the lack of such a correlation is informative. A lack of a correlation between PF and the coefficient of digestibility rules out the possibility that the variation in PF is related to variation in food selectivity. Finally, it also does not seem that food fragmenting represents the same axis of behavior as building nests.

Other clues are revealed by significant correlations with other traits. The amount (not percent) of food fragmented was positively correlated with the amount of food consumed (Figs. 1B,C and 2A). Thus, it seems that food-fragmenting behavior indeed has something to do with eating and is not merely a chewing-anything-at-hand behavior. This justifies our suggestion that the percentage of food fragmented could be regarded as a quantitative measure of "table manners." However, direct, visual observations of behavior will be necessary to confirm the conjecture.

On the other hand, the results revealed similarities of food fragmenting to compulsive, self-reinforcing behaviors, such as wheel running [39]. The percent of food fragmented increased after the mice were deprived of access to wheels (Trial 1 versus Trial 2; Fig. 1D), which suggests that increased food fragmenting could be either a substitute for wheel-running activity or a reaction to novel environment. Although we did not find a difference in PF between the selected and control lines, food fragmenting measured in the trial with wheel access was positively correlated with the amount of wheel running at the level of variation among individuals within lines. This may indicate a shared motivation mechanism, possibly related to dopamine [40], although the lack of difference between selected and control lines may argue against this.

4.4. Limitations of the present study and suggestions for future research

Unlike most "wild" rodents, laboratory mice have evolved for hundreds of generations with typically ad libitum food and hence under conditions of relaxed selection for efficient food consumption. Thus, it might be expected that both the average and the individual variation in the proportion of food wasted by laboratory mice is higher than in wild rodents. A comparative study of food fragmenting, with the information on food habits of the species considered, would increase our understanding of the sources of variation in the behavior. A complementary experimental study could be performed to check whether differences in food fragmenting among individuals within a species are maintained across different types of foods or under limited food availability.

To facilitate measurement of food wasting, mice in the present study were kept in empty cages with food pellets as the only objects available to handle. Mice often fragment any available material, such as carton, straw, or wood to build a nest. Lacking any other material, they might have fragmented food pellets instead. Although we have not found a correlation between nesting scores and PF measured in separate trials on the same individuals, the result does not rule out the possibility because the traits were measured in different environments: the amount of cotton used for nests was measured in cages with wood-shavings as bedding [23].

Because "table manners" in mice clearly vary among families and are apparently correlated with important fitness-related traits, and because similarly large variation in food fragmenting can be observed in other species of rodents including wild ones (Koteja, unpublished data), we believe that our study opens a promising area for further research. The Cinderella work of segregating small pieces of food from feces may be worthwhile.

References

[1] Tagliaferro AR, Levitsky DA. Spillage behavior and thiamin deficiency in the rat. Physiol Behav 1982;28:933–7.

[2] Justice KE, Smith FA. A model of dietary fiber utilization by small mammalian herbivores, with empirical results for Neotoma. Amer Nat 1992;139:398–416.

[3] Hastings IM, Moruppa SM, Bünger L, Hill WG. Effects of selection on food intake in the adult mouse. J Anim Breed Genet 1997; 114:419–34.

[4] Peterson J, Wunder BA. Food sorting by collared lemmings (Dicrostonyx groenlandicus) and prairie voles (Microtus ochrogaster): a cautionary note for digestibility studies. Comp Biochem Physiol 1997; 116A:119–24.

[5] Matsuzawa T, Kitamura K, Iwasaki M. Improvement of a mouse feeder for chemical toxicology testing. Exp Anim 1998;47:123–6.

[6] Batterham RL, Cowley MA, Small CJ, Herzog H, Cohen MA, Dakin CL, et al. Gut hormone PYY3-36 physiologically inhibits food intake. Nature 2002;418:650–4.

[7] Thomas MA, Rice HB, Weinstock D, Corwin RL. Effects of aging on food intake and body composition in rats. Physiol Behav 2002; 76:487–500.

[8] Pelchat ML. Of human bondage: food craving, obsession, compulsion, and addiction. Physiol Behav [special issue] 2002;76:347–52.

[9] Tertil R. Impact of common vole, *Microtus arvalis* (Pallas) on winter wheat and alfalfa crops. EPPO Bull 1977;7:317–39.

[10] Kerley GIH, Erasmus T. What do mice select for in seeds? Oecologia 1991;86:261–7.

[11] Dominguez-Rodrigo M. Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. J Hum Evol 1997;33:669–90.

[12] Dominguez-Rodrigo M. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. Palaeogeogr Palaeoclimatol Palaeoecol 1999;149:373–88.

[13] Morey DF. The early evolution of the domestic dog. Am Sci 1994;82:336–47.

[14] Koteja P, Swallow JG, Carter PA, Garland Jr T. Energy cost of wheel running in house mice: implications for coadaptation of locomotion and energy budgets. Physiol Biochem Zool 1999;72:238–49.

[15] Koteja P, Swallow JG, Carter PA, Garland Jr T. Individual variation and repeatability of maximum cold-induced energy assimilation in house mice. Acta Theriol 2000;45:455–70.

[16] Koteja P, Swallow JG, Carter PA, Garland Jr T. Maximum cold-induced food consumption in mice selected for high locomotor activity: implications for the evolution of endotherm energy budgets. J Exp Biol 2001;204:1177–90.

[17] Swallow JG, Carter PA, Garland Jr T. Artificial selection for increased wheel-running behavior in house mice. Behav Gen 1998;28:227–37.

[18] Garland Jr T. Selection experiments: an underutilized tool in biomechanics and organismal biology. In: Bels VL, Gasc J-P, Casinos A, editors. Biomechanics and evolution. Oxford: Bios Scientific Publishers; 2003. p. 23–56.

[19] Hauschka TS, Mirand EA. The breeder: HA(ICR) Swiss mouse, a multipurpose stock selected for fecundity. In: Murphy GP, Pressman D, Mirand EA, editors. Perspectives in cancer research and treatment. New York: Alan R. Liss; 1973. p. 319–31.

[20] Rice MC, O'Brien SJ. Genetic variance of laboratory outbred Swiss mice. Nature 1980;283:157–61.

[21] Dohm MR, Hayes JP, Garland Jr T. Quantitative genetics of sprint running speed and swimming endurance in laboratory house mice (*Mus domesticus*). Evolution 1996;50:1688–701.

[22] Carter PA, Garland Jr T, Dohm MR, Hayes JP. Genetic variation and correlations between genotype and locomotor physiology in outbred laboratory house mice (*Mus domesticus*). Comp Biochem Physiol A 1999;123:157–64.

[23] Carter PA, Swallow JG, Davis SJ, Garland Jr T. Nesting behavior of house mice (*Mus domesticus*) selected for increased wheel-running activity. Behav Genet 2000;30:85–94.

[24] Henderson ND. Interpreting studies that compare high- and low-selected lines on new characters. Behav Genet 1989;19:473–503.

[25] Sokal RR, Rohlf FJ. Biometry. 2nd ed. San Francisco (CA): Freeman; 1981.

[26] Falconer DS, Mackay TFC. Introduction to Quantitative Genetics. 4th. ed. Essex: Longman; 1996.

[27] Dohm MR. Repeatability estimates do not always set an upper limit to heritability. Funct Ecol 2002;16:273–80.

[28] Hayes JP, Shonkwiler JS. Analyzing mass-independent data. Physiol Zool 1996;69:974–80.

[29] Girard I, Swallow JG, Carter PA, Koteja P, Rhodes JS, Garland Jr T. Maternal-care behavior and life-history traits in house mice (*Mus domesticus*) artificially selected for high voluntary wheel-running activity. Behav Process 2002;57:37–50.

[30] Block E, Kilmer LH, Muller LD. Acid insoluble ash as a marker of digestibility for sheep fed corn plants or hay and for lactating dairy cattle fed hay. J Anim Sci 1981;52:1164–9.

[31] Swallow JG, Koteja P, Carter PA, Garland Jr T. Food consumption and body composition in mice selected for high wheel-running activity. J Comp Physiol B 2001;171:651–9.

[32] Bünger L, MacLeod MG, Wallace CA, Hill WG. Direct and correlated effects of selection for food intake corrected for body weight in the adult mouse. Proc 6th World Congr Genet Appl Livest Prod, Armidale 1998;264:97–100.

[33] Bernardo J. Maternal effects in animal ecology. Am Zool 1981;36:83–105.

[34] Lynch M, Walsh JB. Genetics and analysis of quantitative traits. Sunderland (MA): Sinauer Associates; 1998.

[35] Konarzewski M, Diamond J. Peak sustained metabolic rate and its individual variation in cold-stressed mice. Physiol Zool 1994;67:1186–212.

[36] Hammond KA, Diamond J. Maximal sustained energy budgets in humans and animals. Nature 1997;386:457–62.

[37] Wilson EO. On human nature. Cambridge (MA): Harvard Univ. Press; 1978.

[38] Cooper E. Chinese table manners: you are how you eat. Hum Organ 1986;45:179.

[39] Sherwin CM. Voluntary wheel running: a review and a novel interpretation. Anim Behav 1998;56:11–27.

[40] Rhodes JS, Garland Jr T. Differential sensitivity to acute administration of Ritalin, apormorphine, SCH 23390, and raclopride in mice selectively bred for hyperactive wheel-running behavior. Psychopharmacology 2003;167:242–50.