EFFECTS OF ECONOMY TYPE, REINFORCER MAGNITUDE, AND NICOTINE ON THE ESSENTIAL VALUE OF FOOD IN RATS

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
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To my Mom, who has always supported me

ACKNOWLEDGMENTS

I would like to thank the chair and members of my committee for their mentoring and patient supervision. My lab members also warrant acknowledgment for their hard work running the lab. I would also like to thank my parents for their unwavering support. Finally, I would like to thank Brian Kangas.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
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EFFECTS OF ECONOMY TYPE, REINFORCER MAGNITUDE, AND NICOTINE ON THE ESSENTIAL VALUE OF FOOD IN RATS

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The Exponential Demand Equation proposed by Hursh & Silberberg (2008) included a new quantification of the "essential value", or rate of change in elasticity of demand, of a good. The model predicts that essential value should remain constant across absolute demand level shifts but may change as a function of motivational operations. In Experiment 1, rats' demand for food across a sequence of fixed ratio schedules was assessed during open and closed economy conditions, as well as during one- and two-pellet per reinforcer delivery conditions. The Exponential Demand Equation was fitted to the relation between fixed ratio (FR) value and the logarithm of the absolute number of reinforcers. Estimates of the rate parameter α, the measure of essential value, were compared across conditions. The αs were equivalent across magnitudes during the closed economy, as predicted. The αs showed a slight decrease in essential value across magnitudes during the open economy.

In Experiment 2, the same subjects were administered nicotine via a subcutaneously implanted osmotic minipumps at a dose of 3 mg/kg/day and exposed to both the one- and two-pellet conditions under a closed economy. Estimates of essential value were

more consistent with baseline closed economy values (from Experiment 1) when nicotine was administered during the one-pellet magnitude condition. During the two-pellet magnitude condition essential value increased compared to baseline for three of four subjects. The data from the present experiments provide further evidence for the utility of Equation 1 as a tool for quantifying the rate of change in elasticity of a good apart from changes in absolute level of demand.

CHAPTER 1
INTRODUCTION

Behavioral economics has become an influential theoretical framework by employing the strong empirical tradition of behavior analysis to examine the impact of economic variables on individual behavior (Hursh, 1980; 1984; 2000; Madden, 2000). Behavioral economics has been used to empirically model the effects of such economic variables as the presence of a substitutable or complementary good on responding for a primary good, changes in income, and changes in the price of the given unit of a good (Hursh, 1978; Hursh et al., 1988; Bauman et al., 1996; Foster, Blackman, & Temple, 1997). In addition to empirical work, behavioral economics has also been used to understand and promote behavior change related to socially relevant behavioral problems, perhaps most successfully in individuals suffering from drug addiction (Bickel, Marsch, & Carrol, 2000; Bickel & Vucinich, 2000; Johnson & Bickel, 2003).

In behavioral economics, the primary relationship of interest is between the cost of a good and how much of it is consumed in a given time period. When plotted in graphical space, this relation describes a demand curve. Demand curves describe the relationship between cost and consumption of different commodities in both humans and animals, including demand for food, water, money, and drugs of abuse (Hursh, 1978; 1980; 1984; Hursh & Winger, 1995; Degrandpre et al., 1993; Madden, 2000). All demand curves share certain properties. They are downward-sloping (Madden, 2000): at some point along the curve, consumption begins to decrease as price increases. The rate at which the demand curve slopes downward differs across goods, and this property of the relationship between a good and the behavior that it maintains is termed elasticity (Hursh, 1980). Elasticity can be thought of as measure of a good's current utility, as consumption of goods that are necessary or useful will not decrease as steeply with increases in price as goods that are less necessary. Traditional economic descriptions of elasticity were quantified by computing the slope of the curve at each price point, with slopes of less than -1 deemed inelastic, and slopes of more than -1 deemed elastic. Figure 1 presents hypothetical examples of elastic and inelastic demand. An example of relatively inelastic demand is given by the curve representing food consumption across a range of prices, which declines gradually as price increases. An example of elastic demand is given by the dashed line representing sucrose-flavored water, which declines steeply as price increases (Hursh, 1978; Bauman et al., 1986). Note that computing elasticity by taking the slope of each curve at points marked A and B on the graph would lead to different interpretations of elasticity along the functions.

Another feature of demand curves is the level of demand, or the absolute height of the demand curve. The level of demand may shift up or down without altering the elasticity and this type of shift is often produced by scalar value changes in the good. Scalar value changes are changes in the size, dose, potency, delay, etc. of a reinforcer (Hursh, 2000). Figure 2 presents a hypothetical example of this type of shift. The solid line depicts responding for food deliveries that result in one pellet of food, while the dashed line shows the effects of increasing the size of the reinforcer to two pellets, which shifts the level of demand down while retaining the shape of the function, that is, the degree of elasticity. Until recently, however, the property of elasticity could not be described in one parameter that accurately reflected the shape of the demand function across all price points; this hindered effective comparison of changes in elasticity (Hursh, 1984; 2000).

Hursh & Silberberg (2008) developed a new equation in an attempt to quantify elasticity using a single parameter. The model proposed by Hursh & Silberberg is the Exponential Demand Equation:

$$\log Q = \log Q_0 + k\,(e^{-\alpha \cdot Q_0 \cdot C} - 1) \qquad (1\text{-}1)$$

The equation includes three parameters: Q_0, k, and α. The variables Q and C represent reinforcer consumption and price, respectively. *K* is a constant (usually between the values of 1 and 4) that is set according to the observed range of the dependent variable in logarithmic units, and the parameters Q_0 and α are free to accommodate the data. Q_0 is the estimate of the level of consumption in units of the reinforcer at the lowest price possible (i. e. , an estimate of demand level at theoretical price 0). Scalar changes are accounted for in the model by the parameter Q_0, and absolute changes in this parameter can be examined for changes in the level of demand. The rate constant parameter α of Equation 1 measures the rate of change in elasticity across the function. Hursh & Silberberg (2000) propose that the single parameter α is a measure of "essential value" because it should remain constant across scalar value manipulations of the same reinforcer and represent the overall shape of the demand curve. In this case, essential value is a summary term that encompasses both the precise meaning of the α parameter – a measure of the rate of change in the slope of the demand function – and the more general concept it represents, which is elasticity and its associated assumption of invariance across scalar value manipulations[1]. The authors applied this model retrospectively to fifteen data sets data sets and obtained a

[1] Note that the parameter α is inversely related to essential value, as a small α value indicates a small rate of change in elasticity with increases in price and thus a higher essential value.

median R^2 of 0. 94 (Hursh & Silberberg, 2008; Christensen, Silberberg, Hursh, Huntsberry, & Riley, 2008; Lea, 1978).

One important variable that modulates elasticity, and should therefore change α accordingly, is the economy type (Hursh, 1980; 1984). In the context of an animal experiment, the economy type refers to the availability of the good outside the experimental situation, as well as the correlation between responding and daily intake. In an open economy, sessions are typically short and access to the reinforcer is provided outside of the experimental situation with the express purpose of maintaining a constant level of deprivation with respect to the reinforcer. In contrast, in a closed economy sessions are long, often 24 hours, and all food is obtained in the experimental session (Hursh, 1984; Hursh et al., 1988). Open and closed economies can produce qualitatively different response rates, pause lengths, and other patterns of responding (Hall & Lattal, 1990; Foster, Blackman, & Temple, 1997; Zeiler, 1999). Extensive research has led to the conclusion that open and closed economies represent the ends of a continuum, at the extreme end of which closed economies represent a perfect correlation between responding and consumption. Along the continuum, any of the constellation of factors such as the time to extra-session feeding, session length, and deprivation may vary, and the openness of the economy will vary accordingly (Hursh, 1984; Timberlake, Gawley, & Peden, 1987). These factors, individually or collectively, can contribute to differences in behavior generated by economy types (Timberlake & Peden, 1987; Foster, Blackman, & Temple, 1997; Posadas-Sanchez & Killeen, 2005).

Although economy type per se has not yet been examined in published research with respect to this equation, Hursh & Silberberg (2008) presented re-analyzed data obtained with rhesus monkeys relating to systematic changes in deprivation. The authors demonstrated that providing increasing proportions of in-session free food decreased the essential value of response-contingent food proportionally; demonstrating that α is sensitive to such changes in deprivation. Hursh & Silberberg (2008) also confirmed the prediction that a difference in level of demand, such as a shift in consumption produced by different scalar values of the same reinforcer, should not alter α. The authors showed that the essential value of food did not differ across demand curves generated by food deliveries that resulted in either one or two food pellets per reinforcer. The Q_0 parameter reflected the change in level of demand, while α was identical across the reinforcer manipulation. In the same publication, the authors also demonstrated identical α values across demand curves generated different doses of a drug (alfentanil) that was self-administered by monkeys across a range of fixed-ratio values.

The Exponential Demand model has also been applied to the relationship between responding and food and drug reinforcers in rats. In the first prospective test of the model, rats responded for food and cocaine both separately and in the presence of both goods (Christensen, Silberberg, Hursh, Huntsberry, & Riley, 2008a). The exponential demand model was fitted to the data and the rate of change in elasticity parameter associated with food and cocaine respectively were compared across manipulations. The authors found that the essential value of food was significantly lower when cocaine was concurrently available, as compared to when subjects responded to for food alone. Thus, Christensen et al. (2008a) concluded that cocaine interacted with food in such a way as to decrease its essential value.

The Exponential Demand Equation shows promise in isolating the effects of different variables on elasticity alone, while taking into account changes related to scalar value manipulations. The overall purpose of the present series of experiments was to further test Equation 1 under conditions that may alter the elasticity of the demand function, while also manipulating the scalar value of the good across conditions to further confirm that α remains equivalent across scalar value changes when these changes are properly taken in to account.

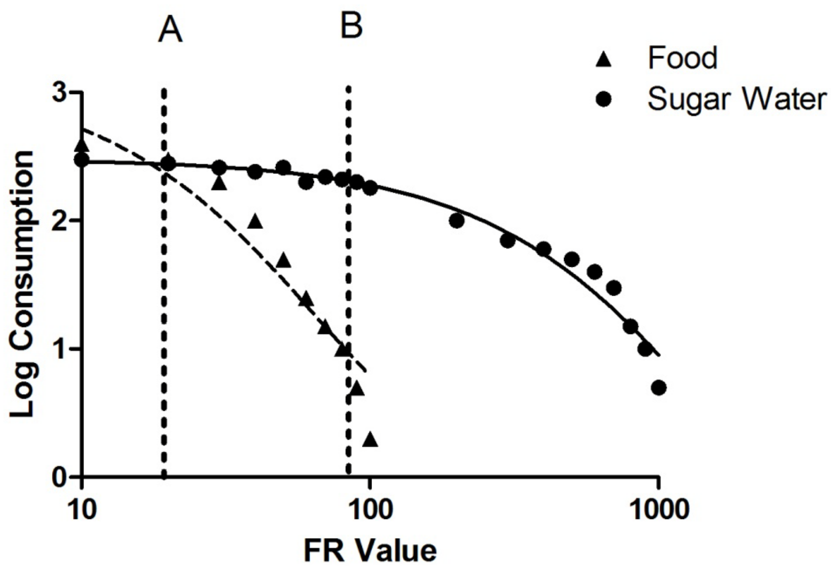

Figure 1-1. A hypothetical example of elastic and inelastic demand . Shown here is an example of the relationship between price (FR value) and the logarithm of consumption for a relatively inelastic good, represented by food, and a relatively inelastic good, represented by sugar water. Note how a calculation of elasticity for each good at points A and B would indicate a similar elasticity for the goods at point A, and dissimilar elasticities at point B. Although this data is hypothetical and menat to be merely illustrative, the data is similar in level and shape to actual data obtained with monkeys responding for these commodities (Bauman, Raslear, Hursh, Shurtleff & Simmons, 1996.)

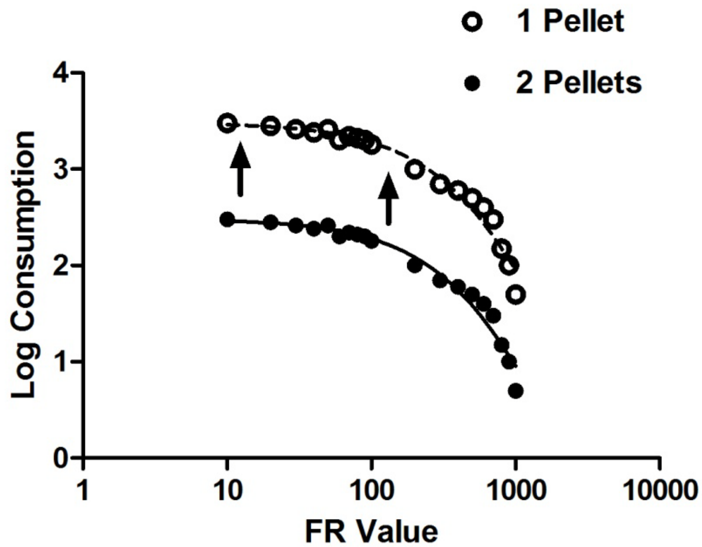

Figure 1-2. A hypothetical example of a change in the level of demand associated with a change in scalar value. Here, both curves represent responding mainted by food reinforcers. The open circles represent food deliveries that result in one food pellet, and the closed circles represent the same relationship when two pellets consititute each food delivery. As the magnitude of the food delivery (scalar value) increases, the level of demand decreases. However, a constant vertical seperation is maintained, denoted by the arrows, that indicates that the shape (elasticity) of the functions are the same.

CHAPTER 2
EXPERIMENT 1

The purpose of Experiment 1 was to compare the effects of economy type (open or closed) on the rate of change in elasticity as measured by the Exponential Demand Equation. Each economy type was tested at two reinforcer magnitudes, either one pellet or two pellets per reinforcer delivery. This was done for two reasons: one, to replicate in a prospective study the findings reported by Hursh & Silberberg (2008) that α remains the same across this manipulation, and two, to assess whether economy type has differential effects on the rate of change in elasticity as a function of reinforcer size. The estimates of α across the two reinforcer size manipulations should be identical during the closed economy; although they may differ somewhat during the open economy if the larger reinforcer size combined with the relatively shorter session time differentially increases local satiation, depressing responding for the larger reinforcer to a greater extent than would be observed in the closed economy (Hursh, 1984; Hursh & Silberberg, 2008).

Experiment 1 Materials and Methods

Subjects

Four male Long-Evans rats, obtained from Harlan Laboratories, maintained at 85% of their free-feeding weight prior to the initiation of each FR sequence, were used as subjects for all experiments. The subjects were individually housed in a windowless colony room and had unrestricted access to water in their home cages. The colony room had a 12:12 hour light/dark cycle, and subjects received any extra-session feeding in their home cages. All subjects had been trained via an automated procedure to press a lever for food pellets as part of a previous unpublished study such that further training was not necessary. All subjects also received subcutaneous nicotine (0.3 mg/kg) and vehicle (potassium phosphate) injections alternately for a period of approximately three weeks prior to the beginning of the present experiments; however, during those sessions in which nicotine was present lever pressing had no programmed consequences; thus any consequences for lever pressing in the presence of nicotine was novel to this experimental procedure for these subjects.

Apparatus

Four Coulbourn Instruments (Whitehall, PA, USA) aluminum and Plexiglas modular rodent operant chambers with steel grid floors, measuring approximately 11"W x10"D x11"H and encased in light- and sound-attenuating outer cases, were equipped with two standard levers. Each lever had an array of three LED lights above it, and were situated approximately 1" from the bottom of the chamber. A houselight provided general illumination during all of the open economy sessions, and alternated off or on according to a 12h:12h light/dark cycle during the closed economy sessions. Also, during the closed economy sessions only, water was freely available in the chamber through a sipper that extended through a hole on the opposite side of the chamber from the levers, and Sani-Chips bedding was present in the chamber. Experimental events were programmed and recorded using a computer operating Graphic State® software.

Procedure

Open economy procedure

During the open economy, sessions lasted for 130 minutes (Winger, Galuska & Hursh, 2007). Sucrose pellets (45 mg, 50% sucrose by weight, Formula AIN-76A, TestDiet) were available according a fixed ratio (FR) schedule that increased across days according to the following sequence: 1, 1, 5, 10, 20, 40, 80, 160, 320, 640, 1280. Data from the first FR 1 day were not included in the demand analyses, and one FR was in effect per session (Hursh et al., 1988; Raslear et al., 1988). Additionally, to better control weight gain across each FR sequence, one day intervened between each FR schedule during which the subjects were not exposed to experimental conditions and were fed to their 85% weight (Posadas-Sanchez & Killeen, 2005). Following each experimental session, subjects were also fed to their 85% weight. This sequence of FRs was repeated twice, with a minimum of three days intervening prior to beginning the next sequence (during which time the subjects were housed in their home cages, given free access to water, and fed to their 85% weight), at each of the two reinforcer magnitude conditions. Sessions were not run to stability as this method of assessing demand provides data similar to that obtained when sessions were repeated until a stable level of consumption was observed (Hursh et al., 1988; Raslear et al. 1988; Foster et al. 1997). Additionally, the sequence of FR presentation was not randomized as the sequence of FRs has been demonstrated to have little effect on overall daily consumption (Hursh et al., 1988; Foster et al. 1997), and preservation of the same schedule sequence across manipulation allowed any sequence effects that may have been present to remain constant across all manipulations (Sidman, 1960).

One – pellet condition procedure

Once the subjects were placed in the experimental chambers, the session began. Upon starting the program, the houselight was illuminated and two colored light emitting diodes (LEDs), one green and one red, were illuminated over the left, active lever. Presses to the right lever had no programmed consequences. Upon completion of the scheduled FR, a food pellet was delivered in the magazine, the center yellow LED flashed above the active lever, and a 2-s blackout period ensued before presses to the active lever could be made. Sessions ended after 130 minutes had elapsed.

Two – pellet condition procedure

The procedure for the two-pellet per reinforcer condition was identical to the one-pellet procedure, with the exception that the feeder mechanism operated twice to drop two pellets into the magazine successively and the yellow LED above the active lever blinked twice prior to the blackout period. The interval between the two pellet deliveries was as short as possible given the time (200 ms) it took for the feeder mechanism to operate.

Closed economy procedure

The closed economy procedure was identical to the open economy procedure with the exception that sessions were 23 hours long and only one FR 1 session was conducted per sequence (Bauman et al., 1996). Prior to beginning each session, the subjects were removed from the experimental chambers and placed in their home cages so that the experimental chambers could be cleaned (3 parts water to 1 part bleach solution) and the water and pellet receptacles refilled. Subjects received no extra-session feeding. As with the open economy procedure, the sequence of FRs was repeated twice, with a minimum of three days intervening prior to beginning the next sequence (during which time the subjects were housed in their home cages, given free access to water, and fed to their 85% weight), at each of the two reinforcer magnitude conditions. The subjects began each FR sequence at 85% of their free-feeding weights, but no further effort was made to constrain deprivation during the remainder of the sequence. As per IACUC regulations, animals were to be removed if their weight fell below 70% of their ad libitum weight; this never occurred. Refer to Table 2-1 for the sequence of conditions.

Experiment 1 Results

Figure 2-1 depicts the absolute number of reinforcers delivered at each FR value for each of the two reinforcer magnitude conditions during the open economy, averaged within subject across both replications. As expected, as the fixed ratio value increased, consumption decreased; and fewer reinforcers were obtained when each reinforcer consisted of two pellets. Figure 2-2 shows the absolute number of reinforcers delivered at each FR value for both reinforcer magnitude conditions during the closed economy. Absolute levels of consumption increased during the closed economy compared to the open economy; this would be expected given the increased session length. Across both economies, the absolute level of demand during both economies decreased as a function of the increase in scalar value of the reinforcer.

Next, the data were normalized and Equation 1 was fitted via least-squares regression (GraphPad Prism version 5) to the relation between the logarithm of normalized daily consumption (total number of reinforcer deliveries) and normalized price (FR value). The normalization procedure as described by Hursh & Winger (1995) sets the maximum observed consumption for each subject as 100%. Decrements from that level of consumption are calculated as percentage decreases from 100%; each subsequent value is divided by the maximum consumption multiplied by 100. Normalized cost is calculated by multiplying each FR value by the maximum consumption and dividing by 100[2]. Normalization thus sets the initial value of all

[2] Because the data are reported here as normalized values, a unit price analysis would be redundant as normalization and unit price are formally similar, and normalizing, according to Hursh (2000) , "[…]

demand curves to 100, greatly simplifying comparison of changes in elasticity across different absolute levels of demand. The Q_0 parameter, however, becomes much less informative as it was artificially constrained to values near 100. Figure 2-3 depicts the obtained data and fitted curve for each of the two conditions of the open economy. Overall, the curves are extremely similar, indicating that essential value was equivalent across the reinforcer magnitude conditions. However, the curve obtained at the two-pellet condition declined more steeply across all subjects, indicating a decrease in essential value.

Figure 2-4 depicts the obtained data and fitted curve for each of the two conditions of the closed economy. Here again, the curves are extremely similar across the two conditions; during the closed economy the essential value of food appears to be even more similar across conditions than during the open economy. For two of the three subjects (277 and 279), the curve obtained at the two-pellet condition declines somewhat more steeply, again indicating a slight decrease in essential value at the two-pellet reinforcer magnitude.

Table 2-2 shows the average obtained α parameter values across all four subjects, as well as the percent variance accounted for by Equation 1. Equation 1 accounted for the data extremely well. The α parameter was also smaller on average for the one-pellet condition than for the two-pellet condition during both economy types, indicating a higher essential value. The average α parameter values obtained at each magnitude during the closed economy are more similar across the two magnitudes than those obtained during the open economy. Next, a model comparison was conducted to

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corrects for any differences in reinforcer magnitude (p.33)" and "[…] normalized price is a kind of unit price based on relative rather than absolute units of reinforcement (p. 34)."

determine quantitatively if α differed significantly across magnitude manipulations. The model comparison approach assessed whether one global α parameter, shared across the two reinforcer magnitudes, would provide a more parsimonious fit to the data compared to two separate parameters. An F-Test, conducted using GraphPad Prism version 5 software, tested the null hypothesis that the simpler, one-parameter model would provide the best fit to the data when controlling for the extra degrees of freedom associated with two parameters. More specifically, the F-ratio compares the relative increase in the sum-of-squares caused by having only one α parameter to fit both sets of data to the increase in the degrees of freedom associated with having two separate parameters, with large positive F-ratios indicating that the null hypothesis should be rejected. Table 2-3 presents the obtained F ratio value, degrees of freedom for the numerator and denominator of the ratio respectively, the associated p-value, and the interpretation of the p-value that indicates whether two separate α parameters are justified for each comparison. The α parameter significantly differed across the two reinforcer magnitudes during the open economy. During the closed economy, the α parameter did not differ significantly, indicating that a global α would provide a more parsimonious fit to the data.

To further investigate the degree to which the Exponential Demand Equation accurately predicted the data, raw residuals were obtained. A residual value is the distance between the obtained data point (Y) and the data point predicted by the equation (Y') at each value of the independent variable. Figures 2-5 and 2-6 show the raw residuals as a function of normalized price obtained during the open economy and closed economy, respectively. Although no systematic deviations from randomness can be observed, the equation's predicted values were more divergent from the obtained data as normalized price increased. That is, during both economy types, the equation did a relatively poor job of accurately predicting consumption at higher prices. The residuals obtained from subject 277 during both economy types show the largest divergences between the obtained data and predicted line.

Experiment 1 Discussion

Essential value was more similar across the magnitude conditions during the closed economy than during the open economy. Additionally, the curves generated by the two different economies did not differ substantially, despite large reported differences in demand curves generated by these economy types (e.g. Zeiler, 1999). One reason for the lack of a larger discrepancy between the two economy types may be due to the relatively long (130 minute) open economy sessions that were used. Although session length per se may not be a factor in determining differential patterns of behavior across economy types (Hall & Lattal, 1990), the ability of the animal to reach satiation in a single session may account for many of the reported differences in behavior. In a recent review and empirical test of open and closed economies, Posadas-Sanchez & Killeen (2005) demonstrated that it was possible to obtain patterns of responding consistent with open economies in the beginning portion of a closed economy in which the animals began hungry, while the remainder of the session more closely resembled a closed economy. From these and other data, they concluded that satiety is a crucial factor in determining the degree of openness of an economy.

To determine the degree to which satiety was achieved in the present open economy, a representative cumulative record from the FR 5 session of the first replication from subject 277 is presented in Figure 2-6 for the first 120 minutes of the session (the last ten minutes, in which no responding occurred, are not shown). From the lack of responding after approximately minute 96, it seems the rat is locally sated; this effect can likely account for the similarity of the curves obtained during both economy types. However, at the higher FR values, the constrained session time did not allow for completion of enough ratios to result in satiety effects, which may explain the small differences found across curves at those values.

Table 2-1. Sequence of conditions for Experiment 1.

FR Sequence	Pellets Per Reinforcer	Economy Type
FR Sequence	1	Open
FR Sequence	1	Open
FR Sequence	2	Open
FR Sequence	2	Open
FR Sequence	1	Closed
FR Sequence	1	Closed
FR Sequence	2	Closed
FR Sequence	2	Closed

Table 2-2. Obtained estimates from Experiment 1 of the α parameter and percent variance accounted for by the Exponential Demand Equation, averaged across all subjects.

Parameter	*Open Economy*		*Closed Economy*	
	1 Pellet	2 Pellets	1 Pellet	2 Pellets
α	1.65E-06	2.70E-06	1.69E-06	2.00E-06
% VAC	0.96	0.95	0.97	0.94

Table 2-3. Results of an F-Test model comparison. For each comparison, the data for all four subjects were included individually. The F-Test compares the increase in the extra sum-of-squares value caused by a shared α parameter to the corresponding increase in degrees of freedom associated with two separate parameters to quantify whether two separate α values are warranted.

Comparison	*F (DFn, DFd)*	*P- Value*	*Does α differ?*
Open Economy, 1 Pellet v. 2 Pellets	19.01 (1,76)	< 0.0001	Yes
Closed Economy, 1 Pellet v. 2 Pellets	2.689 (1,76)	0.1052	No

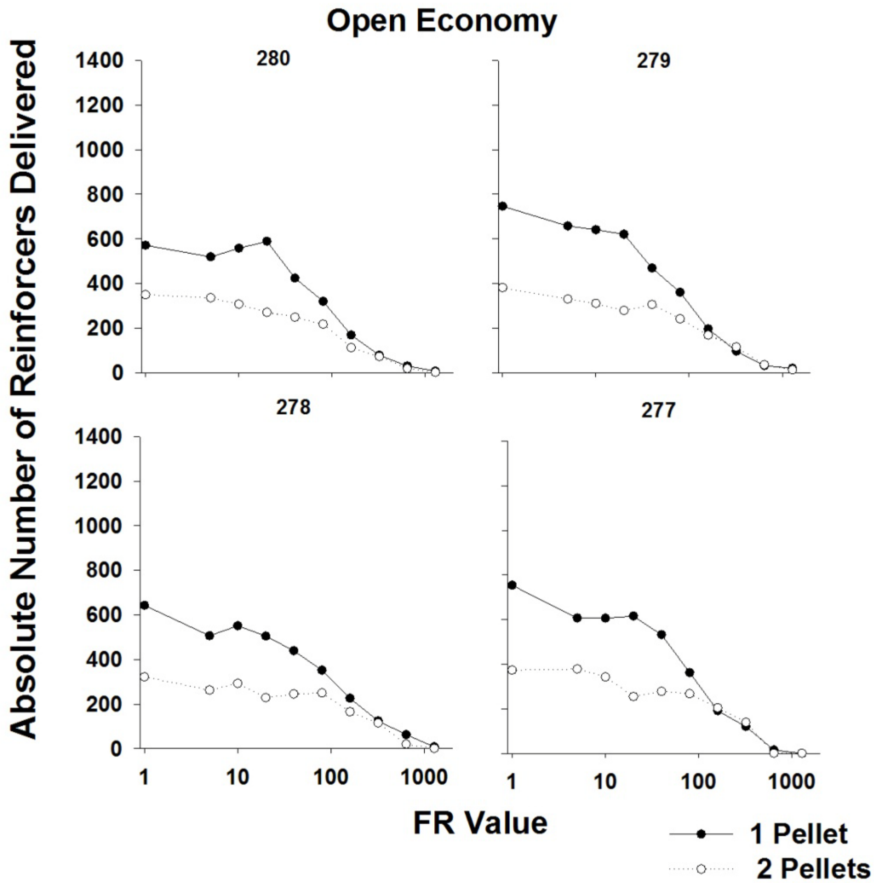

Figure 2-1. The absolute number of reinforcers delivered for each subject obtained during the open economy. The absolute number of reinforcers delivered for each subject was averaged across replications within subject at each schedule value.

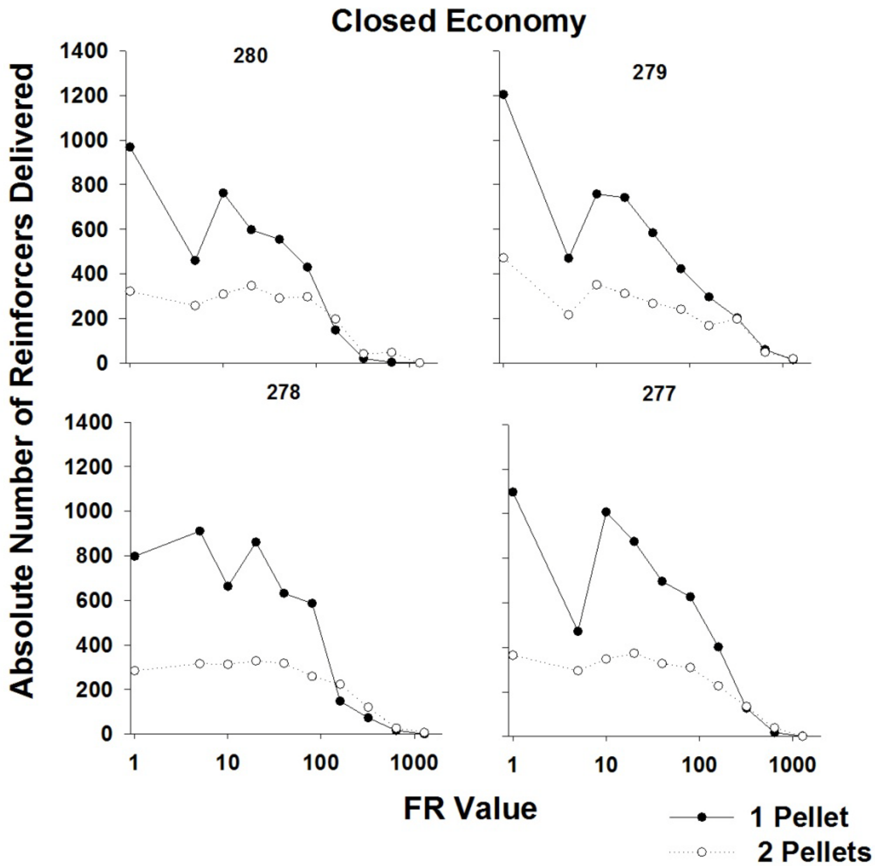

Figure 2-2. The absolute number of reinforcers delivered for each subject obtained during the closed economy. The absolute number of reinforcers delivered for each subject was averaged across replications within subject at each schedule value.

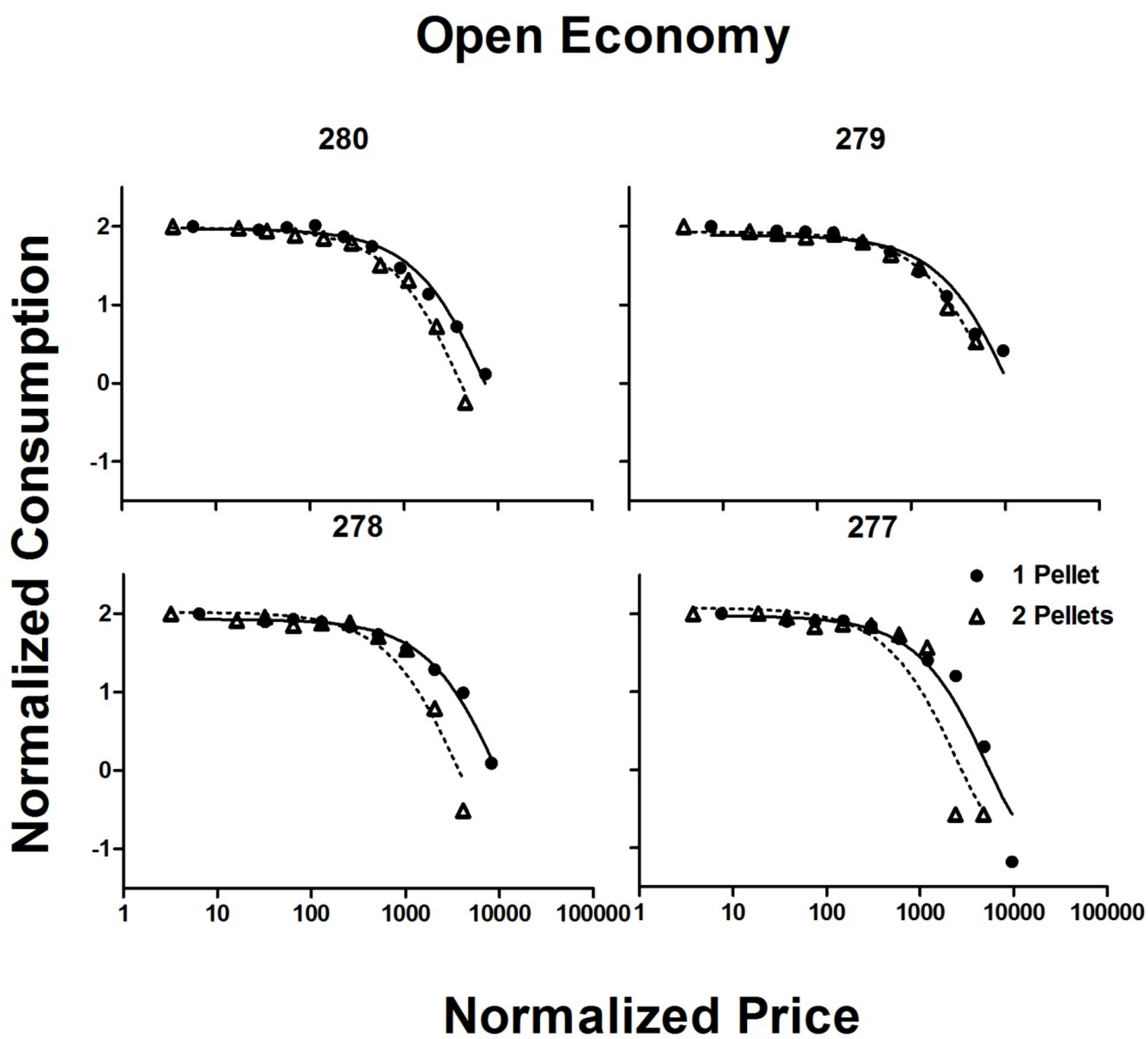

Figure 2-3. The obtained consumption data from the open economy and fitted line. The obtained consumption data from both conditions of the open economy phase were averaged within subject across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the Exponential Demand Equation to the data (see text for details).

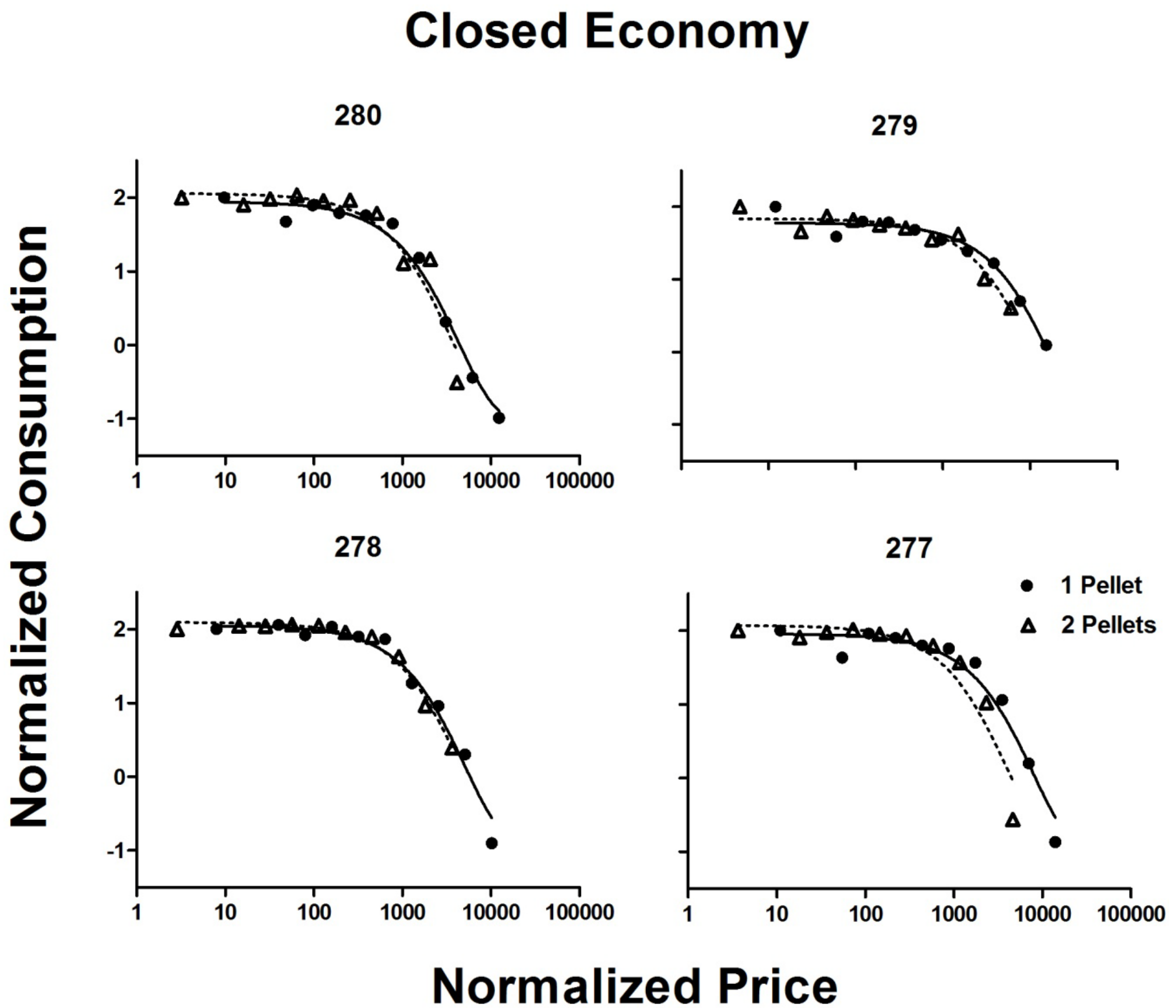

Figure 2-4. The obtained consumption data from the closed economy and fitted line. The obtained consumption data from both conditions of the closed economy phase were averaged within subject across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the Exponential Demand Equation to the data (see text for details).

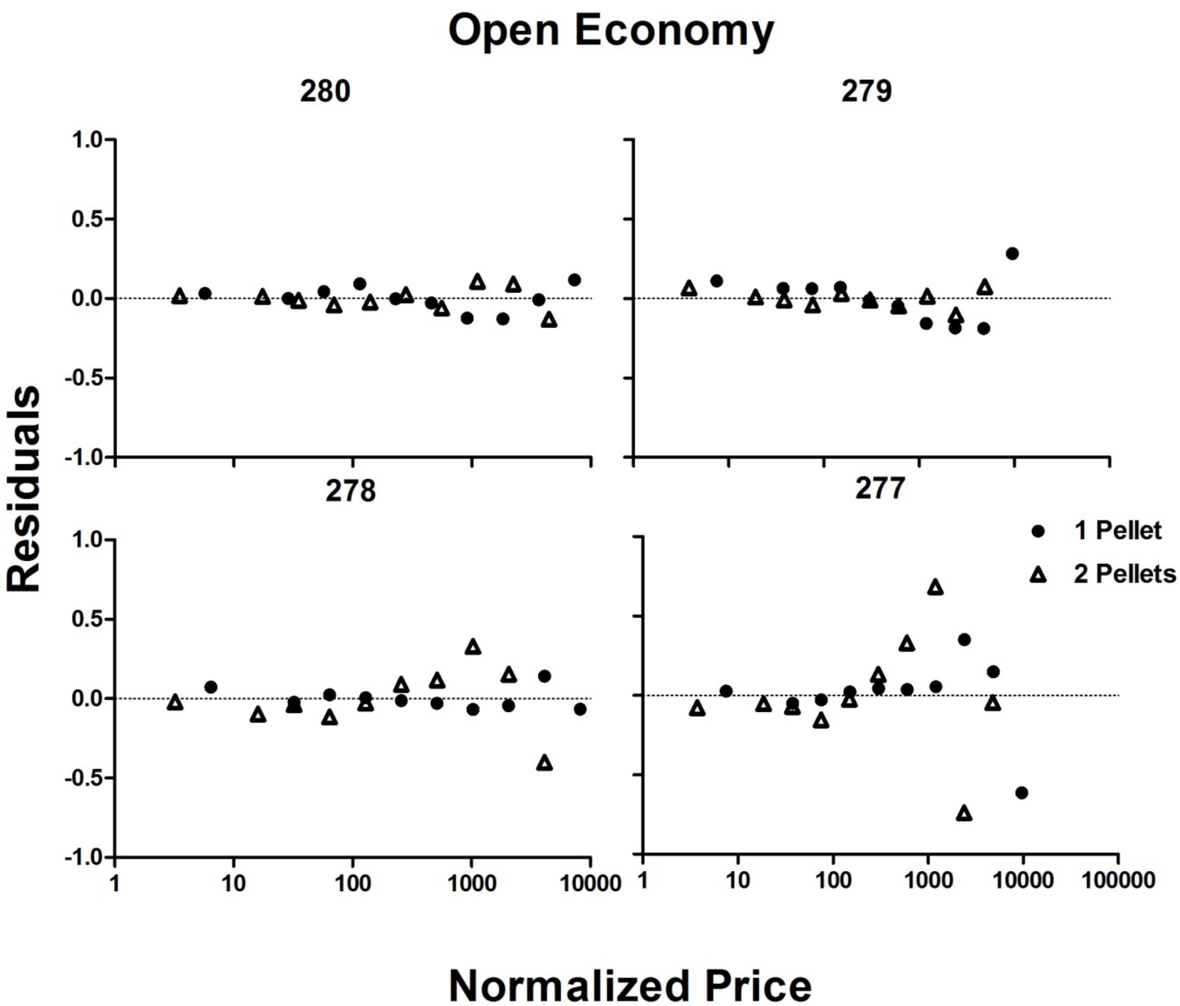

Figure 2-5. Residuals as a function of normalized price during the open economy. Residuals are calculated as the distance from the obtained data point (Y) to its corresponding predicted point (Y').

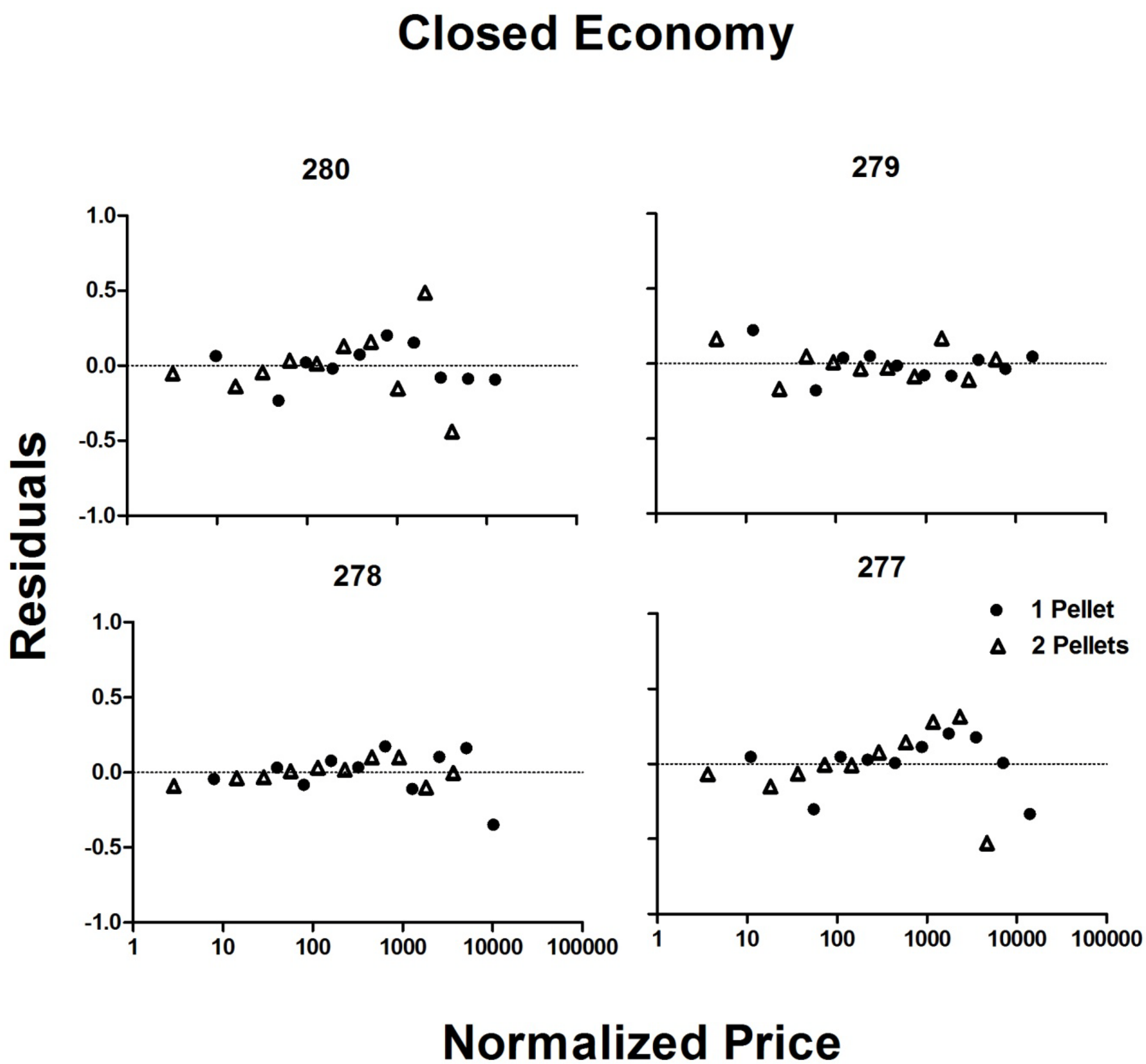

Figure 2-6. Residuals as a function of normalized price during the closed economy. Residuals are calculated as the distance from the obtained data point (Y) to its corresponding predicted point (Y').

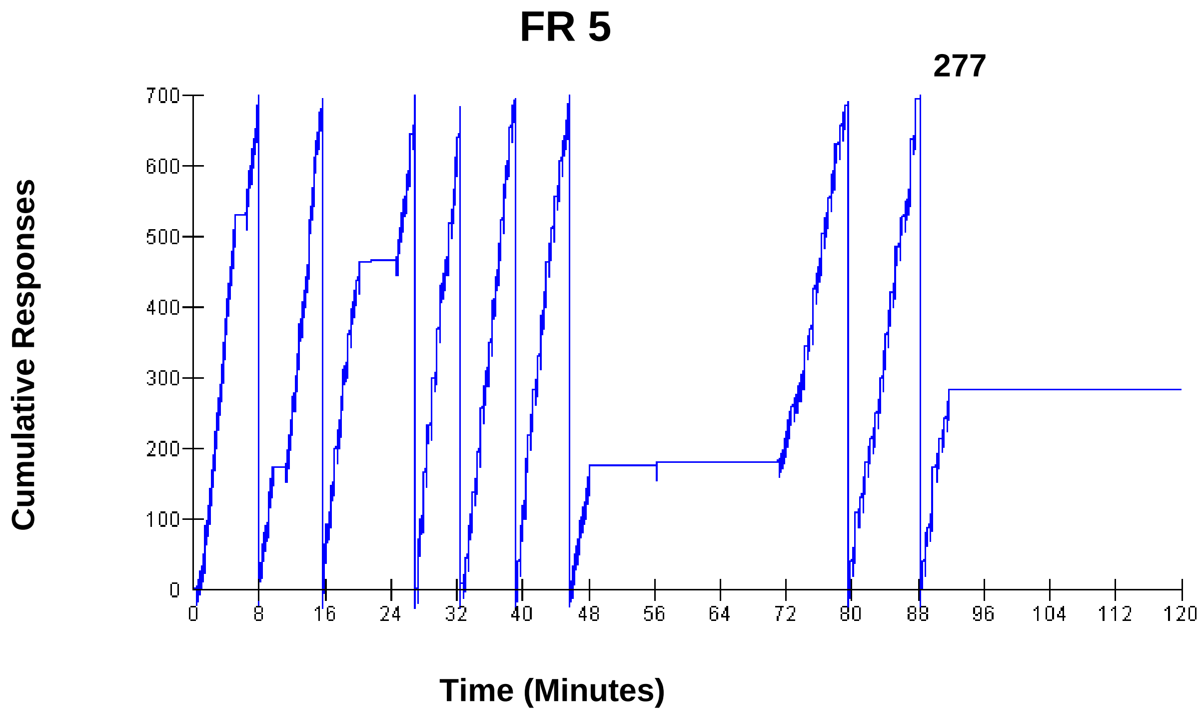

Figure 2-6. Representative cumulative record of response patterns during the open economy. The record is from the first replication of the FR 5 open economy session for subject 277. The first bout of responding ends approximately 49 minutes in to the session, and the second bout ends around the 96th minute. Only the first 120 minutes are shown due to aspect and space considerations; no responding occurred in the last ten minutes of the session.

CHAPTER 3
EXPERIMENT 2

The purpose of Experiment 2 was to determine how nicotine affects the essential value of food. The α parameter may prove useful not only for examining demand for drugs as reinforcers (e.g. Winger, Hursh & Galuska, 2007; Christensen et al., 2008a,b, 2009), but also for understanding how drugs alter the relationship between behavior and other, nonpharmacological reinforcers. Nicotine, one of the most widely abused drugs worldwide, is known to alter both responding for food reinforcers and responding for other, secondary reinforcers. Nicotine has the characteristic effect of decreasing food consumption (e.g. Grunberg, 1982) and this may be an effect similar to a scalar value change that results in only a shift in the absolute level of the demand curve, which would be evident in the raw demand curves. At the same time, research has demonstrated that the administration of nicotine increases responding for other stimuli that have been paired with the availability of food or nicotine (e.g., Donny et al., 2003; Raiff & Dallery, 2006, 2008); this has been interpreted as an effect of enhancing the value of these stimuli (Olausson et al., 2004; Liu et al., 2007; Palmatier et al., 2007). Alternatively, nicotine may alter the rate of change in elasticity of the relationship, causing the demand curve to decline more steeply with increases in price even after the change in level of demand had been taken into account, which would be captured by the α parameter. Or, nicotine may alter both the level and the shape of the function, and this effect may be differential with respect to the size of the food delivery. Thus, in Experiment 2, we aimed to quantify the effects of nicotine on α during a closed economy, again across two magnitudes of food delivery.

Experiment 2 Materials and Methods

Subjects. The subjects were the same four male Long-Evans rats as used in Experiment 1.

Apparatus. The apparatus was the same as that used in Experiment 1.

Procedure. The procedure was identical to the closed economy procedure presented in Experiment 1 with the exception of the presence of nicotine; the data obtained from the closed economy phase served as a baseline. Thus, sessions were 23 hours in length, with one FR in effect per session and water was freely available in the experimental chambers.

Nicotine administration. Following the conclusion of Experiment 1, the subjects were surgically implanted with subcutaneous osmotic minipumps (Alzet® model 2ML4, mean flow rate 2.54 µl/hr, mean fill volume 2125 µl). The subjects were anesthetized via gaseous isoflurane, then an area between the scapulae was shaved and a 2cm incision was made, cleansed with betadine, and gently enlarged such that the pumps could be inserted. The incisions were then closed using Roboz® Surgical Instruments (Gaithersburg, MD, USA) 7mm surgical staples, and the subjects were treated with an injectable analgesic following implantation. The pumps were filled with a solution of nicotine tartrate salt (Sigma Chemical Co., St. Louis, Missouri, USA) dissolved in saline solution such that nicotine was delivered at the behaviorally active dose of 3 mg/kg/day for 21 days (Matta et al., 2007). Two sequences were then conducted at the 1-pellet reinforcer magnitude, and then the pumps were removed and replaced with fresh, identical pumps that remained in place for the two sequences of the 2-pellet reinforcer magnitude sequences. At the conclusion of Experiment 2, the pumps were removed and, per veterinary instruction, all subjects were placed on an ad libitum diet of Purina®

rat chow for 2 weeks. Following this, the subjects were brought back down to their 85% weight and a return to the one-pellet closed economy baseline was conducted with three of four rats (subject 280 died following the conclusion of the nicotine phase). See Table 3-1 for the sequence of conditions.

Experiment 2 Results

Figure 3-1 shows the absolute number of reinforcers delivered at each FR value for each subject, averaged within subject across the two replications, for the one-pellet condition of the closed economy baseline and during the nicotine administration phase. Nicotine consistently reduced the level of consumption, and this effect was particularly pronounced at the smaller FR values. Figure 3-2 shows the absolute number of reinforcers delivered at each FR value, averaged within subject across the two replications, for the two-pellet condition of the closed economy baseline and during the nicotine administration phase. Although consumption decreased as reinforcer magnitude increased, as was shown in Experiment 1, here the effect of nicotine is much less pronounced than at the 1-pellet condition.

The data were normalized and the equation was fitted to the data in the same manner as described in Experiment 1. Figure 3-3 depicts the results of fitting Equation 1 to the relationship between the logarithm of normalized consumption and normalized price for the one-pellet conditions of baseline and the nicotine administration phase. Despite the large difference in the absolute level of demand as shown in Figure 10, the curves are extremely similar, indicating no change in essential value across the conditions. One subject, 280, showed a slight increase in essential value when nicotine was present. Figure 3-4 shows the obtained data and fitted curve for the two-pellet conditions of baseline and the nicotine administration phase, and here again we see extremely similar curves with a slight increase in essential value when nicotine was present observed for subjects 280, 279, and 277.

Following pump removal at the conclusion of the nicotine phase, the animals were placed on an ad libitum diet per veterinary instruction. During this period, subject 280 died; it was unclear if his death was a result of natural causes or complications relating to pump removal. The three remaining subjects were returned to their 85% weights and experienced the FR sequence twice under closed economy conditions. Each reinforcer resulted in one pellet. The data from this return to baseline phase are presented in Figure 8-5. The data have been normalized and Equation 1 fit to the relationship between the logarithm of consumption and price, as described previously. For all subjects, the curves are nearly identical; this further confirms that the essential value of food remains stable over time (Christensen et al., 2009).

Table 3-2 shows the average obtained α values across all four subjects, as well as the percent variance accounted for by Equation 1. As in Experiment 1, Equation 1 accounted for the data well, and the obtained estimates of α were similar across all of the manipulations. At the average level, the estimates of α were smaller for both magnitudes of food when nicotine was present. Table 3-3 shows the results of an extra sum-of-squares F-test that was conducted using GraphPad Prism version 5 software. As in Experiment 1, the test compared whether a global α parameter or two separate parameters would provide the more accurate and parsimonious account of the data. The F-test results suggest that two separate parameters are not warranted when comparing the data from the one-pellet baseline condition to the data obtained when nicotine was present, suggesting that the α parameters were in fact similar enough to be shared globally. When comparing the data from the two-pellet baseline condition to the data obtained when nicotine was present, the F-Test indicated that two separate parameters were justified.

Figures 3-6 and 3-7 show the residual values as a function of normalized price for the nicotine phase and return to baseline phase, respectively. Again, no systematic deviations from randomness were noted; however the equation failed to adequately predict the obtained data for subject 280 in the presence of nicotine, particularly at higher prices. Comparing the baseline and return to baseline values in Figure 8-7, there were no systematic differences in the residuals across phases.

Experiment 2 Discussion

The essential value of food remained consistent across manipulations, despite large differences in absolute levels of consumption. At the one-pellet magnitude, essential value was nearly equivalent in the presence of nicotine as compared to baseline, with the exception of subject 280, for whom nicotine seems to have slightly increased the essential value of food. At the two-pellet magnitude, when comparing baseline to nicotine administration, nicotine seems to have slightly increased the essential value of food for three out of four subjects. The consistency in α values, contrasted with the difference in absolute level of demand noted at the one-pellet magnitude, indicate that nicotine had an effect similar to that of increasing the scalar value of the reinforcer rather than altering the elasticity of the relationship.

Table 3-1. Sequence of conditions for Experiment 2.

FR Sequence	*Pellets Per Reinforcer*	*Nicotine Present?*
FR Sequence	1	No
FR Sequence	1	No
FR Sequence	2	No
FR Sequence	2	No
FR Sequence	1	Yes
FR Sequence	1	Yes
FR Sequence	2	Yes
FR Sequence	1	No
FR Sequence	1	No

Table 3-2. Obtained estimates from Experiment 2 of α and percent variance accounted for by the Exponential Demand Equation, averaged across all subjects.

Parameter	*Baseline (Closed Economy)*		*Nicotine*	
	1 Pellet	2 Pellets	1 Pellet	2 Pellets
α	1.69E-06	2.00E-06	6.94E-07	1.09E-06
% VAC	0.97	0.94	0.92	0.94

Table 3-3. Results of an F-Test model comparison. For each comparison, the data for all four subjects were included individually. The F-Test compares the increase in the extra sum-of-squares value caused by a shared α parameter to the corresponding increase in degrees of freedom associated with two separate parameters to quantify whether two separate α values are warranted.

Comparison	*F (DFn, DFd)*	*P- Value*	*Does α differ?*
1 Pellet, Baseline v. Nicotine	1.845 (1,76)	0.1784	No
2 Pellets, Baseline v. Nicotine	16.09 (1,76)	0.0001	Yes

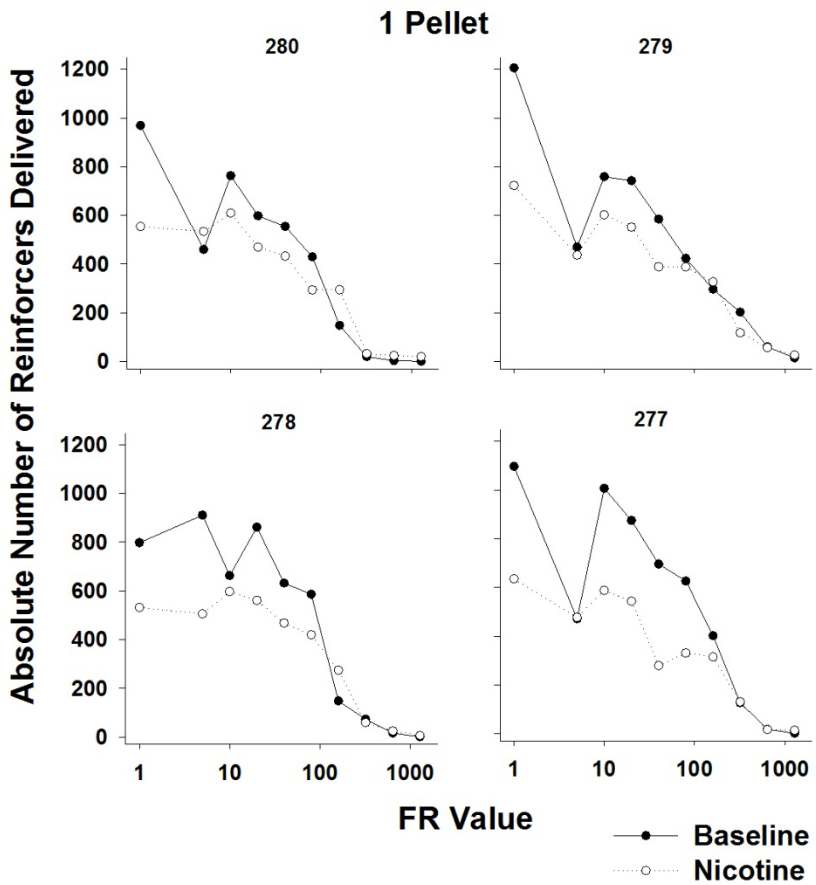

Figure 3-1. The absolute number of reinforcers obtained for one- pellet condition of the closed economy baseline and when nicotine was present. The number of reinforcers delivered for each subject was averaged across replications within subject at each schedule value.

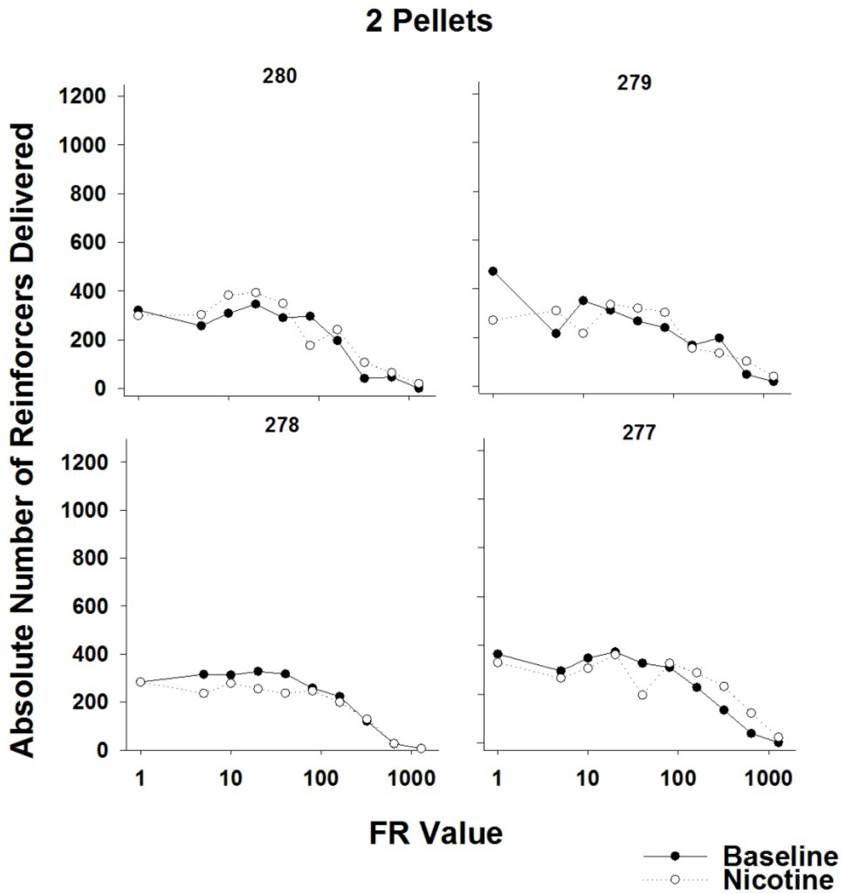

Figure 3-2. The absolute number of reinforcers delivered for each subject obtained from the two-pellet condition of the closed economy baseline and when nicotine was present. The number of reinforcers was averaged across replications within subject at each schedule value,

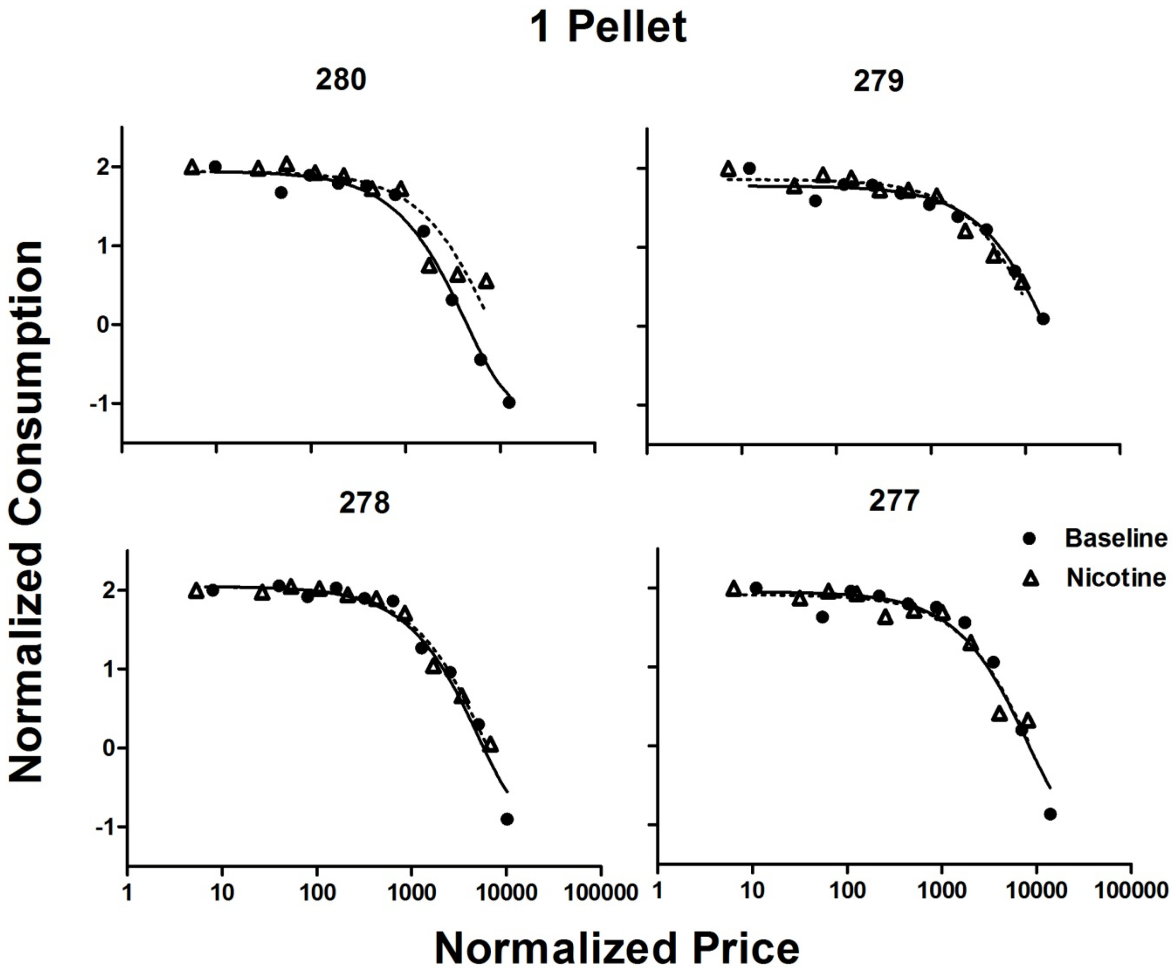

Figure 3-3. The obtained consumption data from the one- pellet condition of the closed economy baseline and the nicotine administration phase and fitted lines. The obtained consumption data from the one- pellet condition of the closed economy baseline and the nicotine administration phase were averaged within subject across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the Exponential Demand Equation to the data (see text for details).

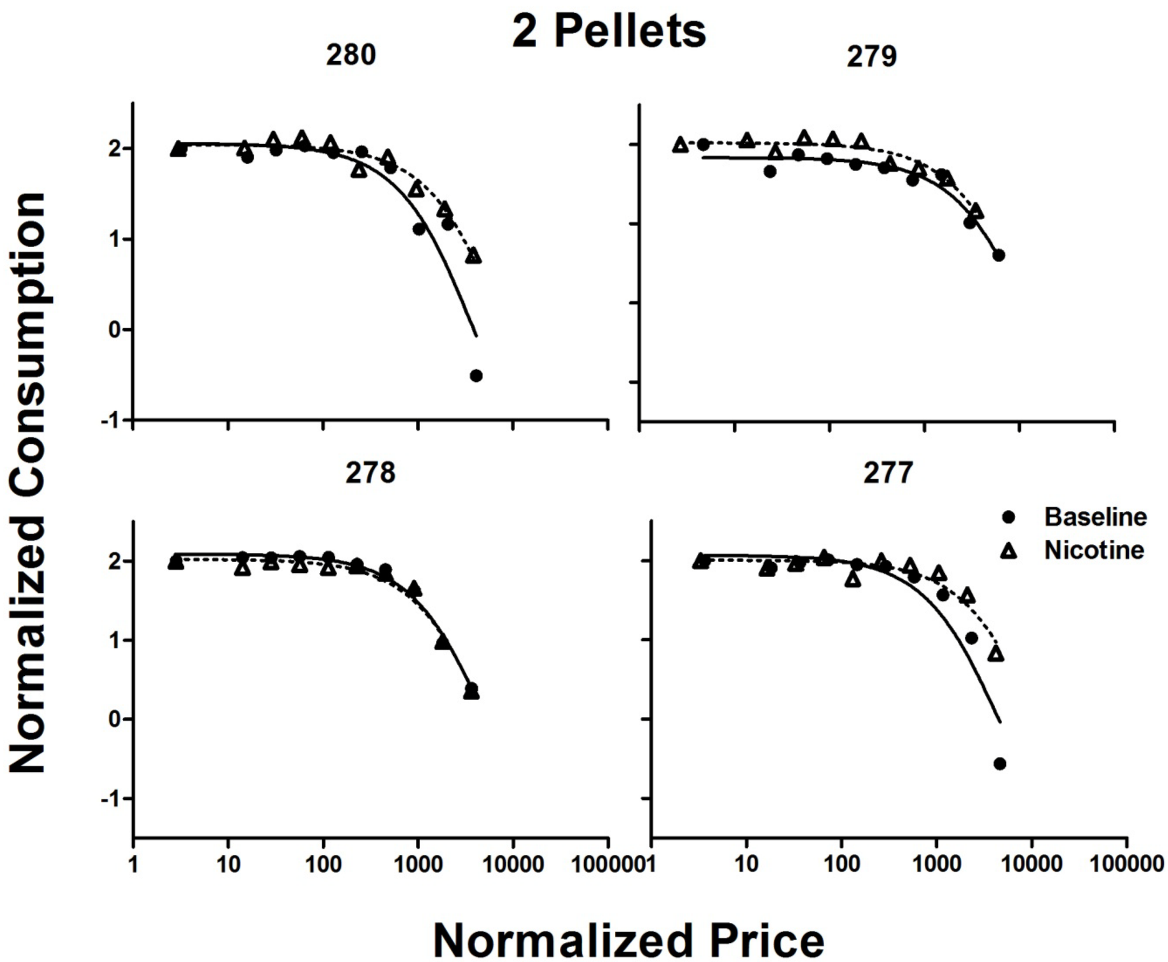

Figure 3-4. The obtained consumption data from the two pellet condition of the closed economy baseline and the nicotine administration phase and fitted lines. The obtained consumption data from the two pellet condition of the closed economy baseline and the nicotine administration phase were averaged within subject across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the Exponential Demand Equation to the data (see text for details).

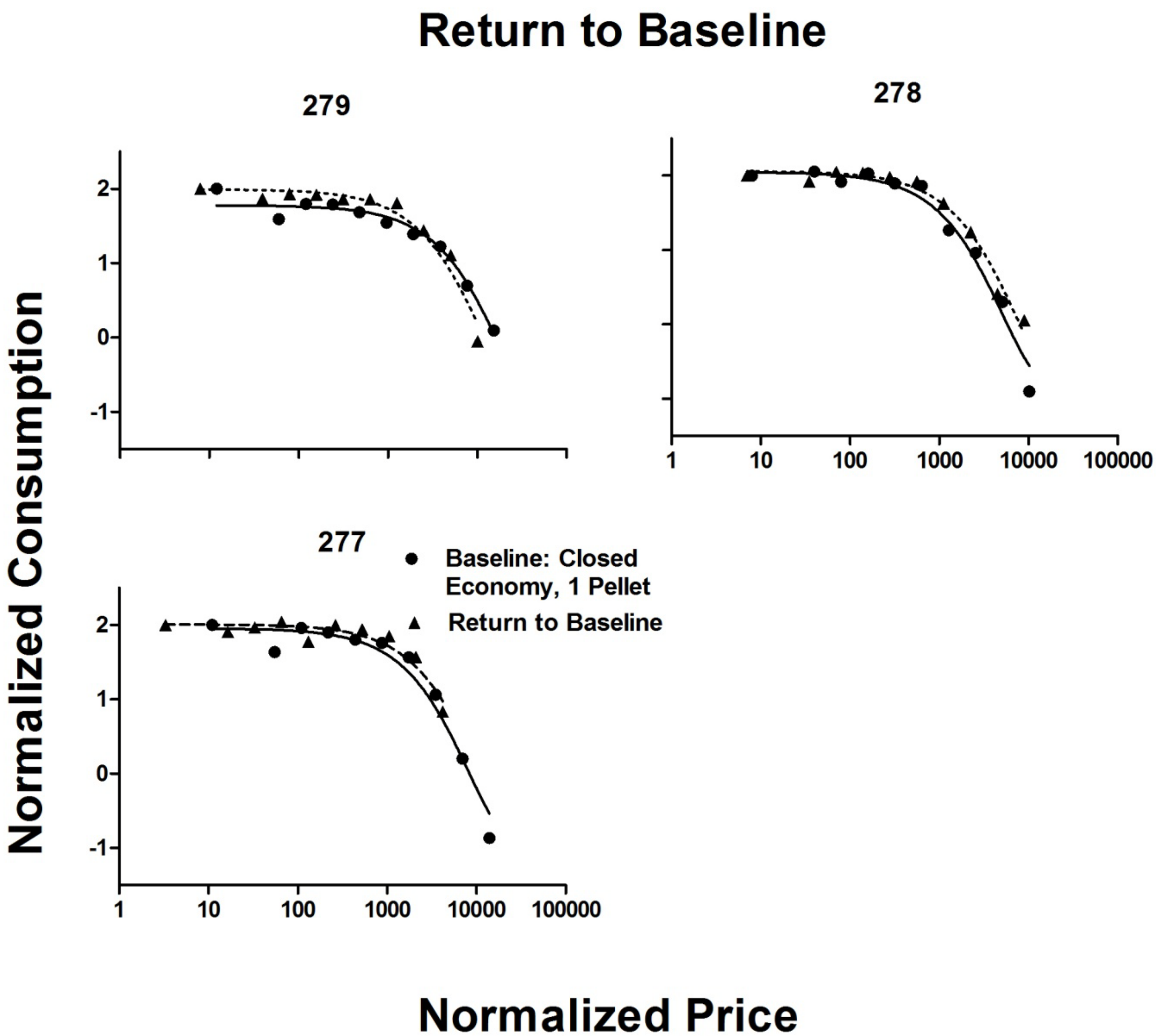

Figure 3-5. The obtained consumption data from the one- pellet condition of the closed economy baseline and return to baseline phase and fitted lines. The obtained consumption data from the one- pellet condition of the closed economy baseline and the subsequent return to baseline phase were averaged within subject across each replication, normalized according to the maximum consumption observed and plotted against the normalized price. The curves represent fits of the Exponential Demand Equation to the data (see text for details).

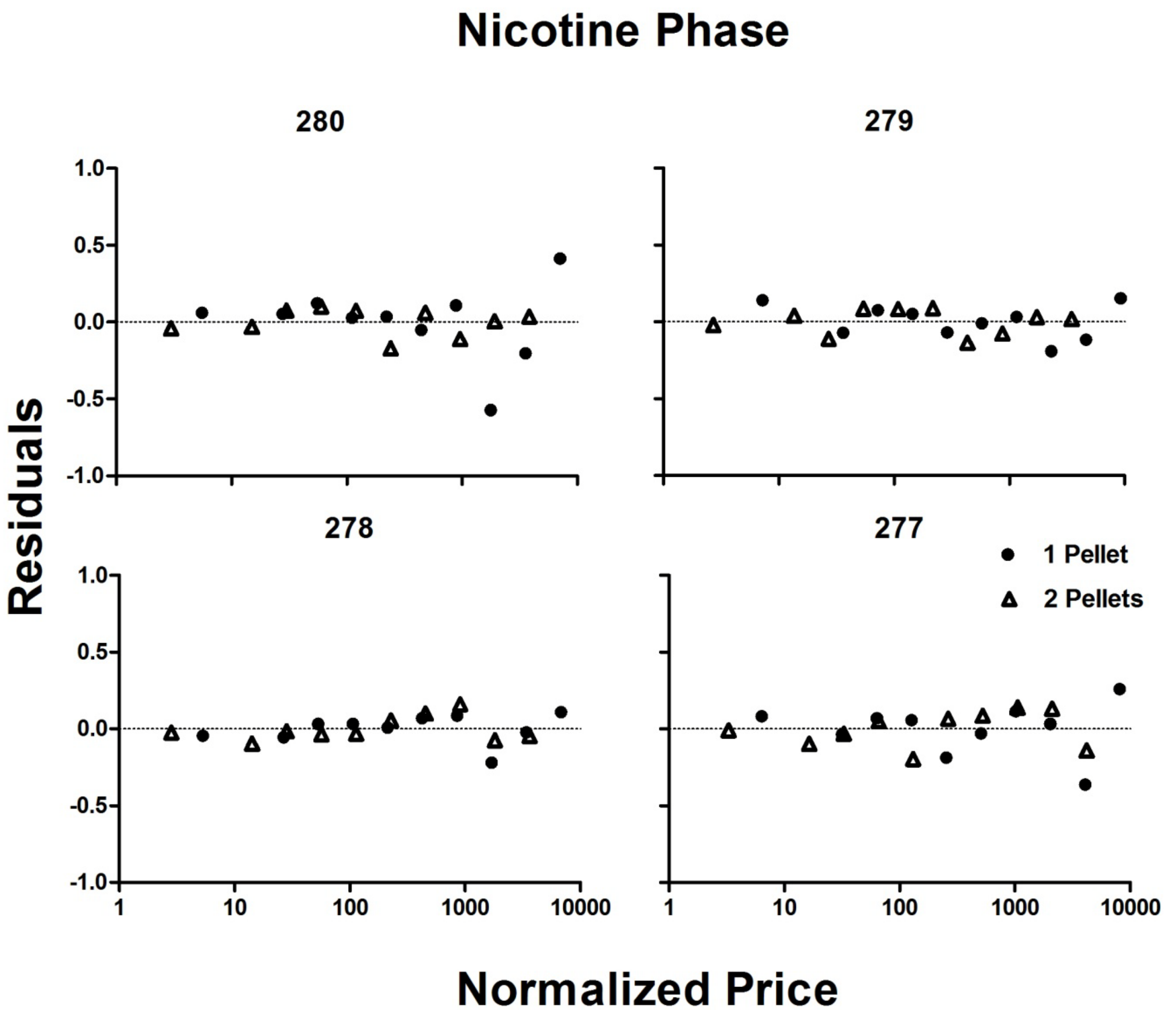

Figure 3-6. Residuals as a function of normalized price during the nicotine phase. Residuals are calculated as the distance from the obtained data point (Y) to its corresponding predicted point (Y').

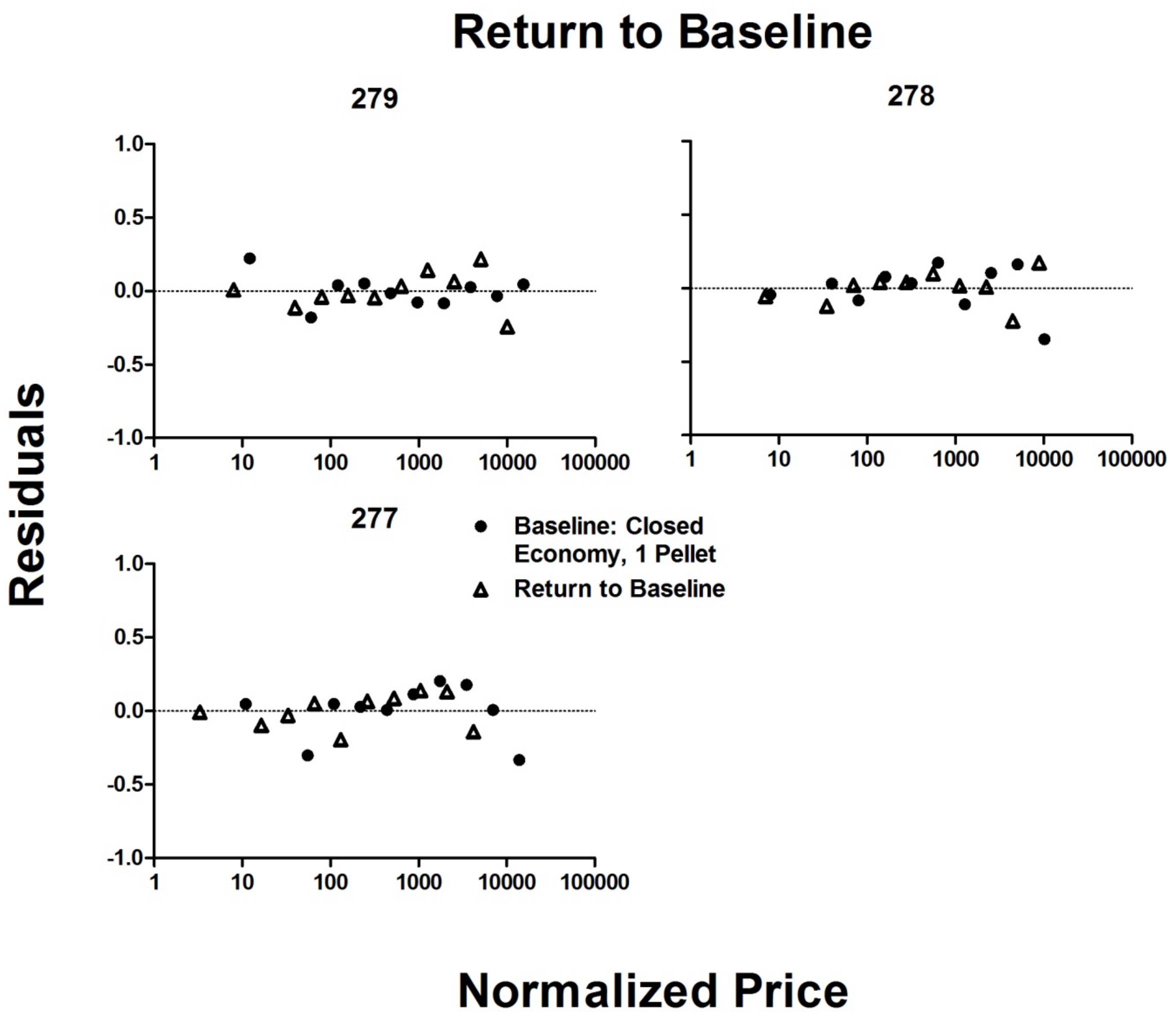

Figure 3-7. Residuals as a function of normalized price during the return to baseline phase. Residuals are calculated as the distance from the obtained data point (Y) to its corresponding predicted point (Y').

CHAPTER 4
GENERAL DISCUSSION

Across both experiments, large differences in absolute level of demand were found as a function of the size of the reinforcer, the economy type, and the presence of nicotine. Specifically, absolute level of demand decreased with increases reinforcer magnitude (scalar value) across all manipulations. The absolute level of demand also decreased in the presence of nicotine compared to baseline at the one-pellet magnitude. Similarly, during the closed economy long session length contributed to larger absolute levels of consumption compared to the open economy. Despite these large differences in the absolute level of demand, essential value remained consistent; in particular, essential value was equivalent across both reinforcer magnitudes of the closed economy and in the presence of nicotine compared to baseline when the reinforcer was one pellet per delivery.

The data from Experiment 1 are consistent with the assumptions of Equation 1 in that an increase in the scalar value of the reinforcer did not alter the essential value of food; rather, the decrease in consumption was evident in the raw demand curves. Although normalizing the data allowed for effective visual comparison of the curves, changes in α would still have been evident in the normalized curves as the procedure does not alter the overall shape of the function. Normalization merely corrects for differences in absolute level of demand. The slight decrease in essential value noted for a few subjects during the open economy was not evident in the data from the closed economy, and differences in essential value between the two economy types are consistent with the assumptions of the equation. The long session duration and lack of extra-session feeding characteristic of the closed economy provided equivalent estimates of essential value across reinforcer magnitude, and this provides further evidence that closed economies are the most appropriate way to adequately characterize demand across all ranges of deprivation (Hursh, 1984; Foster, Blackman & Temple, 1997). The representative cumulative record presented in Figure 9 indicates that the data generated by the two economy types were similar due to the local satiation that occurred near the end of the open economy session, particularly at the lower FR values (Posadas-Sanchez & Killeen, 2005).

Experiment 2 examined nicotine's effects on the essential value of food. Nicotine decreased consumption substantially during the one- pellet condition, while essential value was equivalent to baseline at that level. These data may indicate that nicotine affects demand in a manner similar to merely increasing the size of the reinforcer; thus shifting the demand level down without affecting the rate of change in elasticity. The effects of nicotine in terms of decreasing the overall level of responding for food may thus be dissociated from the stable rate of change in elasticity using the Exponential Demand approach, and the effects of nicotine on food consumption may be functionally equivalent to increasing the scalar value of the reinforcer. The slight increase in essential value observed for some subjects at the two- pellet magnitude may indicate that when the magnitude of the reinforcer is larger, nicotine differentially affects the rate of change in elasticity in a manner distinct from a shift in the level of demand. However, data obtained from a parametric evaluation of different magnitudes of food delivery and across different methods of altering magnitude (i.e. delay) and different doses of nicotine are needed before a firm conclusion can be drawn with regard to differential effects of nicotine across magnitudes.

The data from the present experiments provide further evidence for the utility of Equation 1 as a tool for quantifying the rate of change in elasticity of a good apart from changes in absolute level of demand. Changes in the magnitude of a food reinforcer do not appear to affect the essential value of food, and during the closed economy estimates of the essential value of food were nearly identical across the magnitude manipulation. When nicotine was administered, despite producing decreases in the absolute level of consumption when reinforcers were smaller, estimates of the essential value of food did not differ significantly with respect to baseline. However, when the reinforcers consisted of two pellets, for three out of four subjects the essential value of food appeared to increase slightly in the presence of nicotine. Nicotine may thus have a detectable effect of altering the essential value of food differentially across magnitudes, but whether or not this effect is consistent across different food magnitudes and nicotine doses remains to be seen. Although work remains to gain a fuller understanding of the effects of motivational operations on the rate of change in elasticity, the Exponential Demand Equation appears to be a useful tool for dissociating changes in the level of demand from changes in the degree of elasticity of the relationship between food and the behavior it maintains.

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BIOGRAPHICAL SKETCH

Rachel Cassidy was born in 1986, in Fort Myers, Florida. She graduated from Fort Myers High School with an International Baccalaureate Degree in 2004. She then attended the University of Florida, where she was indicted in to Phi Beta Kappa as a junior and graduated Magna Cum Laude with a bachelor of science in psychology and in sociology in 2008.

Rachel began her research career in behavior analysis in 2006, when she presented a poster at the UF Psychology Undergraduate Research Forum and was awarded Outstanding Poster. In 2007, her application was accepted for the competitive University Scholars Program, which awards stipends to undergraduate researchers. Her final project was published in the Journal of Undergraduate Research. She presented her first poster at a national conference in 2007.

Upon completion of her bachelor's degree Rachel was accepted in to the UF Behavior Analysis Ph.D. program as a student of Dr. Jesse Dallery. In May of 2010, Rachel gave her first paper presentation at a national conference of Behavior Analysts in San Antonio, Texas. When she finishes her doctorate, Rachel hopes to continue teaching and engaging in research activities in an intellectually stimulating academic environment.