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Meal patterns of mice under systematically varying approach and unit costs for food in a closed economy

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Abstract

Several field and experimental studies have investigated the behavioral economics of food intake. In the laboratory, operant behavior has been used to emulate cost and to generate demand functions that express the relationship between the price of food and amount consumed. There have been few such studies of motivated food seeking and intake in mice, and none has reported demand functions. Using albino (CD1) male mice, the present study compares food intake and meal patterns across a series of ratio cost schedules. The first experiment examined unit price. A closed economy was used in which the mice were in the test chambers for 23 h/day and earned all of their food via either a nose poke or lever press response under fixed (FUP5, FUP10, FUP25, FUP50), variable (VUP10, VUP20, VUP50), and progressive (PUP1.25, PUP1.5, PUP1.75) unit prices. Mice were run for 4 days at each cost. There were no consistent differences between the first and last day indicating that behavioral adjustments to schedule changes occurred rapidly. When averaged across all price schedules, mice in the nose poke group consumed more food than their lever press counterparts but the overall shapes of the demand curves did not differ between the two operant responses, with intake decreasing as price increased. The number of meals taken per day differed between two meal-defining criteria that we applied, and there were some differences between the types of unit price schedule. In the second experiment, approach cost in the form of nose poke responses were required to activate a response device (lever) on which a fixed unit price for food was in force. These approach and unit costs were varied systematically. Meal number decreased, and meal size increased, with increasing approach cost even though nose pokes accounted for only a small fraction of the total response activity. Thus, meal patterns in mice are sensitive to approach cost while total amount consumed is more sensitive to unit price. These data are discussed in terms of the concept of foraging cost as either a unitary or a multidimensional variable.

Index terms

foraging; nose poke; lever press; ratio schedules; demand function

1. Introduction

Feeding behavior is highly influenced by the economic structure of the environment, and many studies in animals have described how food intake changes as the price or availability of food changes [1–5]. A demand function describes the relationship between the quantity of a

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commodity consumed and its unit price. For food, demand functions have been most usually determined in animals in which price is the time or effort to obtain uniform morsels of food such as small, nutritionally complete pellets. Effort is usually assessed as the number of behavioral responses required per pellet of food earned. These costs or prices are incurred before food is received and are designed to emulate foraging costs incurred during the appetitive phase(s) of feeding.

In contrast, most physiological studies of feeding have analyzed the intrinsic structure of feeding in the absence of economic variables and have focused on controls of meal size and the number of meals taken in a specified period, often 24 h [6,7]. The product of these two parameters determines the total intake over that interval. Thus, while the economic and physiological approaches both study total intake, they do so using different analytical methods and vocabulary. Collier, Hirsch & Hamlin [8] showed that meal size and frequency could be altered profoundly by relatively small costs imposed during the appetitive phase. Importantly, their results showed clearly that two different types of cost, which they termed procurement and consummatory, had quite different effects on meal structure. In the present paper, to better capture this functional difference and clarify that the appetitive phase should instead be viewed as several phases [9], we introduce a different terminology for these two costs (Table 1). We propose that *approach cost* (procurement) is analogous to travel or effort that occurs while food is still spatially and/or temporally distant, and may be associated with a low probability of success. In contrast, *unit cost* (consummatory) is the effort expended once the food item or patch is reached, such as digging in a substrate or hulling seeds; it occurs in proximity to the food and is usually associated with a higher (but not necessarily fixed) probability of success. Because of these differences, and the results of laboratory emulations showing that they have different effects on meal patterns [8], the 'appetitive phase' may in fact be comprised of several phases [9].

Mice (*Mus musculus*) have become an important species for contemporary basic research into physiology and behavior because of their potential for genetic manipulation. The identification of several genes involved in obesity has generated considerable interest in studies of food intake in mice, yet the number of published works that have examined meal parameters is still small and the results are often inconsistent [10]. This may be in part because mice present some procedural challenges. Methods in which discrete small food items are presented sequentially, as in standard operant behavior protocols, are particularly appealing because they minimize food spoiling behavior for which laboratory mice often show a proclivity. A few such studies have appeared in the recent literature [11–15], but most of these used a low and constant unit price, and did not generate demand functions. In our previous studies using operant response methods in lean and genetically obese mice [10,15–17], we studied the effect of changes in approach cost (we and others [8] previously termed this procurement cost) at a constant but low unit price (previously, consummatory cost); those studies showed that meal parameters in mice are highly sensitive to approach, very similar to results reported in rats [8]. Recently, using wild type mice of mixed background strain, we studied a larger range of approach costs in combination with a fixed unit price [17]. That study showed that increasing unit price had only a small effect on the size and frequency of meals whereas increasing approach cost decreased meal number and increased meal size.

The first objective in experiment 1 is to determine demand characteristics for food over a wide range of unit prices using operant response protocols that may be suitable for moderate capacity screening tests of the structure of feeding behavior using closed economies. In addition to the more usual fixed costs we also study variable costs that emulate uncertainty about unit price and progressive costs that emulate depletion of a resource or patch. A second objective is to compare lever press and nose poke responses; this comparison has not to our knowledge been reported in mice, but in rats a nose poke may support faster task acquisition [18]. In Experiment

2, we examine the effects on demand and meal parameters of a wide range of concurrent approach costs and unit prices. This will allow a more thorough analysis than hitherto of the implications of the hypothetical construct 'appetitive cost'.

2. Materials and methods

2.1. Subjects and housing

A total of 24 male albino (CD1; Harlan, Indianapolis IN) mice, initially about 3 months of age were used, 16 in experiment 1 and 8 in experiment 2. CD1 mice were used because they are of mixed origin and have food intake near the middle of a range of strains of mice [19]. For experiment 1, body weights were 39.7 ± 0.7 g (mean \pm SE) at the beginning and 45.8 ± 1.0 g at the end of the study. In experiment 2, the mean weight of the mice was 40.6 g at the beginning and end of the experiments. All animal use in this experiment was approved by the Institutional Animal Care and Use Committee and was consistent with recommendations in the Guide for the Care and Use of Laboratory Animals [20].

For 1–2 weeks between receipt and the start of the experiments, mice were housed individually in polycarbonate cages with Purina 5001 Chow pellets and tap water available ad libitum. The vivarium was temperature ($23 \pm 2^\circ\text{C}$) and humidity (40–70%) controlled, with a 12:12 light cycle (lights on 0700).

During the experiments, mice lived in test chambers for 23 h per day. The mice were weighed daily and kept in empty holding cages during a 1 h cleaning period without food, although water was available. Mice obtained 20 mg nutritionally-complete pellets (Purina Test Diet 5TUM) when they completed a price that was specified by the particular reinforcement schedule that was in effect.

2.2. Operant behavior chambers and general procedure

Behavior test chambers (Med Associates, St. Albans, VT: $13 \times 13 \times 12$ cm), with Plexiglas and alloy walls and stainless steel grill floor, were used for testing. Each was contained within a ventilated, noise attenuating cabinet with the same 12:12 light cycle as the vivarium via a 7 w bulb in a night light fixture run from a 24 h timer. All chambers were equipped with one lever press and one nose poke device. Each was located approximately 2 cm above the floor and situated on either side of a food receptacle. Water was supplied freely from sipper tubes mounted on the wall opposite the food receptacle.

A record of total pellets obtained and number of responses (nose pokes or lever presses) were acquired by MED-PC IV computer software (Med Associates). Computer recordings allowed an analysis of the number of meals and the amount eaten at each meal. Data were accumulated in 15 min (for fixed and variable unit prices) or 5 min (for progressive unit prices) time bins throughout each 23 h period.

2.3. Experiment 1: Fixed and variable unit prices

Mice were divided randomly in two groups of 8, with one group obtaining food pellets by pressing the lever and the other group by nose poking. For a given individual, only one response device was active throughout the experimental protocol. A small cue light was illuminated above the lever at all times, and then nose poke recess has a small light inside. Prior to the main study, in order to habituate mice to the operant chambers and to the novel pellets a 1 h training period was applied with free food available in the food receptacle at no cost. Then, for the next 1–2 days a fixed unit price (FUP) of one response (a fixed ratio 1 schedule) was in effect in which a food pellet was delivered contingent upon one response on the active device. Mice were deemed to have learned the contingency when they earned enough pellets over 23 h to

maintain their body weight; this typically occurred within 2 days. No food deprivation was imposed at any time during the experimental period.

After this training with the response device, mice were exposed a series of reinforcement or food cost schedules each of which was in effect for 4 consecutive days. Mice were subjected to an incrementing series of fixed unit prices or ratios (FUP1, FUP5, FUP10, FUP25, FUP50), where the number refers to the fixed unit price per pellet. They next were tested with variable unit prices or ratios (VUP10, VUP20, VUP50) in which the cost of any given pellet is varied by the computer program to be 10, 50, 100, 150 and 190% of the mean (*viz.*: 1, 5, 10, 15, 19 for VUP10; 2, 10, 20, 30, 38 for VUP20; and 5, 25, 50, 75, 95 for VUP50) and with the constraint of equal probability of occurrence.

The final phase of testing used progressive unit prices or ratios (PUP1.25, PUP1.5, PUP1.75) in which the number of responses required for the next ($n+1$)th pellet in a series was calculated using the formula $P_{n+1} = P_n \times 1.25$ (PUP.25), $P_{n+1} = P_n \times 1.5$ (PUP1.5), or $P_{n+1} = P_n \times 1.75$ (PUP1.75), where P_n = price or response requirement for the n^{th} pellet in a meal. The result was rounded to the nearest integer (Table 2). The mean price per pellet within a meal escalates as the meal gets larger. When 15 min elapsed without a response the price was reset to the initial value (one) of the schedule. At the end of the PUP series we ran an additional block of PUP1.5 using a 30 min reset condition instead of 15min, but these data will not be presented in detail.

2.4. Experiment 2: Concurrent approach cost and unit price

Eight naïve mice were tested in a concurrent schedule of approach cost (AC) and unit price (UP). Both lever and nose poke response devices were present and active. For all mice, nose poke was designated as the approach cost response and lever press as the unit price response. Following separate initial training at FUP1 with both lever and nose poke devices, mice were tested in a series of fixed unit prices (FUP5, 10, 25, 50, 100) with an approach cost of 5 (AC5), then the series was repeated with AC25 and then with AC100. After completion of the designated approach cost on the nose poke device, a cue light was illuminated above the lever indicating its availability for food responding at the prevailing unit price. Subsequently, whenever 15 min elapsed without a response on the lever, the lever was inactivated and the cue light extinguished. Total pellets and responses were recorded every 15 min throughout 23 h sessions.

2.5. Data analysis

The raw data showed the number of responses emitted each 23 h period (1380 min) and the number of pellets earned with a resolution of 15 min (FUP and VUP) or 5 min (PUP) intervals in Experiment 1, and 15 min in Experiment 2. Non-responding (non-eating) episodes were defined as time bins with zero pellets received. The data stream from Experiment 1 was then separated into meals using either 15 min (at least one zero separating non-zero bins) or 30 min (at least two zeros separating non-zero bins) minimum criteria. Only the 15 min inter-meal interval (IMI) criterion was used for analysis of the PUP data (because the reset was 15 min) and for Experiment 2. It is important to note that, on average, an animal will have stopped in the middle of the interval preceding a zero entry and will have started eating in the middle of the interval following a zero entry; thus, our 15 min criterion in fact defines an average minimum IMI of 30 min, but with a range from 15–45 min. After the numbers of meals per day were determined for each mouse, the mean meal size was derived by dividing the number of total pellets by the number of meals for each day. With only one exception, no statistical difference was found across the 4 days of each schedule for either total intake or the meal parameters. Thus, for each mouse, the mean number of meals, total pellets earned and meal sizes were averaged across the 4 days of each cost or reinforcement schedule. These data were

then treated using a repeated measures analysis of variance (ANOVA; SPSS) with the operant (nose poke vs lever press) as a between-subject variable and the cost schedules as a within-subject variable. For the analyses within each ratio schedule type (FUP, VUP and PUP), one-way ANOVAs were used. Follow up Bonferroni tests were employed to assess specific differences; in all cases, $p < 0.05$ was considered significant.

3. Results

3.1. Experiment 1: Fixed and variable unit prices

We [10,17] have previously reported that mice often earn far more pellets than they consume at low unit prices because they spill excessively and intake is impossible to measure accurately. This was also true in the present study, so data from the FUP1 phases were not analyzed. For all of the other phases, spilled pellets found beneath the cage floor were subtracted from the total earned; in every case spillage was small (typically <5% of the number earned). The meal numbers, meal sizes and the number of pellets consumed did not differ significantly across the 4 days that a given schedule was in force with the exception of the number of pellets consumed at FUP10 [$F(3,57) = 8.19; p < 0.01$]. Thus, to reduce the data for presentation, intakes or meal parameters were averaged across the 4 days to give a single mean value for each mouse at each price, and a group mean (\pm SEM) computed from the individual means.

When averaged across schedules, mice in the nose poke group consistently consumed approximately 10% more pellets than those in the lever press group [$F(1,173) = 13.09; p < 0.01$], although the initial body weights and average weight change across the experiment did not differ between the groups.

3.1.1. Fixed unit price (FUP) schedules—The numbers of pellets taken in the FUP phases are shown as the demand functions in the left panel of Figure 1. Across all four FUP schedules, mice in the nose poke group consumed more pellets than those in the lever press group [$F(1,61) = 7.82; p < 0.01$]. For both lever press and nose poke groups, the number of pellets earned per day differed significantly across the four FUP schedules, with fewer taken at FUP50 than at FUPs 5, 10 or 25 (Figure 1) [$F(3,31) = 2.89$ and $4.47; ps < 0.05$ for lever press and nose poke groups].

The number of meals and corresponding meal sizes during the FUP series are shown in Figure 2. Meal numbers were approximately 50% higher using the 15 min compared with the 30 min IMI criterion, and meal sizes were correspondingly smaller. When the data from both response types were combined, meal number declined slightly across the FUP series using both the 15 and 30 min IMI criteria [$F(3,57) = 5.57$ and $3.52; ps < 0.01$ and < 0.05 , respectively]. In contrast, meal size did not change across the FUP series. It follows that the demand functions (Fig 1) are determined more by meal frequency than meal size.

3.1.2. Variable unit price (VUP) schedules—The numbers of pellets taken in the VUP phases followed the demand functions shown in the middle panel of Figure 1. For both lever press and nose poke groups, the total pellets earned per day differed significantly across the three VUP schedules, with fewer pellets taken at VUP50 than either VUP10 or VUP20 (Figure 1) [$F(2,23) = 10.19$ and $6.70; ps < 0.01$ for lever and nose poke groups respectively]. The shapes of the demand functions did not differ between FUP and VUP series, indicating that the degrees of uncertainty represented in these VUPs were insufficient to alter the overall structure of feeding.

The number of meals and the corresponding meal sizes during the VUP series were similar to those shown for the FUP series (Figure 2), and so will not be presented.

3.1.3. Progressive unit price (PUP) schedules—The numbers of pellets taken in the PUP phases followed the demand functions shown in the right panel of Figure 1. Across all PUP schedules, mice in the nose poke group consumed more pellets than those in the lever press group [$F(1,61)=6.64$; $p < 0.05$]. Total pellets earned per day differed across the three PUP schedules for only the lever press group, with more pellets taken at PUP1.25 than at PUP1.5 or PUP1.75 (Figure 1) [$F(2,23)=6.93$; $p < 0.01$].

The number of meals and the corresponding meal sizes during the PUP series are shown in Figure 3. Because the reset time was 15 min, only the 15 min IMI criterion was applied. Meal number averaged 27 per day and meal size was reciprocally related to meal number. The total number of responses per day is shown in the bottom panel of Figure 3. By dividing the total presses by the pellets earned, the mean price per pellet at PR1.25 was 4.1 and 4.4 for lever press and nose poke groups; from Table 2, this should correspond to 11–12 pellets/meal, consistent with the observed result (Figure 3). Corresponding mean prices for PR1.5 were 11.0 and 12.2, for meal sizes of 9–10 pellets. Corresponding mean prices for PR1.75 were 19.7 and 21.2, for meal sizes of about 9 pellets. Thus, mean meal size declined slightly across the PR while the mean price paid per pellet increased approximately 5-fold.

The comparison between 15 min reset condition and the subsequent 30 min reset condition at PUP1.5 did not result in significant changes in meal pattern. However, total number of pellets earned per day did was higher in nose poke than lever press groups (Fig 1 for 15 min reset; 290 vs 220, $P < 0.01$, for 30 min).

3.1.4. Comparison between schedule types—Daily intake differed significantly between the three types of unit price schedule. Mice took more pellets per day under PUP schedules compared to FUP or VUP schedules [$F(2,171)=17.85$; $p < 0.01$]. However, body weight may have been a factor in this effect, as will be presented in section 3.1.5. Mice showed larger meal numbers on PUP than FUP or VUP schedules when the 15min IMI criterion was used [$F(2,171)=233.99$; $p < 0.01$].

3.1.5. Body weight—The main part of the experiment took several weeks to complete and mice gained some weight over this period of time. It is thus relevant to examine the extent to which changes in food intake, at least between schedule types in experiment 1 (Fig 1), was due to changes in body weight. During the first price block of each schedule type (*viz* PUP5, VUP10, PUP1.25), the mean intakes for the lever pressing group were 232, 290 and 312 pellets (see Fig 1) and their corresponding mean body weights were 37.8, 42.0 and 47.2 g. The linear correlation coefficient for these points is $r=0.95$ with a slope of 8.34 (pellets per g body weight increase). A similar but weaker relationship was evident in the nose poke group.

3.2. Experiment 2

The results are shown in Figure 4 and Figure 5. The left panel of Figure 4 shows the mean number of lever presses per day as a function of unit price (UP) and concurrent approach cost (AC). This log-log plot is approximately linear, and indicates that up to 20,000 presses per day are well within the work capacity of mice. The right panel of Figure 4 shows the number of nose pokes (the approach response) per day as a function of UP and the concurrent AC. As was expected, the total number of approach responses per day increased as the AC ratio increased, but not in a proportional fashion: the average number of nose pokes at AC25 and 100 were approximately 2x and 6x those at AC5, respectively.

Food demand curves under these schedules are shown in the top panel of Figure 5. Demand declined only slightly at the highest unit prices (UP50 and 100), and this was significant only for the lowest approach cost (AC5) [$F(4,35)=8.97$; $p < 0.01$] during which the mice lost ~7% body weight.

The corresponding numbers of meals per day are shown in the middle panel of Figure 5. Meal number differed significantly as a function of AC when analyzed separately for each UP (*all* $P_s < 0.01$). Mean meal size (Figure 5, bottom panel) showed generally reciprocal changes, and meal size differed significantly as a function of AC under each UP ($P_s < 0.01$ except $P < 0.05$ for FUP100).

Some individual variability was noted, and the results from two mice are shown in Figure 6. One mouse (m2) showed very little change in number of meals per day (or meal size, not shown) across the FUP range, but showed a significant reduction in meal number at AC100 compared with AC5. Another mouse (m4) showed great change in meal frequency with change in FUP, but only a small effect of changing AC. Most other mice showed intermediate patterns, so generating the means in Figure 5.

Meal parameters were analyzed across the four days that each schedule was applied. No statistical significance was found for meal sizes across days except at AC5FUP100 when mice ate smaller meals the first day compared to the three subsequent days at this schedule [$F(3,82) = 4.67$; $p < 0.05$]. This trend was present, although not significant, in all of the schedules.

4. Discussion

The main purpose of the present study was to design an instrumental response protocol that would allow us to conduct a systematic analysis of demand functions and meal patterns in mice as a function of effort, including an explicit comparison of two response types. Averaged across unit price schedules, the nose poke response group had a slightly higher food intake than the lever press group, but both groups changed intake comparably across the various unit price schedules, suggesting that nose poke and lever press may be used interchangeably as cost devices for the study of food demand. These findings agree with studies in rats comparing nose poke and lever press operants in which acquisition of the nose poke response often occurs more rapidly, but response rates in trained rats are usually comparable [21,22]. In mouse studies, a nose poke operant might also be more useful if minimal training time is a consideration.

The demand for food was comparable in experiments 1 and 2 and, at the ratios used, was relatively constant except at the highest unit prices (Figure 1 and Figure 5). Presumably, had we gone to higher prices, a further decline in demand would have occurred as it does in rats [3], but we were limited in our ability to do this because of restrictions on maximal weight loss (~10%) due to welfare considerations. In Experiment 1, food demand increased across the phases of the study as a linear function of increase in body weight. This linearity may be in part a reflection of the restricted range of ages and weights represented in this study, but within these limits a linear correction factor appears to be adequate.

Similar to food demand, which varied relatively little (~20%) across the range of unit prices imposed in Experiment 1, meal number and meal size were also relatively constant across the 10-fold range of FUP costs (Figure 2). However, the meal parameters were sensitive to the IMI criterion (Figure 3), with overall means of 15.1 and 10.3 meals/day (collapsed across all FUPs and both responses) at the 15 and 30 min IMI criteria, respectively. The corresponding mean meal sizes were 16.4 and 24.0 pellets. Recall that the 15 and 30 min IMI criteria based on zero pellets obtained in 1 or 2 consecutive 15 min intervals represent true average intervals of 30 and 45 min, respectively, and so the number of meals appears to be reciprocally related to the minimum IMI criterion. We additionally made a preliminary examination of the distribution of meal sizes for a subset of the data, namely FUP5 with IMI 15 min. The fraction of meals in bin sizes of 1–5, 6–10, 11–15, 16–20 pellets were all similar (~20%) with a sharp decline at larger sizes so that <5% of all meals were >30 pellets. Thus, there are not an excessive number of very small meals, and so we did not impose a minimum criterion.

As we have noted previously [10], meal numbers that have been reported by different laboratories for free-feeding mice vary up to 5-fold. An updated list of meal parameters that have been reported in mice is presented in Table 3. The high variability between studies contrasts with relatively good convergence among studies measuring meal numbers in rats [6,23–25]. Closer analysis of feeding, as well as the relationship of activity or rest periods to eating in mice [26] will be needed to better understand these discrepancies. The absolute meaning of a particular meal pattern in mice may be unclear at the present time, but differences in patterns across conditions using a uniform criterion should be meaningful.

In the PUP series in Experiment 1, because the reset criterion was 15 min, then only the 15 min IMI criterion was used for meal analysis. The number of meals was about 50% higher than in the FUP study, indicating that the PR does cause mice to show a breaking point at which they cease responding; this may be seen in the relatively small error bars on meal size at the higher PR schedules (Fig 3). Since 80% of all meals in the FUP series were 20 pellets or less, then only the two higher PR schedules may have been effective in altering mean meal size. One strategy to minimize average unit price on a PUP schedule would be to take many small meals separated by the minimum reset time. Optimal application of this strategy was not evident in the data. In order to maintain the same unit price across the PR series, mice should have decreased meal size about 2-fold (cf Table 2), whereas the data show little change (Fig 3).

A consistent finding in the present study was that, for each price schedule, the intake and meal pattern did not differ across each of the four days of each schedule, with the single exception of FUP10. The statistical significance at FUP10 was accounted for entirely by a lower intake on the first day, so we believe that mice had a temporary difficulty adjusting to this higher price since this was the first time it had been encountered. With this exception, mice adapted within the first day of a new schedule, although this may in part be due to increased experience with escalating costs.

To examine further the rapidity of adaptation to a new schedule, mice from experiment 1 subsequently were run through the schedules in the same price sequence as before, but with only one day at each schedule. The results, both in terms of food demand and meal parameters, were similar to those in the 4 day study. This could be because these mice were by now experienced with changing price schedules. We then studied 8 naïve mice run through the same price sequence with 1 day at each schedule. Their intake during the initial FUP series was lower than in the subsequent VUP or PUP series, presumably because they were still adapting to price schedules. In the VUP and PUP series the intakes were similar in profile to those shown in Figure 1. For example, from Figure 1 the intake at VUP50 was 73% that at VUP10; the corresponding number in the naïve mice was also 73%. In the 4 day groups (Fig 1), intake at PUP1.75 was 88% that at PUP1.25; the corresponding number in the naïve group was 78%. Thus, in both experienced and relatively naïve mice, the adaptation to different price schedules appears to be very rapid. This agrees with a report by Raslear *et al* [27] in which rats showed a stable relationship between food consumption and operant price for food on each of seven consecutive days after a change in price.

In experiment 2, in which concurrent approach and unit costs were imposed, food demand again varied relatively little across the range of parameters studied (Figure 5). In contrast, meal number and meal size were profoundly affected by approach cost. This is illustrated in Figure 7. The left hand panels of Fig 7 show the meal size and number data redrawn from figure 5 as a function of unit price, and include for comparison the comparable data from Experiment 1 (lever press group, 15 min IMI criterion) when no approach cost was required. Meal numbers per day (top panel) were relatively invariant across the unit prices, and the meal sizes (bottom panel) were likewise reasonably constant except at the highest unit price when demand fell. In contrast, the right hand panels show the mean meal numbers and sizes (collapsed across unit

prices 5 through 50) as a function of the approach cost. Meal number and size show a 2-fold and reciprocal change across the range of approach costs. Further, depicted in Figure 7 as hatched circles, are mean data from experiment 1 in which no approach cost was in force. This graph suggests that zero approach cost may be regarded as an extrapolation of the functions shown; the zero approach cost points fall on the log-linear regressions at extrapolated approach cost nose poke costs of about 1–2 per meal. It should be noted that the maximum number of approach responses emitted in this experiment was about 1000 nose pokes, whereas the maximum number of consummatory or unit prices emitted was about 20,000 lever presses.

We also noted some individual variability in Experiment 2 (Fig 6). Thus, one mouse (m2) can be considered to have “learned” the contingency well, by varying meal number with approach cost while maintaining invariant meal size across FUP change, similar to rats with only FUP in Experiment 1 (Fig 2). In contrast, another mouse (m4) seems to have been confused, and its meal pattern was driven more by the FUP than by the imposed approach cost. It would be interesting in the future to examine whether more extensive pre-training would lead to more uniform results, or whether this result indeed reflects a true individual variation in response to a complex foraging schedule.

Even though the approach cost appears to be a trivial part of the overall food cost, it had a profound effect on meal patterns. Absolute approach cost may be important to the subject not only as responses but also or instead as elapsed time. The amount of time spent in the two responses was not measured in this study, but an average of 600 nose pokes per day spent to initiate 6 meals (data derived from Figure 4 and Figure 6) would very likely account for less than 2 min of total approach response time per meal. More detailed temporal analysis will be needed to assess further the contribution of elapsed time on meal parameters. Consistent with this analysis, time itself has been shown to be an effective cost parameter in rats [29,32]. Overall, these results are similar to previous results in rats [28,29] and mice [10,17]. One of these studies [10] did not vary approach cost. The other study [17] examined a limited range of both approach costs and unit prices in a mixed strain of mouse, and used slightly different analytical criteria than the present, but the results were quantitatively very consistent with the present data. Although it would be hard to determine which of the meal defining IMI criteria is more appropriate for analysis of meals in this strain of mice, the 15min IMI criterion produced results consistent with several earlier studies (Table 2). Strain differences cannot be excluded as a source of at least some of the variance [19,30,31].

Lastly, these data give further support to the idea that foraging or appetitive cost should not be considered a unitary phenomenon [9], but instead consists of at least two phases that affect behavior quite differently. We have introduced the terms approach cost and unit price to make this distinction clear insofar as it relates to behavioral economics, but presumably there are as yet unknown underlying neural structures that support such a distinction.

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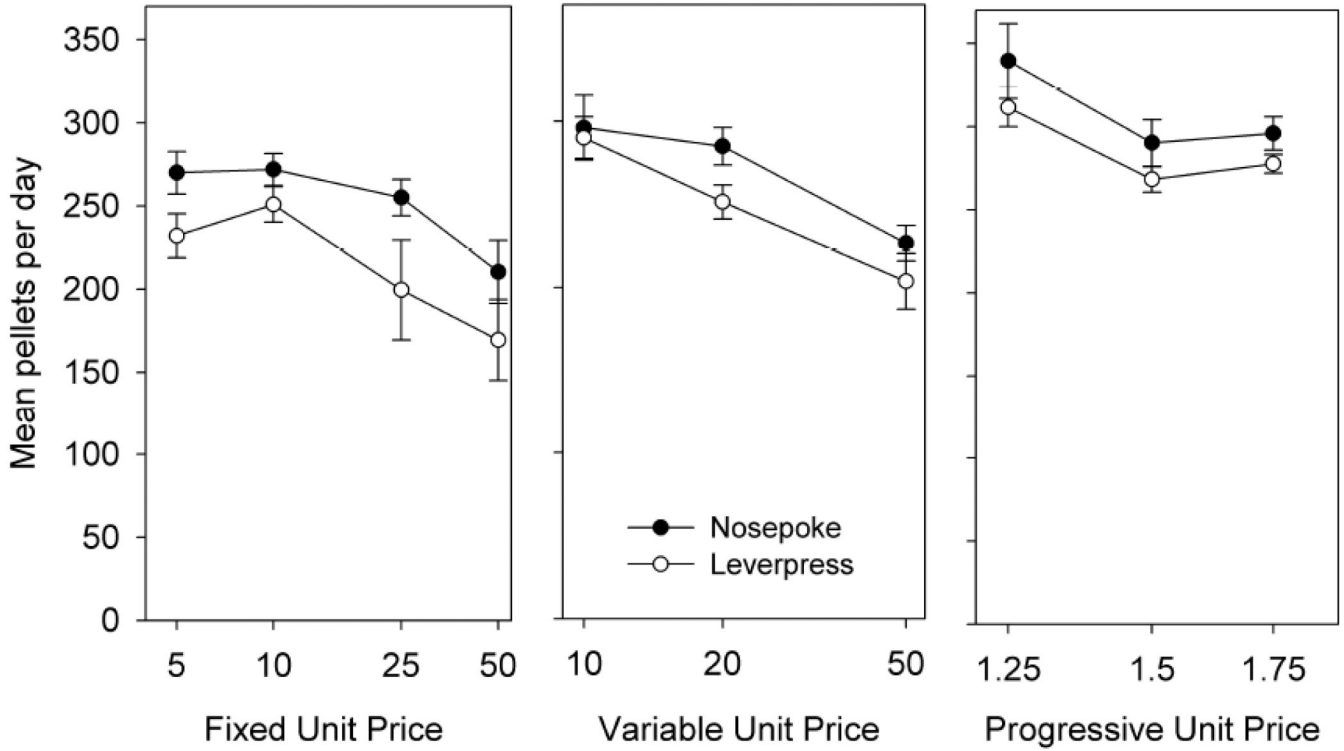


Figure 1. Mean (\pm SEM) number of pellets taken per day as a function of unit price under fixed (left panel), variable (middle panel), and progressive (right panel) ratio schedules. Data are for separate groups ($N_s=8$) required to emit either nose poke or lever press responses to obtain food, but for the same animals is left-to-right progression across costs and schedules. Note that the fixed price axis is scaled logarithmically.

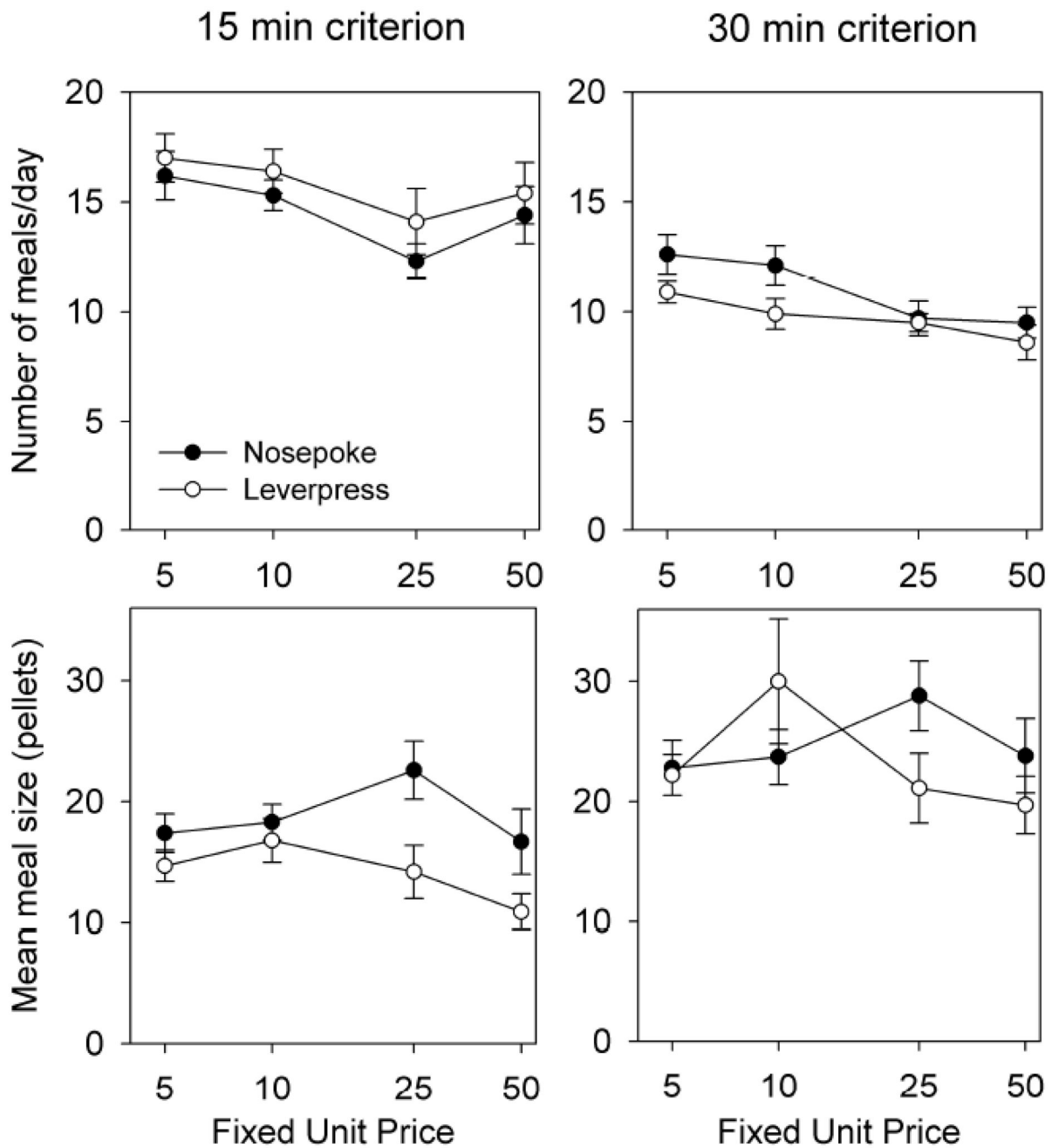


Figure 2. Mean (\pm SEM) number of meals per day (top panels) and corresponding mean meal sizes (bottom panels) during four fixed unit price schedules in groups of mice ($N_s=8$) required to emit either nose poke or lever press responses to obtain food. The left panels show the data analyzed using a 15 min inter-meal interval criterion, while the right panels show the same data analyzed using a 30 min criterion.

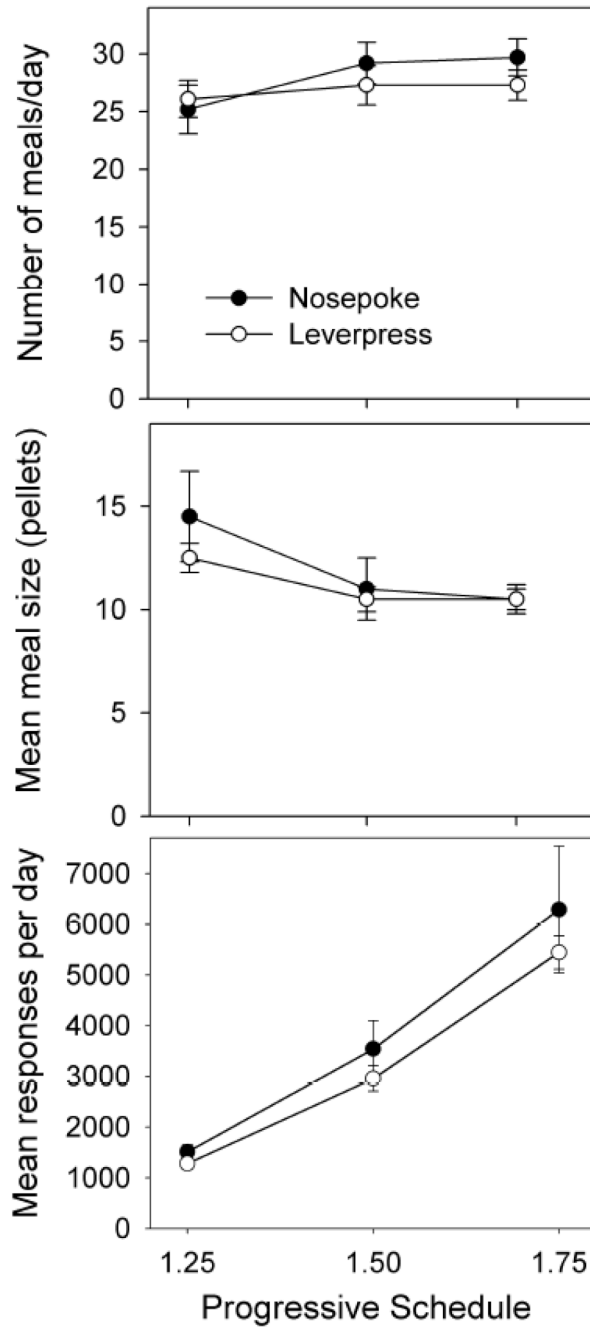


Figure 3. Mean (\pm SEM) number of meals per day (top panel), mean meal size (middle panel) and responses emitted (bottom panel) during three progressive unit price schedules (Table 2) in groups of mice ($N_s=8$) required to emit either nose poke or lever press responses to obtain food

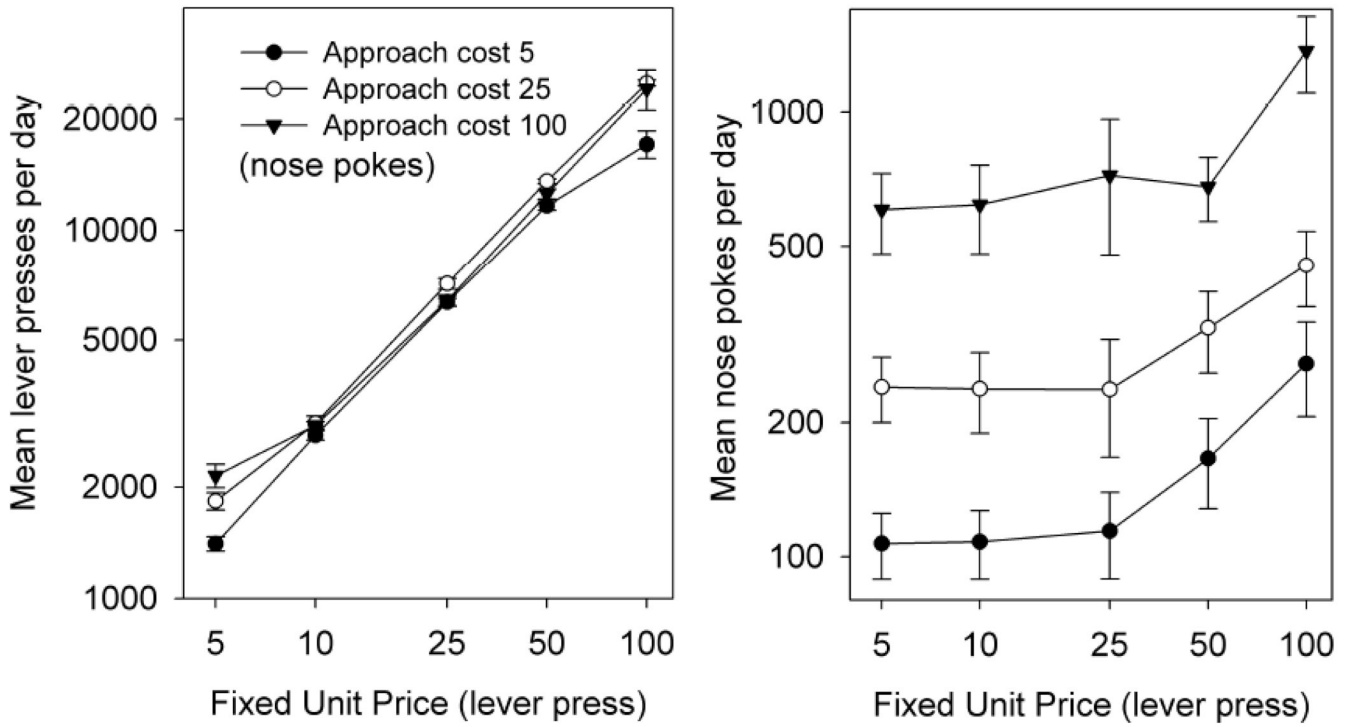


Figure 4. Mean (\pm SEM) number of lever presses (left panel), the unit price response, and nose pokes (right panel), the approach response, as a function of varying unit prices and approach costs (N=7). Note that these are both log-log scaled plots.

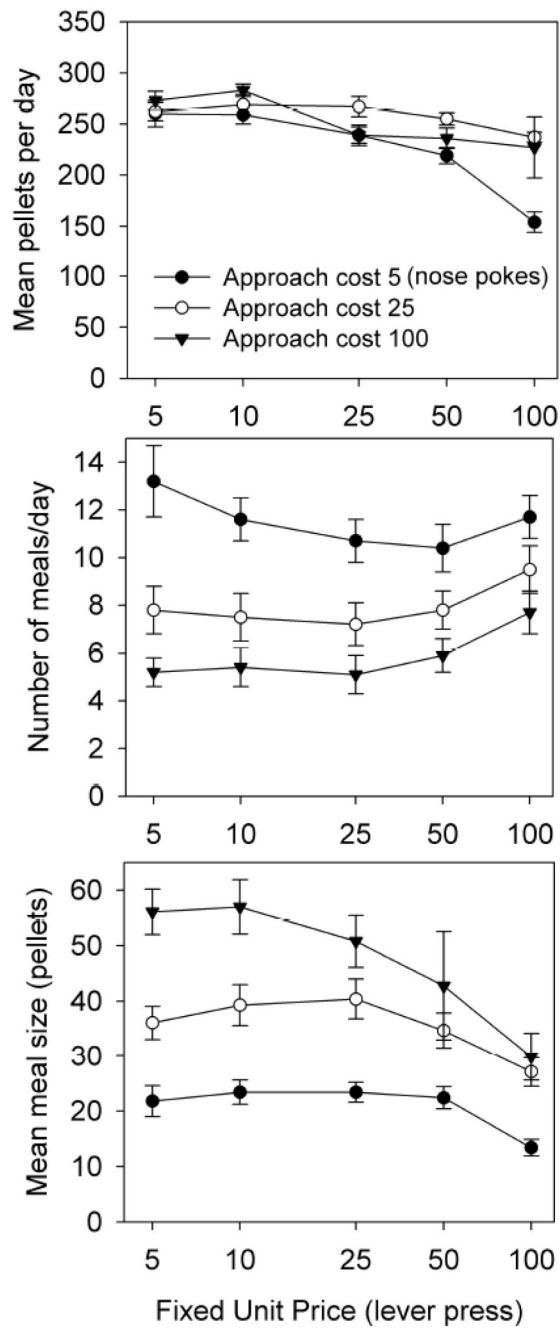


Figure 5. Mean (\pm SEM) food intake (top panel), meals per day (middle panel), and meal size (bottom panel) of 7 mice in three approach cost and five fixed unit price conditions (log scale).

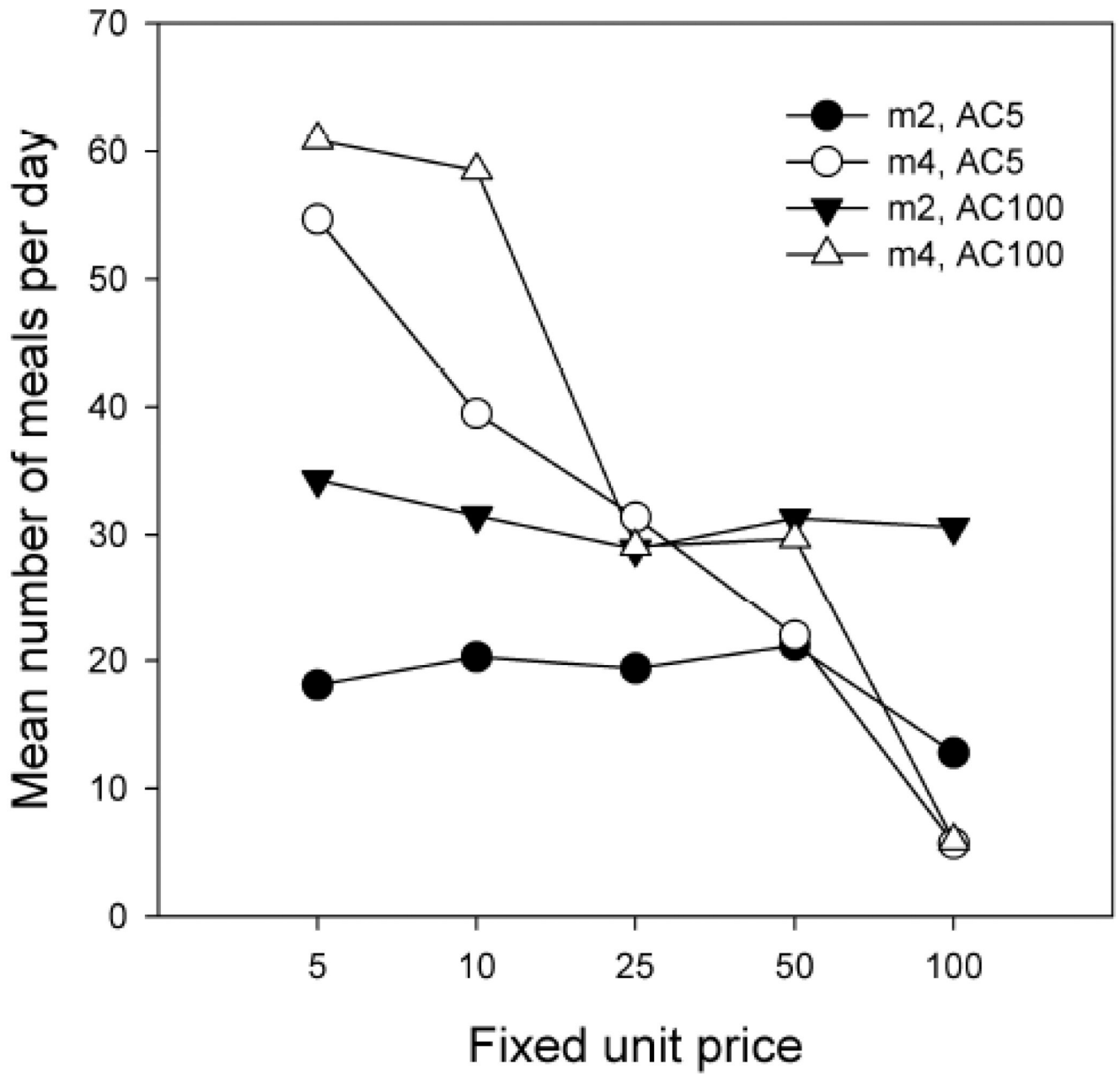


Figure 6. 4-day mean number of meals taken per day by two mice (m2, m4) during the five fixed unit price conditions at the two extreme approach cost conditions (AC5, AC100).

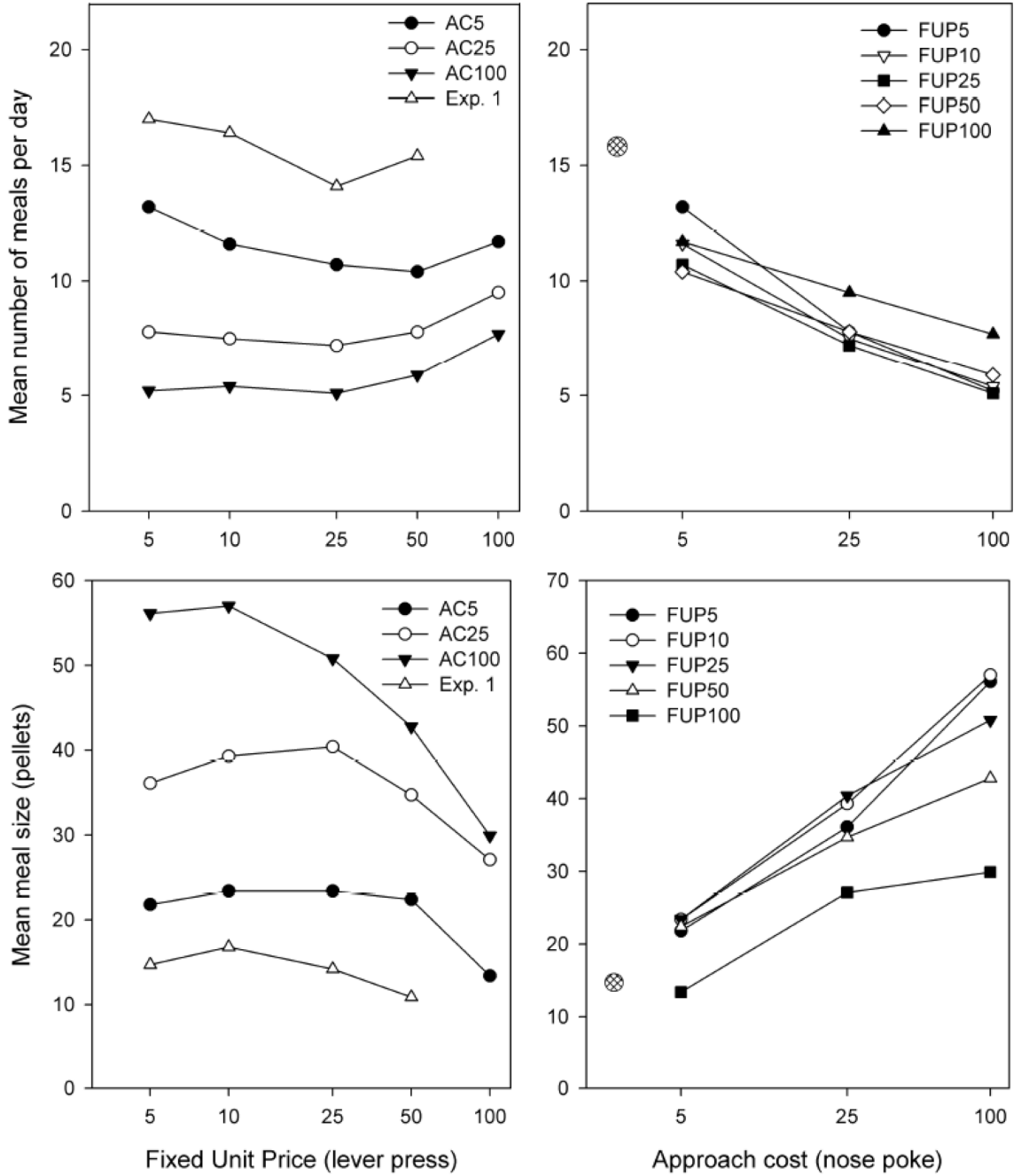


Figure 7. Left panels: Mean meal numbers (top panels) and meal sizes (bottom panels) from Experiment 1 (data from Fig 2, approach cost AC=0) and Experiment 2 (data from Fig 5, AC=5, 25, or 100) as a function of the fixed unit price in lever presses. Right panels: mean meal numbers and sizes in Exp. 2 (data from Fig 5) and Experiment 1 (large round circle, shown at a small but non-zero cost) as a function of approach cost in nose pokes.

TABLE 1
APPETITIVE COSTS, ALTERNATE NAMES, AND DEFINITIONS

Term used in this paper	Alternate term(s)	Functional description or examples
Approach cost (AC)	Procurement cost Anticipatory activity Travel cost Distal foraging	Searching for a remote food source. May have low probability of success. May include moving food to a hoard.
Unit price (UP)	Consummatory cost Ratio requirement Proximal foraging	Effort in proximity to food such as hulling seeds or nuts; picking fruit. Relatively high probability of success.

Table 2

Properties of Progressive Ratio schedules

Pellet number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14
PR 1.25														
Successive price	1	2	2	2	2	4	4	5	6	8	10	12	15	19
Cumulative price	1	3	5	7	9	13	17	22	28	36	46	58	73	92
Mean price	1	1.5	1.7	1.8	1.8	2.1	2.4	2.7	3.2	3.6	4.2	4.8	5.6	6.6
PR 1.5														
Successive price	1	2	2	3	5	8	1	17	26	38	58	86	130	195
Cumulative Price	1	3	5	8	13	21	32	49	75	113	171	257	385	578
Mean Price	1	1.5	1.7	2.0	2.6	3.5	4.6	6.1	8.3	11.3	15.5	21.4	29.6	41.3
PR 1.75														
Successive price	1	2	3	5	9	16	29	50	88	154	269	471	825	nc
Cumulative price	1	3	6	11	20	36	65	115	203	357	626	1097	1923	nc
Mean Price	1	1.5	2.0	2.7	4.0	6.0	9.3	14.4	22.6	35.7	56.9	91.4	148	nc

Note: Successive price refers to the number of responses required for consecutive pellets within a meal. Cumulative price are the total responses during the meal to that point. Mean price is cumulative price divided by pellet number. Nc= not calculated.

Table 3

Summary results from previous studies of meal patterns in mice

MOUSE STRAIN	RESPONSE	DIET	# OF MEALS/DAY (CRITERION)	REFERENCE
Small `S` and large `L` inbred	Overhead door panel	Powdered rodent chow	12 (5min)	Petersen and McCarthy [33]
SWR/J	Recess at the floor level	Powdered rodent chow	36 (5min)	Gannon et al [34]
C57BL/6J (lean and ob/ob)	Sipper spout in cage	Liquid diet EC116	50(male);30(female) (1 and 5min)	Strohmayr and Smith [35]
C57BL/6J	Lever press	20mg pellets	~8 (24 h food access fixed price schedules)	Vaughan and Rowland [36]
C57BL/6J (lean and ob/ob)	Lever press and food receptacle	20mg pellets	2–10, function of procurement/approach cost (10min)	Vaughan and Rowland [10]
129/B6 (wild type for BNDF +/-)	Pellet removal from trough	20mg pellets	~12 (18 hr food access)	Fox and Byerly [13]
129/B6 (wild type for BNDF +/-)	Liquid diet from 0.02ml dipper	Isocal-High fat liquid	~15 (18 hr food access)	Fox and Byerly [13]
129/B6 (wild type for MC4R +/-)	Lever press and food receptacle (approach cost)	20mg pellets	2–7, function of procurement/approach cost (10min)	Vaughan et al [15]
129/B6 (wild type for MC4R +/-)	Lever press and food receptacle (progressive ratio)	20mg pellets	25–50, function of reset condition (20 vs 3min)	Vaughan et al [16]
129/B6 (wild type for MC4R)	Lever press or nose poke , food receptacle (approach and unit price costs)	20 mg pellets	10–35 depending on imposed costs and analytic criterion	Chaney & Rowland [17]