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ABSTRACT

INTERSPECIFIC AND INTRASPECIFIC COMPARISONS OF SINGLE-BOTTLE SUCROSE INTAKE IN PEROMYSCUS

By

Douglas W. Bloomquist

The postulated roles of taste for animal survival suggest that animals exposed to different selection pressures should differ in their response to taste solutions. Comparative taste studies have focused largely on domesticated species, however, and the measurement of taste thresholds and preference for sugars with the laboratory rat has received particular attention. Several studies have examined sugar preferences among various species of deer mice and other rodents, and interspecific comparisons have been based usually upon quantitative differences in average relative intake from solutions. Sources of intraspecific differences which could possibly explain quantitative species differences have not been examined.

The present research was undertaken to measure acceptance of 2%, 4%, and 8% sucrose solutions in two

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species of *Peromyscus* and to determine by correlational techniques the relation of age, weight, water intake, and "preference" threshold to individual differences in intake from the suprathreshold concentrations. A degree of explanatory value by thresholds was predicted on the basis of Fechner's psychophysical scaling law and assumptions about the relation of sucrose intake to stimulus (concentration) and sensory (sweetness and "hedonic intensity") factors.

A single stimulus procedure was used to measure 24-hr. intake of water and sucrose solutions by *P. m. bairdi* (n = 36) and *P. polionotus* (n = 29). In Experiment 1 *P. m. bairdi* were found to drink significantly less water than *P. polionotus* and were less responsive to sucrose as indicated by higher "preference" thresholds. Sucrose thresholds were defined by a variety of criteria involving either amount of increase in intake from or percentage of subjects drinking more from the low concentrations of sucrose. By all criteria the *P. polionotus* threshold estimates were lower than the corresponding *P. m. bairdi* threshold values. In Experiment 2 no significant species differences were found in 2%, 4%, and 8% sucrose intake for the same animals. Intake increased significantly over the range of concentrations, but differences in sweetness accounted for only an estimated 10% of the variance in sucrose consumption by either species.

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Multiple correlation and regression analyses revealed that 65% or more of the variance in *P. polionotus* intake from each of the three concentrations could be explained by differences in voluntary water intake, age, weight, and threshold, while for *P. m. bairdi* 37% or less was accounted for by these variables. Both water intake and threshold in that order explained a significant proportion of the variability in *P. polionotus* sucrose intake. Only the threshold was uniquely associated significantly with intake among individual *P. m. bairdi*. The results suggest that taste and satiety factors operated differently in these species to determine similar levels of sucrose intake. It is uncertain whether taste factors were more important in determining amounts of sucrose consumed among individual *P. m. bairdi* or whether *P. polionotus* were able to exchange fluids less rapidly than *P. m. bairdi*. The results provide indirect support for the extension of psychophysical laws to the scaling of taste in deer mice.

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INTERSPECIFIC AND INTRASPECIFIC COMPARISONS OF SINGLE-BOTTLE SUCROSE INTAKE IN *PEROMYSCUS*

By

Douglas W. Bloomquist

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology

1971

TO MY PARENTS

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Many persons at Michigan State University, at the U.S. Army Natick Laboratories where I was stationed when earlier stages of the writing was accomplished, and at State University College, Oneonta, New York, where the work was completed, contributed generously of their time and talents to assist in the completion of this dissertation. I am particularly grateful to those I have chosen to acknowledge here for their substantive contributions at various stages of the project--from the inception of the problem in October, 1967, through the typing of the final draft in September, 1971.

I am indebted to my major professor, Dr. Ralph Levine, who carefully supervised all stages of the research and who prodded me effectively at such times that it was necessary. I am also appreciative of the assistance and patience extended by the other members of the committee: Dr. Theodore Forbes; Dr. Mark Rilling; Dr. John King, who also generously supplied the animals used in the research; and Dr. Glenn Hatton, who offered constructive suggestions on data analysis.

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I wish to express my gratitude to those persons who contributed their time and skills to the analysis of data and to typing of various drafts of the dissertation. I am particularly thankful to Dr. Gerald Gillmore, who provided extensive consulting on the use of the computer and who prepared various programs for data analyses; to Mrs. Laura Crane, who wrote the computer programs for the analyses of water intake; and to Mrs. Penny Vedder for assistance in stepwise regression and other analyses. Mrs. Rhonda York and Miss Carol Russell helped to prepare the data for analysis. I wish to acknowledge the conscientious efforts of the women who were responsible for preparing readable versions of the drafts: Mrs. Rosalind Kopelman, Mrs. Virginia Eldredge, Mrs. Eloise Maguire, Mrs. Thelma Apicella, Mrs. Sandy Bilka, and Mrs. Peggy Fuente.

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LIST OF TABLE

LIST OF FIGUR

Chapter

I. INTROD

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II. SUCROSE

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TABLE OF CONTENTS

Page

LIST OF TABLES viii

LIST OF FIGURES xi

Chapter

I. INTRODUCTION 1

The Problem of Individual Differences in Taste 3
Sources of Individual Differences 8

Age, weight, and water intake 11
Sucrose thresholds and Fechner's Law 12

The Subjects 17
Purposes of the Research 19

II. SUCROSE THRESHOLDS 21

Threshold Measurement Procedures 23
Reported Sucrose Thresholds for the Rat 24
Evaluation of Threshold Methods 28
The Problem of Defining Thresholds . . . 31
Definitions of Rat Taste Thresholds . . . 33

Single-bottle thresholds 36

Experiment 1 40

Method 42

Subjects and Housing Conditions 42
Preparation of Solutions and Apparatus 44
Design 45
Procedure 46

Chapter

Res

M

Water
Estim
Sucro
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III. SUPRATH

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Subje
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Desig
Proce

Re
Di

Chapter Page

Results 48

Missing data 49

Water Intake 49
Estimates of Proportion of Variance . . . 50
Sucrose Intake 53
Sucrose Thresholds: Group Data 58

Definitions 58
Threshold estimates 59

Sucrose Thresholds: Individual Data . . 63

Definitions 63
Assignment of threshold values above 2% 71
Threshold estimates 72

Discussion. 75

Water Intake 76
Sucrose Intake and Threshold Estimates 78

Group threshold estimates 80
Individual threshold estimates 81
Limitations of threshold criteria . . 83
Comparison of deer mice and rat thresholds 85

III. SUPRATHRESHOLD SUCROSE INTAKE 88

Sucrose Preference in the Rat 88
Sugar Preference in Deer Mice 93
Methodological Problems and Experiential Effects 95
Experiment 2 98

Method 99

Subjects 99
Concentrations 99
Design 99
Procedure 100

Results 101
Discussion 107

Chapter

Sati
Co

C
C

Expe
Compa

IV. SOURCES
SUCRO

Inter
Multi
Reg

S

Inter

A
T
T

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Summa

ADDENDUM . . .

LIST OF REFERE

APPENDICES

Appendix

A. Data f
Indi

B. Data f
Indi

C. Abstra

Chapter Page

Satiating Factors in Sucrose Consumption 110

Osmotic dehydration 113
Caloric constancy 114

Experiential Effects 119
Comparative Taste Data 121

IV. SOURCES OF INDIVIDUAL DIFFERENCES IN SUCROSE INTAKE 124

Intercorrelation Matrices 128
Multiple Correlation and Multiple Regression 135

Stepwise regression 137

Interpretations and Limitations 151

Age, weight, and fluid intake . . . 156
Thresholds and Fechner's Law . . . 158
The roles of water and energy regulation 162

Implications and Further Research . . . 165
Summary of Research Findings 167

ADDENDUM 171

LIST OF REFERENCES 173

APPENDICES

Appendix

A. Data from Experiments 1 and 2 for Individual _P_. _M_. _Bairdi_ 181

B. Data from Experiments 1 and 2 for Individual _P_. _Polionotus_. 187

C. Abstract of Dissertation Research 193

Table

2.1 Report
Labo

2.2 Result
of D

2.3 Analys
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a Fu

2.5 Analys
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Conc

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2.9 Analys
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2.10 Thres
Bas

2.11 Resul
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2.12 Inter
Est

LIST OF TABLES

Table		Page
2.1	Reported Sucrose Thresholds for the Laboratory Rat	25
2.2	Results of Water Intake as a Function of Days for *Peromyscus*	51
2.3	Analysis of Variance of Water Intake for *Peromyscus*	51
2.4	Analysis of Variance of Water Intake as a Function of Days for *P. polionotus* . .	52
2.5	Analysis of Variance of Water Intake as a Function of Days for *P. m. bairdi* . .	52
2.6	Results of Intake from Threshold Test Concentrations by *Peromyscus*	55
2.7	Analysis of Variance of Intake from Threshold Test Concentrations	55
2.8	Analysis of Variance of Intake from Threshold Test Concentrations for *P. polionotus*	57
2.9	Analysis of Variance of Intake from Threshold Test Concentrations for *P. m. bairdi*	57
2.10	Threshold Estimates (Concentration) Based upon Group Data in *Peromyscus* . .	59
2.11	Results of Threshold Estimates (Concentration) Obtained with Different Criteria for *Peromyscus* . . .	72
2.12	Intercorrelation Matrix of Threshold Estimates for *P. polionotus*	74

Table

2.13 Interco
Esti

3.1 Results
Sucro

3.2 Analysi
Supra
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P. m
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4.5 Predic
of 2
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P. p

Table Page

2.13 Intercorrelation Matrix of Threshold Estimates for *P. m. bairdi* 74

3.1 Results of Intake from Suprathreshold Sucrose Concentrations by *Peromyscus* . . 102

3.2 Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *Peromyscus* 103

3.3 Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *P. polionotus* 105

3.4 Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *P. m. bairdi* 105

4.1 Intercorrelation Matrix of Predictor Variables for Intake of 2%, 4%, and 8% Sucrose Solutions in *P. polionotus* 130

4.2 Intercorrelation Matrix of Predictor Variables for Intake of 2%, 4%, and 8% Sucrose Solutions in *P. m. bairdi* 130

4.3 Proportion of Variance in 2%, 4%, and 8% Sucrose Intake Accounted for by Water Intake, Age, and Weight for *P. polionotus* by Using Stepwise Regression 143

4.4 Proportion of Variance in 2%, 4%, and 8% Sucrose Intake Accounted for by Water Intake, Age, and Weight for *P. m. bairdi* by Using Stepwise Regression 143

4.5 Prediction with Raw Score Coefficients of 2%, 4%, and 8% Sucrose Mean Intake by Water Intake (X_1) and AL 4 (X_2) in *P. polionotus* 145

Table

4.6 Predict
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Inta

4.7 Regress
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Table Page

4.6 Prediction with Raw Score Coefficients of 2%, 4%, and 8% Sucrose Mean Intake by AL 4 (X) in P. m. bairdi 145

4.7 Regression Analyses for Prediction of 2%, 4%, and 8% Sucrose Intake by Water Intake and Threshold Value (AL 4) in P. polionotus 147

4.8 Regression Analyses for Prediction of 2%, 4%, and 8% Sucrose Intake by Threshold Value (AL 4) in P. m. bairdi 147

A1 Water Intake for Six Days in Experiment 1 by P. m. bairdi 181

A2 Intake from Threshold Test Solutions during First and Second Presentations in Experiment 1 by P. m. bairdi 182

A3 Age, Weight, Mean 6-Day Water Intake, and Threshold Values for P. m. bairdi . . 185

A4 Intake from Suprathreshold Sucrose Solutions during First and Second Presentations in Experiment 2 by P. m. bairdi 186

B1 Water Intake for Six Days in Experiment 1 by P. polionotus 187

B2 Intake from Threshold Test Solutions during First and Second Presentations in Experiment 1 by P. polionotus 188

B3 Age, Weight, Mean 6-Day Water Intake, and Threshold Values for P. polionotus . . 191

B4 Intake from Suprathreshold Sucrose Solutions during First and Second Presentations in Experiment 2 by P. polionotus 192

Figure

2.1 Percenta
intake
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2.2 Three hy
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4.2 Distribu
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LIST OF FIGURES

Figure — Page

2.1 Percentage of subjects for which sucrose intake exceeded water intake as a function of concentration 62

2.2 Three hypothetical intake curves illustrating different ways a threshold criterion could be satisfied (explained in text) 67

4.1 Percentage of variance in sucrose intake accounted for by voluntary water intake, threshold value (AL 4), weight, and age in *P. polionotus* and *P. m. bairdi* by stepwise regression 141

4.2 Distribution of residuals in ml. for *P. m. bairdi* and *P. polionotus* as a function of concentration 149

4.3 Residuals in ml. as a function of concentration for the three *P. m. bairdi* and *P. polionotus* individuals which demonstrated the smallest (A), the largest positive (B), and the largest negative (C) deviations from predicted 2% sucrose intake 153

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Chapter I

INTRODUCTION

Comparative studies of taste behavior have been undertaken for a variety of reasons and with an assortment of substances, particularly sugars. The incentive or reward properties of sucrose have been studied in motivational and learning studies (e.g., Guttman, 1953; Young & Shuford, 1954, 1955). As carbohydrates, glucose and sucrose contain calories, and they have been used as a liquid foodstuff in studies of appetite and food regulation (e.g., Jacobs, 1962; Young & Greene, 1953). For wild animals taste is ascribed a role in the ingestion of nutrients (Kare, 1961) which means that in order to survive animals must be able to detect food, to reject poisons, and to discriminate between edible and inedible substances (Young, 1968). Because of the assumed biological significance of taste, detection thresholds for various substances representative of the four primary taste qualities (for man, at least) have been measured in order to determine differential sensitivity to various chemicals. In general, though most comparative taste

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studies have been concerned with relative acceptability or preference functions for taste substances (especially sugars) differing in concentrations.

Species differences in response to taste solutions have been reported both in kind and in degree. For example, Kare (1961) reported that the rabbit, hamster, rat, calf, and man respond positively to sucrose, while the chicken and cat, under non-deprived conditions at least, are relatively indifferent. Species differences have been reported in other studies (e.g., Carpenter, 1956; Fisher, Pfaffmann & Brown, 1965) to other substances. Among rodent species, however, the response to sugars has reportedly varied more in degree than in kind. For example, the response to sugars in wild and domesticated rats (Maller & Kare, 1965) or among various subspecies of the *Peromyscus* deer mouse (Wagner & Rowntree, 1966, 1970) have been expressed as qualitatively similar, but quantitatively different. Because various rodents generally have shown a preference for sugars differing in kind (e.g., sucrose, glucose, fructose) and in sweetness (concentration, or amount of solute in solution), it has been observed that rodents share in common a "sweet tooth" (Wagner & Rowntree, 1970).

Intraspecific differences in taste responses have been noted, also. Ficken & Kare (1961) found a considerable range of thresholds in chickens for chloride

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substances. Kare (1961) reported individual differences in acceptability of fructose in calves, of quinine, saccharin, and sucrose solutions in pigs. Pronounced strain and individual differences have been observed for alcohol preferences in house mice (Rodgers & McClearn, 1962). Young (1966) reported consistent differences among individual rats in preferences for compound solutions which contained both sucrose and sodium chloride. Levine (1968) found that a group intake curve for five sucrose solutions presented simultaneously did not correspond to the curve of a single one of 15 house mice used and that none of the individual curves was the same. Wagner (1968b) noted individual differences within several species of deer mice (*Peromyscus*) and Kangaroo rats to fructose and glucose.

The Problem of Individual Differences in Taste

The incidence of both interspecific and intraspecific differences prompted Kare (1961) to conclude that it is reasonable to assume that each species lives in an isolated taste world and ". . . the unique taste patterns of species or individuals can be a natural opportunity to explain the mechanisms . . ." (p. 15). However, little attention has been given to the importance of individual differences or to their determinants. The apparent lack of interest in individual differences is

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not unique to comparative studies of taste behavior, though. Vale & Vale (1969) recently complained of the failure to incorporate individual differences into general laws of psychology. Indeed, they point out, interaction effects involving subjects in analyses of variance designs seem to be a "nuisance" to investigators interested in determining the effects of some variable on behavior. They add that "interaction often still retains the taint of 'messiness' that derives from main effects thinking."

Other problems with what Vale & Vale (1969) would refer to as "main effects thinking" have been raised. For example, highly reliable results (i.e., statistically significant main effects) may represent weak effects. That is, replicable differences may be found among means due to differences in the values of the independent variable(s), but variability among the individual subjects within the groups or treatment conditions may be comparatively greater than the variability of means for the levels of the treatments. Consequently, the strength of an effect will be weakened to the extent that such individual differences are found.

In taste studies, a Treatment X Subjects design with repeated measures is commonly employed in which each subject is presented with several concentrations of the same substance individually (either singly or with water)

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in a random order. Typically, the amount of fluid consumed (intake) is the dependent variable, although preference may be expressed in relative intake terms when paired with water (see Chapters II and III). Across the range of concentrations presented, intake for sucrose usually is found to increase within a certain range. Accordingly, the appropriate analysis of variance produces a significant Treatment (i.e., Concentration) effect. Individual differences in intake with a sample of animals is revealed both by the Subjects effect, which represents differences in level of fluid intake averaged across all concentrations, and by the Treatment X Subjects interaction which represents differences in the intake patterns or "profiles" of individual subjects to the taste solutions presented (see Lindquist, 1953). Where significant interactions are found, the interpretation of the Concentration effect should be tempered, for it reveals that subjects are not affected similarly by differences in treatments, i.e., their intake patterns differ.

Hays (1963) and others have described procedures for estimating the strength of association between independent and dependent variables. Such procedures which are applicable to designs amenable to analyses of variance provide information similar to that obtained by coefficients of determination used in correlation and regression analyses; they enable one to estimate the

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proportion of variance accounted for by the independent variable(s), which, therefore, provides a measure of the strength of the main effect(s). One survey of published psychological studies found that statistically significant effects accounted for surprisingly little of the total variance in many experiments (Dunnette, 1966).

While individual differences have been observed in comparative taste studies, inquiry into underlying determinants of interspecific and intraspecific differences in taste behavior has not been seriously undertaken. Unfortunately, the majority of taste studies with animals have been performed with a few domestic (e.g., chicken) and laboratory (e.g., rat) species (see Kare & Ficken, 1961). The usefulness of these data for evaluating the postulated functional significance of taste is, therefore, diminished. Indeed, attempts to establish the adaptive function of taste for animals have been generally unsuccessful, although the postulated assumptions are reasonable. While a seemingly disproportionate number of taste studies have been performed on the laboratory rat, more work is needed because of conflicting conclusions over the roles of taste and post-ingestional "regulatory" and satiety factors in determining preference functions (see Chapter III).

Mechanisms found to underlie the taste behavior of laboratory rats may or may not be appropriately

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extended to other rodent species which also exhibit a positive response to sweet substances. McClearn (1967, p. 309) presenting a view shared by behavior geneticists points out that:

> failure to appreciate the implications of biological individuality has resulted in a state of affairs wherein many investigators expect that an obtained result has universal application--to all rats, or all monkeys, or even to all mammals. The explanation of discrepant results from other investigations is usually sought in terms of subtle differences in apparatus to technique, and the possibility is rarely considered that there exist different subgroups within a species to which different rules apply.

In apparent contrast with McClearn's position, Vale & Vale (1969, p. 1096) argue:

> It is true that the organisms with which we deal are in most instances both biologically and environmentally unique, but it does not follow that all differences among organisms express differences in basic processes.

The extent to which taste behavior can be generalized across species is partially a matter of what kinds of data one chooses to consider. It seems to be widely accepted that sucrose and other sugars, for example, are universally preferred substances for a wide variety of rodents and other mammals. Moreover, quinine substances, which are discriminable in much smaller quantities than sucrose, generally are found also to be aversive to most animals. Accordingly, these data suggest that a wide variety of species share certain taste processes or mechanisms in common. Curiously, among a variety of rodents

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and other mammals similar shaped taste preference patterns to sucrose solutions of varying concentrations have been obtained with a wide variety of experimental designs, methods, procedures, and dependent variables (see Chapter III).

Support for the former view which suggests that permissible generalization may be narrow in scope comes from comparative data showing quantitatively different, though qualitatively similar, responses to preferred substances. In addition, the fact that the general shape of preference curves is relatively impervious to departures in experimental procedure does not necessarily mean that similar behaviors are being measured or that the underlying determinants are similar, even within a species. For example, in relatively long-term intake studies (e.g., 24-hr. intake) certain postingestional consequences are said to influence intake (see Chapter III) which would be diminished or eliminated in brief-exposure or short-term intake (e.g., 1-hr.) tests.

Sources of Individual Differences

Where interspecific and intraspecific differences are found with respect to degree of preference for a particular taste substance, the question arises: what is the source of these differences? What are the underlying determinants? Different selection pressures and energy

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requirements have been cited as probably being responsible for species differences in sugar preference (e.g., Maller & Kare, 1965). With respect to individual differences within a species, however, Young (1968) observes that "the correct interpretation of such differences is an open problem."

Because investigators are not in agreement over the relative roles of taste and postingestional factors in determining sucrose intake functions, even for the widely studied rat (see Chapter III), it seems appropriate to inquire into possible sources of individual differences in rodents. While it is convenient to dismiss such differences as "biological uniqueness," it would be useful if individual differences in relatively genetically heterogeneous groups of animals could be accounted for to a respectable extent by factors which do not require genetic manipulation, and which might reasonably be expected to underlie intake of taste solutions.

Surely genetic factors play a role in determining responses to taste substances. A genetic basis for saccharin preference in rats (Nachman, 1959) and for the ability of human beings to taste the synthetic compound, PTC (Blakeslee & Fox, 1932), has been found, for example. However, while the individual differences observed in thresholds and preference for taste substances may have a

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genetic basis, it is not so easy to link underlying genetic causes to a complex of more observable variables which may be related in varying degrees to ingestion of taste solutions. Thus, whereas the basis of individual differences in taste thresholds may be largely genetic, the variability in intake from concentrations may be related to other and more measurable factors, including thresholds.

Not surprisingly, taste preferences can be modified by experience. Young (1959) has summarized the roles of deprivation, satiation, habituation, and learning in altering preferences for foodstuffs such as sucrose, for example. But, in the usual taste preference experiment, experimentally naive and, commonly, nondeprived animals are used. Frequently in such studies the investigators do not examine the effects upon intake of repeated presentations to the same or different taste solutions. Instead, potential experiential effects are averaged out by pooling intake recorded over two or more test periods to depict the role of "taste" factors in preference curves. However, it is clear that experiential effects do occur which probably contaminate conclusions (see Chapter III).

While genetic factors, dietary manipulations, and experience will underlie individual differences and variability in taste behavior, it was of interest in the

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present research to determine by correlational techniques (see Chapter IV) to what extent several demographic and behavioral variables may be associated with interspecific and intraspecific differences in long-term (24-hr.) single stimulus intake of sucrose solutions in two rodent subspecies. The variables deemed as probably possessing a certain degree of explanatory value for acceptance of sucrose solutions measured by fluid intake were age and weight, voluntary 24-hr. water intake (apparent water need), and a sucrose "preference" threshold estimate (taste related).

Age, weight, and water intake. In the situation where amount of fluid consumed is the measure of acceptance, individual differences in levels of fluid intake may be expected to vary with differences in age and weight, which in turn may be associated with voluntary consumption of water. Age and weight are normally highly correlated, of course. But, few studies have examined solution ingestion and preferences as a function of age. Bloomquist & Candland (1965) found that deprived rats 10-months old consistently made fewer licking responses to water and solutions of varying palatability in comparison with 1- and 5-month old rats. However, fluid consumption of rats maintained on *ad libitum* water was found to be an increasing function of age for rats ranging in age from 1- to 25-months (Goodrick, 1969).

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Wagner (1965) found that absolute intake of glucose solutions was affected by weight, though age alone produced no differences in relative preference for two sweet solutions.

Differences in levels of voluntary water consumption would be expected to be related to amounts of sugar solution ingested if palatability factors were relatively equivalent among the animals. That is, if the palatability of the taste solutions stimulate similar levels of "affective arousal" or "hedonic intensity" (Young, 1959) among individuals, and if it can be assumed that intake from sweet solutions will be proportional to hedonic intensity, then individual differences in amount of solution ingested from a given concentration may be largely accounted for by levels of voluntary water intake. In other words, an animal with a relatively high level of water intake would be expected to exhibit relatively greater intake from a sucrose solution than an animal with a lesser apparent water need, if the solution possesses equal incentive value for each subject.

Sucrose thresholds and Fechner's law. Variation in the slopes or shapes of intake patterns across a range of concentrations among individuals would be revealed by the Concentration X Subject interaction. To the extent that such an interaction effect is found it would indicate that sucrose intake was determined by

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more than constant palatability (taste) factors combined with level of water intake. Moreover, the assumption of an equal palatability effect for all animals itself is questionable on the basis of psychophysical principles.

Taste preference studies may be viewed as a psychophysical scaling situation in which magnitude of sensation is related to stimulus intensities. Young (1959, 1968) argues that taste solutions of different concentrations (and, therefore, different sweetness) will differ in "intensity of positive affectivity" or in "relative hedonic intensity" which they arouse. More sustained drinking in two-choice tests is found for a sweeter concentration because, in Young's motivational terms, the solution arouses greater hedonic intensity. Because animals will generally consume more of sweeter sucrose solutions, for convenience let it be assumed that the increases in intake are proportional to the "hedonic intensity" aroused by the palatable characteristics of the substance. Accordingly, a taste preference function may be viewed as a scaling situation in which the magnitude of sensation for sweetness or sweet solutions ("hedonic intensity") as measured by level of intake is related to stimulus intensity (concentrations).

The earliest expression of a lawful relationship between sensation and stimulation was formulated by Fechner in 1860 (see Woodworth & Schlosberg, 1954).

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Fechner's Law simply states that magnitude of sensation is directly a function of the logarithm of stimulus intensity. In other words, sensation is not directly proportional to stimulus intensity; instead, it is logarithmically proportional.

Beginning with Fechner's Law, the history of psychophysics has been characterized by a search for a universal law intended to be general for all modalities (Stevens, 1962). While such laws have been generated for the human population, there is some basis for expecting that Fechner's formulation may prove useful for explaining individual differences in taste preference among rodents. Young & Greene (1953) presented pairs of sucrose solutions to rats in brief exposure tests and they found that rats selected the higher of the concentrations in preference to the lower. Moreover, when the choice results were scaled by a modified pair comparison procedure and plotted against the logarithm of the concentration, they found a nearly straight line function. Accordingly, the level of acceptability of sucrose with this procedure was found to be directly proportional to the logarithm of the concentration. In addition, Young (1959) suggested that this relationship holds all the way up the scale from the preference threshold which is the lowest concentration at which a preference for sucrose to water is evident.

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Although Young & Greene (1953) did not point out the agreement, their conclusion is a statement of Fechner's psychophysical scaling law. Since their choice data of sucrose pairs conformed to Fechner's formulation, it is tempting to consider the possibility that other measures of sucrose preference, e.g., absolute intake, may conform similarly to a logarithmic relationship. Young (1968) appropriately points out that brief-exposure tests should isolate taste factors more clearly than long-term intake tests of preference. However, sucrose intake functions for concentrations ranging up to about 8% are generally monotonically increasing for concentrations varying in logarithmic steps and they are explained in terms of increasing taste (palatability) factors (Beck, 1967). For example, the intake curve for the rat obtained by Owings _et_ _al_. (1967) is a nearly logarithmic function.

Although an overall logarithmic relationship may be found between intake and concentration for the rat, it is not at all certain that the relationship will hold so nicely for individual subjects or for other rodent species. But, the basis for adopting Fechner's psychophysical law to account for individual differences in sucrose intake is that individuals with different thresholds for sucrose should experience different "hedonic intensities" (i.e., sensation magnitudes) for a given

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concentration of sucrose above threshold. Because an undetectable concentration would arouse a sweetness sensation of "zero" intensity, and because sensation magnitude increases logarithmically according to Fechner's Law, then it follows that animals with different sucrose "preference" thresholds should exhibit similar slopes in their intake functions, although the intercepts of these functions will differ. For example, if two animals are found to have different thresholds, then the increase in sucrose intake to concentrations above the thresholds should be inversely related to their sensitivity to, or initial preference for, tasting sucrose. The animal with a lower threshold should experience a greater "hedonic intensity" to a given suprathreshold concentration than an animal with a higher threshold; consequently, the greater "hedonic intensity" should be translated into a proportionally larger increase in intake for the individual with the greater sensitivity. Therefore, thresholds would be expected to correlate inversely with sucrose intake.

The relationship between sucrose taste thresholds and intake from suprathreshold concentrations has not been empirically established, although both thresholds and intake have been exhaustively studied independently, for the rat at least. Typically, experimenters have focused on one problem or the other. The extent to which

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this model derived from psychophysical scaling laws will be useful for explaining sucrose intake behavior will depend upon a variety of factors, of course, including the adequacy of Fechner's law to taste, the validity of the underlying theoretical assumptions about the interrelationships of palatability, hedonic intensity, and intake, and also the reliability of the intake measures. However, on both theoretical and empirical grounds it is considered likely that this kind of linear psychophysical model will provide a certain degree of explanatory power for individual differences in sucrose intake, in addition to knowing an animal's age, weight, and voluntary water intake.

The Subjects

The use of inbred strains of laboratory rats or mice presumably would preclude the genetic variability desired in the subjects of the present research. For, while genetic factors would be expected to underlie individual differences in sucrose "preference" thresholds which are assumed to approximate detection ability for the substance (see Chapter II) and levels of daily water intake, the intent of the present research is to examine the association of these other variables with sucrose intake among a relatively heterogeneous sample of animals within a particular species. In addition, because

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of the questions raised about the generality of sucrose preference in rodents, it was deemed desirable to make interspecific comparisons of rodents not far removed from their wild state.

Two subspecies of deer mice were chosen for interspecific and intraspecific comparisons. *Peromyscus maniculatus bairdi* and *Peromyscus polionotus* are two of 38 species which are taxonomically classified in the *Peromyscus* genus, subgeneus and species, and which belong to the *maniculatus* group. According to Hooper (1968) *P*. *polionotus* and *P*. *maniculatus* are closely related genetically, as they are thought to be derived from the same parental stock. However, ecological barriers have kept the two species relatively distinct and presumably they have been exposed to different selection pressures. *P*. *m*. *bairdi*, a grassland animal, is found in the east-central region of the United States. *P*. *polionotus*, also mainly a grass-dwelling animal is distributed in the southeastern region of the United States, both on the mainland and along coastal regions (Baker, 1968, p. 114; Hooper, 1968, p. 42).

Both species have proved to be ideally suited for laboratory conditions. All mice used in the present study were laboratory stock several generations descended from wildcaught parents.

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The literature on habitat selection, population dynamics, physiology and behavior is more comprehensive for *P. m. bairdi* than *P. polionotus*. For both subspecies, however, there is an evident lack of information on the perceptual and sensory capabilities of these animals (King, 1968, p. 523). Moreover, only a few studies have examined deer mice preferences for various sugars (see Chapter III), and no systematic studies of threshold determinations or other measures of taste discrimination have been reported.

Purposes of the Research

On the basis of empirical data and psychophysical theory, it was argued that age, weight, voluntary water intake, and threshold estimates would be likely to account to an unknown extent for individual differences in sucrose consumption. The relative explanatory value of these variables has not been systematically established for any population of animals. Moreover, it is possible that the amount of variability which these variables can explain may vary for different species. Accordingly, the major purposes of the present research were as follows: For *P. m. bairdi* and *P. polionotus*, (1) determine intake and reliability of intake for water and a range of sucrose concentrations up to 8%; (2) obtain estimates of a sucrose "preference threshold" for the individual

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animals and assess the agreement among thresholds defined by different criteria; and (3) determine the proportion of variance in sucrose intake from three suprathreshold concentrations (2%, 4%, and 8%) accounted for by age, weight, voluntary water intake, and a threshold estimate for each subspecies. Finally, the usefulness of the psychophysical model derived from Fechner's law for describing sucrose intake functions is to be considered.

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Chapter II

SUCROSE THRESHOLDS

In general terms a "threshold" refers to an organism's ability to detect the presence of some stimulus, and it is usually expressed in units of the physical stimulus. Specifically, with respect to taste behavior for which the stimulus is invariably presented in a fluid medium, the threshold is expressed as the minimal concentration (amount of taste chemical substance dissolved in water) to which a specified behavioral response is obtained.

When one considers the interest in the biological adaptive function of taste, it is surprising that so few species have been tested for their sensitivity to sucrose and other substances. Virtually all such rodent data have been concerned with the laboratory rat. No taste thresholds for sucrose or other taste substances have been reported for *Peromyscus*. And, while the sensitivity of the rat for sucrose is well documented, the reported threshold values vary considerably. This variation can be attributed partially to the fact that widely different

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psychophysical procedures, response measures, and threshold definitions have been employed in these studies. Accordingly, to a certain extent the discrepancies in results are understandable. Because the problems involved in determining the rat's sucrose threshold are the same for other rodent species, it is appropriate here to examine the data and problems associated with the measurement of the rat's threshold.

The concept of a "threshold" is, itself, somewhat controversial. Some opponents argue that a threshold is a meaningless concept because of the fact that it is so variable in nature and it is variable depending upon how it is measured. At the other extreme, though, investigators have demonstrated, perhaps unwittingly, a tendency to regard thresholds as invariate entities, the values of which will vary only with differences in methodology.* However, estimates of individual and group thresholds have proven to be useful for delineating relative differences in sensitivity to various substances of a given taste quality (e.g., sugars) or of different taste qualities (taste, sour, bitter, salty). Moreover, if relative

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*The term "threshold estimate" is probably a more appropriate term for describing an animal's ability to discriminate sucrose in water. Accordingly, the term "threshold estimate" shall be used generally in presenting and discussing the results of Experiment 1. However, for convenience the term "threshold" will be used elsewhere in this dissertation with the understanding that it is always considered to be an estimate.

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differences in the discriminative ability of different species for a single substance (e.g., sucrose) can be observed with the use of one or more procedures, then it can be argued that such determinations are useful for making interspecific comparisons of taste sensitivity.

Threshold Measurement Procedures

Essentially three different methods have been employed to measure thresholds, and a variety of modifications have been used with each. The methods can be characterized as (1) the preference or free-choice method, (2) the discrimination or forced-choice method, and (3) the electrophysiological recording method. In the preference or free-choice method the animal is allowed to drink *ad libitum* from either of two bottles, one containing the taste substance and the other containing water (Campbell, 1958; Richter & Campbell, 1940a,b). The total intake from each solution is measured over a relatively long period (e.g., 2- to 24-hr.). A more recent modification of the free-choice procedure, first described by Young & Kappauf (1962), utilizes a series of brief exposure tests in which the number of tongue licks rather than fluid intake is measured; Beck, Self & Carter (1965) and Burright & Kappauf (1963) have used this procedure to determine sucrose thresholds.

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In the discrimination method the animal is presumably motivated either to discriminate between the solution and water for food reward or to avoid punishment for failure to discriminate. Carr (1952) and Harriman & MacLeod (1953) used this general procedure for determining salt thresholds, and Koh & Teitelbaum (1961) used both procedures to compare thresholds for a variety of solutions including sucrose.

Electrophysiological procedures have been used to obtain the "nerve response threshold" by measuring the "whole nerve" response to solutions of different concentrations (e.g., Hagstrom & Pfaffmann, 1959).

The usual procedure with any of these methods is to present a range of concentrations of the solution varying from subliminal to supraliminal values. The concentrations are presented in either an ascending and/or descending series, or in a random or counterbalanced order. The former procedure is sometimes called the "up-and-down" or "staircase" method (Guilford, 1954), and it is analagous to the psychophysical method of limits; the latter procedure resembles the method of constant stimuli.

Reported Sucrose Thresholds for the Rat

The sucrose thresholds reported for the laboratory rat are presented in Table 2.1. They are ordered

Threshold & Method
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.43% p
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TABLE 2.1

Reported Sucrose Thresholds for
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Threshold & Method	Motivation	Dependent Variable	Reference
.15% p	dep	intake 20-hr.	Campbell (1958)
.21% p	dep	intake 2-hr.	Campbell (1958)
.21% d	dep	"tracking"	Koh & Teitelbaum (1961)
.32% p	nondep	licks 4-min.	Burright & Kappauf (1963)
.34% e	nondep	nerve response	Hagstrom & Pfaffmann (1959)
.43% p	nondep	licks 4-min.	Beck *et al*. (1965)
.45% p	nondep	intake 20-hr.	Campbell (1958)
.47% d	nondep	"tracking"	Koh & Teitelbaum (1961)
.50% p	nondep	intake 24-hr.	Richter & Campbell (1940b)
.57% p	nondep	intake 24-hr.	Richter & Campbell (1940a)
.75% p	nondep	intake 2-hr.	Campbell (1958)
1.16% p	dep	licks 4-min.	Beck *et al*. (1965)

Note: Motivation refers to whether the rats were deprived (dep) or nondeprived (nondep).

[p] Preference or free-choice method.

[d] Discrimination or forced-choice method.

[e] Electrophysiological method.

by the magnitude of threshold value expressed in terms of concentration. Threshold concentrations are generally expressed as a percentage (weight/volume, or gm. solute/100 ml. solution x 100). It is not always clear, however, particularly in reports of early studies, whether the percentage specified is by weight/volume or weight/weight.

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The former is the most common way of preparing concentrations, but this lack of conformity in preparation and specification of solutions is what prompted Pfaffmann, Young, Dethier, Richter & Stellar (1954) to suggest that all solutions be expressed in molar concentration.* It was assumed for present purposes that the concentrations were prepared by weight/volume. The general method (preference or two-choice, discrimination or forced-choice, and electrophysiological), motivational state (deprived or satiated), and type of dependent variable used are also indicated in Table 2.1.

The summary of results presented in Table 2.1 shows that no one type of method consistently produced similar results. For example, the lowest and highest threshold values were obtained with deprived animals using a preference method. The results do not favor one type of dependent variable over another, either, for variably high and low thresholds have been obtained with 2- to 24-hr. intake and 4-min. tongue lick measures. One pattern does seem to emerge from these results, however; higher thresholds were generally found with nondeprived animals, regardless of the method or dependent variable used (although they are somewhat lower with 4-min. tests).

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*Sucrose concentrations expressed as weight/volume can be converted to molarity by the equation

(gm. per 100 ml.) X 10/ 342.3 = molarity,

where 342.3 is the molecular weight for sucrose (Pfaffmann _et_ _al_., 1954).

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It is noted that the twelve threshold values presented in Table 2.1 were obtained from only seven studies. Thus, in some cases two (e.g., Beck et al., 1965; Koh & Teitelbaum, 1961) or even four (e.g., Campbell, 1958) different threshold estimates have been reported in the same study. Such results afford an opportunity to compare more readily the consequences of using different procedures. Accordingly, it is seen that Campbell (1958) who used 2-hr. and 20-hr. intake measures found the two lowest threshold values in deprived rats. Koh & Teitelbaum (1961), using a discrimination method, obtained similar results. Beck et al. (1965), though, found the opposite results with tongue lick measures on deprived and non-deprived rats.

It is generally assumed that a preference method will provide higher threshold values than a discrimination method. The thresholds obtained with the free-choice or preference method are generally described appropriately as "preference thresholds" (Beck et al., 1965; Burright & Kappauf, 1963; Campbell, 1958), for such a threshold represents the lowest concentration for which the animal initially showed a preference for the taste solution to water. Pfaffmann & Bare (1950) have argued that a distinction should be made between the physiological threshold and the more variable preference threshold. Campbell (1958) agrees that the preference threshold is not

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synonymous with, or even necessarily related to, the sensory threshold. Behind this distinction is the reasonable assumption that the rat may not necessarily demonstrate a preference for a taste substance at a concentration at which it is just discriminable from water. Harriman & MacLeod (1953) suggested that "one might even argue that even the absolute threshold is really a preferential threshold under optimum conditions of stimulation and motivation."

Evaluation of Threshold Methods

The distribution of threshold values in Table 2.1 suggests that the rat's sensitivity for sucrose is not necessarily overestimated by a "preference threshold" estimate. The rat's sucrose threshold is commonly reported as approximately .50%, which is the concentration reported by Richter & Campbell (1940b) and is nearly the median threshold of those presented in Table 2.1. However, the wide range of thresholds (.15% to 1.16%) raises questions about which procedure will reliably provide the best measure of the rat's threshold for sucrose. Unfortunately, standard errors of the mean and confidence intervals have not been reported in a single study of taste thresholds. Moreover, in some studies, such estimates would be impossible to obtain, because the reported thresholds are based upon the pooled data of individual

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subjects, rather than upon means of individual thresholds. It is difficult, therefore, to determine how discrepant many of the reported thresholds may be.

One reasonable criterion for selecting the best single procedure for estimating the rat's sucrose threshold would be the method which produces the lowest threshold. In this respect, Campbell's (1958) 20-hr. or 2-hr. preference test for hungry rats, or Koh & Teitelbaum's (1961) tracking procedure for hungry rats would appear to be equally suitable, for thresholds between .15% and .21% were obtained with these entirely different procedures. Another criterion would be the method which yields a threshold corresponding closest to the absolute physiological threshold in nondeprived rats. Indeed, Burright & Kappauf (1963) suggested that their 4-min. test may, in fact, be more sensitive than the 2-hr. test used by Campbell (1958), and they point out that their threshold of .32% "agrees very closely with the 'nerve response threshold' as reported by Hagstrom and Pfaffman (1959)."

Such comparisons may be fortuitous, however. The implications from these kinds of comparisons is that there is a relatively stable taste threshold among laboratory rats and that some methods lend themselves to tapping the "true" threshold better than others. Moreover, implicit in this kind of reasoning is the questionable assumption

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(McClearn, 1967, p. 309) that laboratory rats of diverse strains do not differ in their response to sucrose.

Clearly, methodological differences will provide different results. It appears that deprived animals in either preference or discrimination tests will produce somewhat lower sucrose thresholds (e.g., Campbell, 1958; Koh & Teitelbaum, 1961), although it is not clear whether deprivation produces a lowered sensitivity to the taste substance, or whether lower thresholds result from an increased motivation to obtain food or to avoid shock. In nondeprived animals the duration of the intake measure in preference tests may make a difference (Campbell, 1958). In addition, some taste solutions are prepared with tap water and others with distilled water. Young & Falk (1956) found tap water to be more palatable than distilled water for rats. Schnorr & Brookshire (1965) and Brookshire & Schnorr (1965) acknowledged that rats can discriminate between the two, but they found that experience with either prior to testing can influence preference.

Investigators have been inclined to point primarily to many of the major methodological differences in their studies to reconcile different findings. Quite appropriately, Harriman & Macleod (1953) suggested that comparable thresholds would not be expected with various procedures because different motivational conditions influence psychophysical judgments (or responses); therefore,

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they conclude that "there are as many preferential thresholds as there are conditions that motivate choice." However, little or no consideration has been given to the implications of using different response measures and threshold definitions. The criteria which investigators have used to determine thresholds have differed as much as the general methods and motivational conditions employed with the rat. Yet, for some unexplainable reason the consequences of using different measures of taste behavior as well as different criteria for determining threshold concentration has been virtually ignored as a factor which may partially explain the differences obtained.

The Problem of Defining Thresholds

The so-called "preference" thresholds which presumably provide a measure of the rat's sensitivity for sucrose are less related to absolute thresholds than they are to difference thresholds which represent the minimum amount of stimulus change required for a stimulus to be perceived as different. For, analagous to classic psychophysical procedures for determining difference thresholds (DL), all sucrose threshold studies have employed two-bottle choice tests in which the animal's response to a sucrose solution is compared to water. Water, then, is used as a standard stimulus and the sucrose concentrations

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are the variable comparison stimuli. Accordingly, the so-called sucrose taste threshold is more appropriately regarded as a difference threshold for water, i.e., the minimal amount of sucrose required to be dissolved in water (gm./100 ml.) for the solution to be discriminable from water alone. After all, the threshold presumably is an estimate of the concentration at which a "preferred" substance in solution is just discriminable from water.

While the procedures employed for determining thresholds generally resemble the classic psychophysical methods of limits and constant stimuli (see Woodworth & Schlosberg, 1954, or Candland, 1968), practical limitations make it impossible to obtain more than a few estimates of an individual rat's threshold. Because of the variability in a single subject's judgments with repeated presentations of the stimuli, classic procedures require administering many trials and taking into account the systematic errors which have been identified with such procedures. In the method of limits, for example, it is generally found that thresholds will differ depending upon whether the stimuli are presented in an ascending or descending order. Rather than averaging the "thresholds" on all trials to obtain the estimated threshold value for a single subject, the threshold is interpolated between the average of the ascending and descending trials. A similar observation has been noted in one sucrose thr

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threshold study; Campbell (1958) presented two ascending and two descending series of sucrose concentrations and found that thresholds were higher on the ascending series than descending series. Yet, in most taste threshold studies on the rat only one or two ascending or descending series of concentrations is presented to the animal. For sucrose and salt thresholds ascending concentrations are given, while concentrations of aversive solutions such as quinine are usually presented in descending order.

The way in which the threshold value will be determined with classic psychophysical procedures will vary with the procedure used, for the data are treated differently. But, basically it is conventional with such procedures to define the DL as the amount of change in the value of the standard stimulus required for a comparison stimulus to be perceived as different from the standard on 75% of the trials. The assumption underlying this criterion is that a 50% criterion would represent chance guessing, while perfect discrimination (100%) is greater than the minimal discriminable difference.

Definitions of Rat Taste Thresholds

It has been common in recent taste studies to adopt a 75% response criterion for defining thresholds. However, in most cases the definitions of sucrose thresholds with the rat have shared only a superficial

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resemblance with the conventional definitions of a DL. Partially because the psychophysical judgments by the rat are expressed by its intake or licking behavior to the solutions, the 75% criterion adopted in some studies is too arbitrary to be psychophysically sound. Generally, with two-bottle free-choice preference procedures two criteria for defining thresholds have developed which utilize a 75% concept. Thresholds have been determined by noting the concentration of sucrose for which either (1) by interpolation, 75% of the relative intake (sucrose intake/sucrose + water intake) occurs, or for which (2) 75% of the subjects drank (licked) sucrose more times than water. Using free-choice preference tests Campbell (1958) defined the threshold by interpolation as the concentration where 75% of the relative intake occurred. Burright & Kappauf (1963) and Beck *et al*. (1965) used a more precise procedure involving a series of short-term tests in which the animals had to choose between sucrose and water; however in both studies the threshold was defined as the concentration at which, for 75% of the animals, more tongue licks were recorded for sucrose than for water.

Perhaps the soundest procedure for determining taste thresholds from a psychophysical point of view is the discrimination method used by Carr (1952) for salt. Carr used a forced-choice procedure in which the animals

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were shocked for failure to discriminate salt from water, and he conducted a series of 20 tests for each concentration. His threshold was determined for the average concentration for which the animals responded correctly on 75% of the trials (i.e., 15 of 20). Koh & Teitelbaum (1961) used a "tracking" procedure with hunger and shock motivation which would appear to be a precise procedure for determining a rat's ability to discriminate sucrose. They suggested, however, that shock may be a disruptive stimulus in threshold studies.

The thresholds obtained from two-bottle tests by these various definitions not only are derived from different dependable variables (e.g., intake, number of tongue licks, correct choice), but they clearly convey different kinds of numerical information about sucrose discrimination. For example, the Burright & Kappauf (1963) and Beck _et_ _al_. (1965) definition (2 above) with free-choice tests reveals what percentage of the animals preferred sucrose to water, but not by how much it was preferred. On the other hand, the relative preference measured (1 above) used by Campbell (1958) reveals the relative magnitude of preference on the average for a particular sucrose concentration, but it does not convey information about what percentage of subjects exhibited that magnitude of preference while discriminating that sucrose solution from water. Meanwhile, the discrimination

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procedure used for salt (Carr, 1952) yields the average concentration which can be discriminated as different from water 75% of the time. Thus, the adoption of the 75% relative intake criterion seems to be more arbitrary and less satisfactory a criterion than 75% correct discriminations. Designating the threshold as the concentration for which 75% of the subjects reveal a preference for sucrose ignores individual differences in both discrimination ability and relative amount of preference at the threshold level. Therefore, it seems to be the least psychophysically defensible definition of a threshold.

Single-bottle thresholds. Taste thresholds for salt and quinine, though not for sucrose, have been determined with single-bottle procedures. The single-stimulus or one-bottle method was originally introduced by Beebe-Center, Black, Hoffman & Wade (1948) for the measurement of taste preference. With this method the animal is presented with a different test fluid each day or test period. For the determination of salt and quinine thresholds rats were given 1-hr. tests following water deprivation of 15- or 16-hr. Weiner & Stellar (1951) determined the rat's salt threshold merely by noting the lowest concentration at which mean intake of salt exceeded mean water intake. This criterion for a salt threshold was similar to that used by Richter & Campbell (1940b) with a two-bottle procedure for sucrose; that is, they defined the

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threshold (.50%) as "the concentration at which rats began drinking more sugar solution and less distilled water." Benjamin (1955) presented water on alternate days and defined single-bottle quinine thresholds for individual rats "as the lowest concentration at which the test-period intake of quinine solutions was less than the water intake on the preceding or following test periods."

Because of the fact that single-bottle tests have not been used to determine sucrose thresholds, it is not possible to know how such thresholds would compare to preference thresholds obtained by a similar two-bottle procedure. Only one taste study has directly compared thresholds obtained on the same animals with both a two-bottle and one-bottle procedure. Benjamin (1955) found that the one-bottle (1-hr.) procedure yielded significantly higher quinine thresholds than the two-bottle (24-hr.) test in intact rats. However, it is apparent from the data presented in his report that the two threshold estimates were not linearly related. That is, a Spearman rank order correlation coefficient derived from the individual data presented produced an r = +.21 (n = 16) which is not statistically significant.* Therefore, the

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*The correlation coefficient was calculated by the present writer from the data presented in Benjamin's (1955) report.

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animals with higher thresholds determined by one method did not necessarily have higher thresholds as measured by the other.

Curiously, no investigator has compared sucrose thresholds obtained by different procedures and definitions. It may be found, for example, that ingestion measures with a long-term preference method may yield thresholds comparable to the somewhat lower thresholds obtained in short-term tests which use licking as the dependent variable if the relative intake criterion were arbitrarily changed to something less than 75%. It may be that at least 75% of the subjects show a preference for sucrose at the concentration for which the average relative intake is 60%, for example. Moreover, it could be determined statistically that 60% relative intake represents reliably greater intake than 50%, thus indicating that the animal is discriminating between the solutions. It would be possible, of course, to determine the percentage of subjects drinking more sucrose than water at the concentration at which 75% of the relative intake is found for sucrose. Similarly, an index of the amount of preference in the Burright & Kappauf (1963) and Beck _et_ _al_. (1963) studies could be determined by recording how many tongue licks were made for water and sucrose during each of their 4-min. test periods.

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There is no single threshold method or definition which would be suited for all purposes. An evaluation of the desirability of a particular procedure should take into account the purposes for which it is intended. For example, if the purpose is merely to obtain threshold estimates which delineate differences in the effectiveness of various taste substances, then many of these procedures may be adequate. However, if the investigator is asking questions about the cortical mechanisms underlying taste sensitivity and wishes to compare pre-operative and post-operative thresholds, then time limitations and other considerations dictated by the experimental questions should determine the choice of procedure. For example, the Burright & Kappauf (1963) procedure which gives merely a group threshold estimate at the expense of individual threshold estimates obviously would not be useful for determining the effects of surgical operations, which would have to be verified histologically. The uncertainty over the reliability of threshold estimates, over the relationship of thresholds determined by one procedure to thresholds determined by another, and over the consequences of using different criteria in defining thresholds clearly provide problems for further research into the measurement of animal taste thresholds.

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Experiment 1

Because the major purpose of the present research was to account for individual differences in sucrose intake of Peromyscus, it was imperative that reliable measurements of fluid intake and of individual threshold estimates derived from the intake behavior of P. m. bairdi and P. polionotus be obtained. Sources of intraspecific variability needed to be reduced as much as possible. The results of a pilot study using a two-bottle 24-hr. intake procedure indicated that some animals did not show a consistent position preference which would be required to obtain reliable estimates of preference thresholds for sucrose. In a two-bottle test, position preferences are usually controlled by alternating the positions on which the test fluids and water are presented. However, in cases where an animal alternately or unpredictably tends to consume most of his daily fluid intake from one drinking tube or another an undesirable source of "error" is introduced. Although this variability possibly would average out across individuals and not seriously jeopardize interspecific comparisons of sucrose thresholds, it would provide a more serious problem for determining individual thresholds; spuriously low thresholds could be obtained if close to 100% relative intake on repeated occasions was recorded for concentrations which were actually subthreshold.

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In order to eliminate the problems associated with two-bottle preference tests, a single-bottle procedure was used in the present research. Weiner & Stellar (1951) pointed out that one advantage of the single-bottle procedure is that it prevents the development of position habits and eliminates elaborate controls. In addition, providing each animal with the same drinking tube daily is a precaution that possibly would reduce another source of intrasubject variability in intake. Accordingly, the single-bottle procedure was deemed practical because it would eliminate some unwanted sources of individual variability.

The purposes of Experiment 1 were (1) to determine voluntary 24-hr. intake from water and low concentrations of sucrose in *P. m. bairdi* and *P. polionotus*, (2) to evaluate the reliability of the intake measure by presenting each solution twice, and (3) to compare the results of sucrose threshold estimates obtained with a variety of criteria for defining them. Accordingly, the major purpose of Experiment 1 was to compare sucrose intake and sucrose thresholds in the two species and to determine to what extent the threshold defined by different criteria agree. Water intake and a threshold estimate for individual subjects measured in Experiment 1 will be related to intake from suprathreshold sucrose solutions (Experiment 2) in order to determine how intake from su

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sucrose solutions is associated with apparent water needs and ability to discriminate sucrose (Chapter IV). For reasons explained in Chapter I it is of interest to test the predictive power of psychophysical laws for individual subjects by relating thresholds to intake.

Method

Subjects and Housing Conditions

A total of 73 male deer mice (33 *Peromyscus polionotus* and 40 *Peromyscus maniculatus bairdi*), supplied by the Animal Behavior Laboratory, Department of Zoology, Michigan State University, served as subjects. All animals were laboratory-reared descendants of wild-caught parents. Seventeen matings from 11 different parent pairs produced the 33 *polionotus*, while the 40 *bairdi* were obtained from 21 matings and 11 parent pairs. At various ages after weaning (23 days) the mice were imported into the Mouse Laboratory in the Department of Psychology at Michigan State University.

Prior to the experiment the animals were housed communally by litters in 11.5 x 7 in. x 5 in. clear plastic cages (Maryland Plastics) which were provided with metal gridded tops. Wood shaving bedding and cotton (for nesting) were provided in each cage. Purina Mouse-Breeder Chow and tap water were available *ad libitum*. A

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12-12 hr. light-dark cycle (8:00 a.m. to 8:00 p.m.) was employed at all times. The minimum and maximum temperatures in the Mouse Laboratory were recorded daily during the experiment; the average minimum and maximum temperature for all testing days was 69 and 73 degrees F.

At the beginning of testing the ages of the *polionotus* ranged from 54 to 140 days (mean = 86.1), while the *bairdi* were between 58 and 148 days of age (mean = 97.4). The average weights at this time were 13.6 and 16.1 grams for the *polionotus* and *bairdi*, respectively.

Originally it was planned to use a total of 60 subjects, 30 of each species, and to run two squads of animals at different times. When subjects of both species were selected for the first squad, no more than two animals from each litter were selected for testing. However, some difficulty was encountered in procuring additional animals for assignment in the second squad, and therefore it was necessary to select siblings of the first squad for assignment to the second. Accordingly, 11 *bairdi* and eight *polionotus* tested in the second squad were siblings of subjects which began testing 33 days earlier.

Preparation of Solutions and Apparatus

Six different sucrose concentrations were used: 0%, .125%, .25%, .50%, 1%, and 2% (weight/volume). All solutions were prepared with commercial cane sugar (Domino) and cold tap water. The .125%, .25% and .50% solutions were made by diluting a 1% stock solution. That is, 125, 250, and 500 ml. of a 1% sucrose solution was poured into a 1500 ml. beaker which was then filled to 1000 ml. with tap water. The 1% and 2% solutions were prepared by the liter by adding the required amount of tap water to 10 gm. and 20 gm. of sucrose, respectively. All solutions, including tap water (0%), were stored in 1-liter plastic bottles and kept in a refrigerator. A minimum of 20-hr. was allowed before the newly mixed solutions were used in the experiment. Fresh solutions were mixed every four days. A Mettler electronic balance (model P-6), accurate to 0.5 gm. was used to weigh the sucrose.

Metal testing racks, each with four shelves, accommodated the cages in which the subjects were tested. Four cages were placed on each shelf. A 2 in. x 1 in. piece of scalloped pine wood was attached to the rear of each shelf which assured stable support for the bottles.

During testing the subjects drank from 25 ml. graduated glass cylinder bottles which permitted readings of fluid level to the nearest 0.1 ml. The bottles were fitted with size 0 rubber stoppers and 3 in. straight metal drinking tubes. The bottles were inverted and placed at approximately a 45 degree angle through slots in the metal wire top the animals were tested individually in the same type of cage in which they were housed prior to testing.

Design

Pilot work indicated that a range of sucrose concentrations from 0% to 2% would be sufficient for obtaining threshold estimates for both species with a single stimulus 24-hr. intake procedure. Accordingly, six different sucrose concentrations between 0% and 2% in logarithmic steps were used. The experiment was designed so that each subject would be given each of the six sucrose concentrations twice; a different solution was presented daily for six days in a random order which differed for each subject and then the procedure was replicated.

Each subject was tested for 16 days in Experiment 1. Following one day of acclimation to the test cage, water was presented for the first two testing days. In the following six days the six sucrose concentrations were given. A day of water alone preceded and followed the replication of the procedure in which the sucrose solutions were presented in a different random order for six days. To summarize, the 16 testing days were scheduled as follows: days 1 and 2 (water), days 3 to 8 (sucrose concentrations), day 9 (water), days 10 to 15 (sucrose concentrations), and day 16 (water). Water intake (including 0% sucrose solutions), therefore, was recorded for a total of six of the 16 days. Thus, a 2 (species) x 6 (sucrose concentration) design with repeated measures and replication on the same subjects was used in this experiment.

Procedure

It was impractical to test all subjects at one time; therefore, the subjects were tested in two squads. The first squad consisted of 15 polionotus and 15 bairdi. The second squad contained 18 polionotus and 25 bairdi. The animals were randomly assigned to test cage positions on the testing racks with the restriction that individuals of each species occupy alternate spaces within a shelf and between shelves. Therefore, if a bairdi assumed the first position on the left on the top shelf, then a polionotus was assigned the first position on the second shelf, etc. The randomization of position was accomplished by arbitrarily assigning odd numbers to bairdi and even numbers to polionotus subjects between 1 and 30 (first squad) and 31 and 79 (second squad); an animal was then assigned a cage space in either rack according to the order in which its number appeared in a table of random numbers.

All subjects were weighed on the day that they were placed individually into test cages. Although 30 or more animals were tested daily, the required readings, removal, and change of solutions was staggered in such a way that only the animals occupying cages on two shelves (i.e., no more than eight subjects) were treated at a time. This procedure provided flexibility and it also assured that no animal was without a solution for more than a few minutes. Solutions were changed daily beginning at 2:00 p.m. for the first 16 subjects and 3:00 p.m. for the remaining animals in each squad.

Before the level of fluid in the bottles was recorded, clean bottles were filled with fresh refrigerated solutions. The solutions were not allowed first to stand until they reached room temperature. Because the cylinders were narrow and had a capacity of only 25 ml., it was assumed that the solutions would reach room temperature relatively soon after being presented. Moreover, because 24-hr. intake was recorded, it was believed that the total amount of fluid ingested from each solution would not differ from the amount that would be recorded if it were presented initially at room temperature each day.

After the new bottles were filled with the appropriate solutions, the level of fluid in the bottles presented 24-hr. earlier was recorded and each bottle was then removed. New drinking tubes were not provided daily, however. Instead, each tube and stopper was rinsed individually in tap water in order to remove any sugar which possibly may have accumulated around the tip of the tube. The stopper and tube was then inserted into the new bottle, and the bottles were placed into the cages at approximately a 45 degree angle. The new levels of fluid were recorded to the nearest 0.1 ml.

Results

The data from this experiment were analyzed to provide information about 24-hr. fluid intake of water and of sucrose solutions by both species. Specifically, the first matter to establish was the level of 24-hr. voluntary water intake in _bairdi_ and _polionotus_. Secondly, the shapes of their respective sucrose intake functions were compared. Also, because intake for both water and each sucrose concentration was recorded on repeated occasions, the stability or reliability of intake was examined. Finally, the sensitivity or responsiveness of the animals of each species to sucrose was determined by a variety of procedures, and the agreement among the resulting "preference" threshold estimates was evaluated.

Missing data. It is necessary to point out here that although 33 polionotus and 40 bairdi were tested, complete data were obtained on four fewer animals of each species. That is, one day's data on four polionotus and four bairdi subjects inadvertently were not recorded. Because the data from this experiment were indispensable for the analyses presented in Chapter IV, it was decided to exclude the data on these animals from all analyses. Accordingly, the data presented in Chapters II, III, and IV are based on 29 polionotus and 36 bairdi subjects, not 33 and 40. In addition, as will be pointed out later, in order to provide equal samples sizes it was necessary to randomly eliminate seven bairdi from analyses of variance in which species differences in intake were evaluated.

Water Intake

Table 2.2 shows the results of 24-hr. water intake by each species for the six days that water was presented. It can be seen from this table that polionotus averaged greater intake on each of the days than bairdi and that for each species water intake progressively increased slightly over days. Three analyses of variance (Tables

2.3 to 2.5) were performed on these data. The analyses were run to determine the significance of species differences in intake (Table 2.3), and also to evaluate the effect of the increase in water intake as a function of days in each species separately (Tables 2.4 and 2.5).

Estimates of Proportion of Variance

Estimations of the proportion of variance in intake accounted for by each source of variance in the analyses of variance was estimated by dividing the sums of squares of each effect by the total sums of squares. This procedure was used to provide an estimate of eta squared, a statistic analagous to the coefficient of determination used in correlational analyses to estimate the proportion of variability in one variable associated with changes in another. Levine (1968a) used this index of relative variability to determine sources of variation in sucrose intake of house mice. Accordingly, estimates of eta squared are presented in each analysis of variance summary table.

Table 2.3 reveals that the difference in intake between species and the increase in intake over days for both species were statistically significant effects. No Species X Days interaction was evident, however. The kind of information provided by the proportion of sums of squares in conjunction with significance levels is

TABLE 2.2

Results of Water Intake as a Function of Days for *Peromyscus*

	Days						
	1	2	3	4	5	6	Total
Polionotus							
Mean	5.07	5.20	5.47	5.76	5.82	5.94	5.54
SD	1.51	1.74	1.98	1.89	2.15	2.08	1.89
SE	.28	.32	.37	.35	.40	.39	.35
Bairdi							
Mean	3.78	3.98	4.14	4.22	4.29	4.41	4.14
SD	.72	.86	.94	.88	1.03	1.05	.91
SE	.12	.14	.16	.15	.17	.18	.15

TABLE 2.3

Analysis of Variance of Water Intake for *Peromyscus*

Source	SS	df	MS	F	eta^2
Species (SP)	193.2	1	193.2	16.27**	.20
Subjects w/i Sp (S)	664.8	56	11.9		.69
Days (D)	24.1	5	4.8	17.08**	.03
Sp X D	1.7	5	.3	1.19	.00
D X S	78.9	280	.3		.08
Totals	962.7	347			1.00

Note: Seven *bairdi* were randomly dropped from analysis; n = 29 for each species.

**p<.01.

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TABLE 2.4

Analysis of Variance of Water Intake as a Function of Days for _P_. _polionotus_

Source	SS	df	MS	F	eta^2
Days (D)	18.2	5	3.6	9.09**	.03
Subjects (S)	552.9	28			.88
D X S	56.0	140	.4		.09
Totals	627.1	173			1.00

**p<.01.

TABLE 2.5

Analysis of Variance of Water Intake as a Function of Days for _P_. _m_. _bairdi_

Source	SS	df	MS	F	eta^2
Days (D)	9.4	5	1.9	11.85**	.05
Subjects (S)	150.1	35			.80
D X S	27.6	175	.2		.15
Totals	187.1	215			1.00

**p<.01.

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illustrated in Table 2.3. For example, although both main effects were highly significant statistically ($p<.01$), these effects combined contributed less than 25% to the total variance. The largest source of variance in water intake was the Subjects effect (nearly 75%), which indicates that the variation in intake among the animals within both species was substantially greater than the overall intake difference between species or across days. Thus, the variation in water intake within species was found to be rather extensive relative to differences between species.

Tables 2.4 and 2.5 show simple analyses of variance on the water intake data for each species separately. These analyses illustrate further that although the small increase in water intake over days was significant, the extent of individual differences in subjects' intake nullified the experiential effects of time and experience with low sucrose concentrations on water intake variability. In summary, the results show that polionotus consumed significantly more water daily than bairdi. The increase in water intake over days was statistically significant, but of relatively small magnitude compared with subject variability.

Sucrose Intake

For purposes of presenting the sucrose intake functions of the six concentrations the intakes recorded from the two different test periods were averaged for each animal. Therefore, the means, standard deviations, and standard errors of sucrose intake as a function of concentration presented in Table 2.6 were obtained on the basis of the average intake recorded for each animal.

Because this procedure of averaging data is common in studies in which repeated measures are obtained, it is of interest to inquire about the reliability of such measurements. Accordingly, correlation coefficients which provide an index of the reliability of intake from one test period to the next for each solution i.e., test-retest reliability, are presented in Table 2.6 also. It is noted that the high correlations (.83 to .93) indicate that averaging both intake measurements for each subject was a defensible procedure; that is, the means adequately reflect the intake behavior for these animals to the sucrose solutions tested in this experiment.

An analysis of variance on the data presented in Table 2.6 is summarized in Table 2.7. For purposes of the analysis of variance each of the two days per concentration on which intake was recorded was considered to be replication of the procedure. The resulting replication term provided an error term for testing the significance of the Subjects effect in this and other analyses of variance (e.g., Tables 2.8, 2.9, 3.2, 3.3, and 3.4). Table 2.7 shows that <u>polionotus</u> ingested significantly

TABLE 2.6

Results of Intake from Threshold Test Concentrations by *Peromyscus*

	Concentrations (%)					
	H_2O	.125	.25	.50	1.00	2.00
Polionotus						
Mean	5.64	5.93	6.23	6.73	8.35	10.36
SD	2.03	2.12	2.21	2.35	3.43	4.30
SE	.38	.39	.40	.44	.63	.80
r	.93	.91	.88	.87	.89	.93
Bairdi						
Mean	4.21	4.20	4.25	4.53	5.17	6.51
SD	.96	.86	.86	.93	1.31	2.55
SE	.16	.14	.15	.16	.22	.43
r	.90	.90	.83	.85	.89	.84

Note: All correlation coefficients (r) are significant at the .01 level for both species.

TABLE 2.7

Analysis of Variance of Intake from Threshold Test Concentrations

Source	SS	df	MS	F	eta^2
Between					
Species (Sp)	1029.1	1	1029.1	22.20**	.17
Concentrations (C)	1124.3	5	224.9	75.04**	.19
Sp X C	107.6	5	21.5	7.18**	.02
Within					
Subjects w/i Sp (S)	2596.2	56	46.4	67.60**	.44
C X S	839.0	280	3.0	4.37**	.14
Replications	238.6	348	0.7		.04
Totals	5934.7	695			1.00

Note: Seven *bairdi* were randomly dropped from analysis; n = 29 for each species.

**p<.01.

more fluid than bairdi across the range of concentrations tested, and that both species increased their intake significantly from sucrose. Moreover, Species X Concentration and Concentration X Subjects interactions were found to be significant.

The source of the Concentration X Subjects interaction is evident upon an examination of individual intake functions (Appendices A and B). While the majority of animals displayed monotonic intake functions for these concentrations, the intake patterns differed markedly. Moreover, it is clear from examining the separate analyses of variance shown in Tables 2.8 and 2.9 that bairdi were much more variable than polionotus in their drinking of sucrose concentrations up to 2%. Indeed, the proportions of sums of squares in these tables indicate that although the Concentration X Subjects interaction was highly significant for each species, the interaction was a substantially greater source of the overall variance in intake for bairdi (37%) than for polionotus (11%); for the latter animals, the individual differences in subjects' intake across all concentrations (i.e., Subjects effect) accounted for more than half of the total variance alone.

In summary, the results show that for concentrations up to 2%, at least, polionotus intake was relatively greater in terms of the average curve. Although both species displayed an increase in intake from sweeter

TABLE 2.8

Analysis of Variance of Intake from Threshold Test Concentrations for *P. polionotus*

Source	SS	df	MS	F	eta^2
Concentrations (C)	957.6	5	191.5	61.94**	.25
Subjects (S)	2329.2	28	83.2	81.12**	.60
C X S	432.9	140	3.1	3.01**	.11
Replications	178.4	174	1.0		.05
Totals	3898.1	347			1.01

**p<.01.

TABLE 2.9

Analysis of Variance of Intake from Threshold Test Concentrations for *P. m. bairdi*

Source	SS	df	MS	F	eta^2
Concentrations (C)	298.3	5	59.7	23.89**	.25
Subjects (S)	367.0	35	10.5	32.04**	.31
C X S	437.0	175	2.5	7.63**	.37
Replications	70.7	216	.3		.06
Totals	1173.0	431			.99

**p<.01.

solutions, polionotus exhibited a more accelerated increase; that is, the general slope of the polionotus function was steeper. Intake from each concentration for both species was highly reliable as indicated by correlation coefficients calculated on the intake recorded in two different 24-hr. periods.

Sucrose Thresholds: Group Data

It was pointed out earlier that the variability in thresholds reported for the rat may be a consequence not only of differences in methodology, but also of the criteria adopted for defining them. Since more than one threshold estimate rarely has been reported within a single investigation, it was of interest to evaluate the extent of agreement among threshold estimates obtained by various criteria on the data from the same group of subjects.

Definitions. The criteria adopted in the present study were suggested from various sources. First, two group threshold estimates were obtained by pooling individual data and using criteria similar to those employed by Weiner & Stellar (1951) in their single-stimulus study of salt thresholds, and also by adopting the criteria used in a different situation by Burright & Kappauf (1963) and by Beck et al. (1965). Accordingly, two threshold estimates for each species were found (1) by noting the concentration for which mean sucrose intake first exceeded water intake, and (2) by interpolation, the concentration for which 75% of the subjects consumed more sucrose than water.

Threshold estimates. The threshold estimates obtained with both criteria from the collective data are presented in Table 2.10. The lowest concentration at which mean sucrose intake exceeded water intake (AL G1) was found simply by consulting Table 2.6.* With this criterion it is clear that for *polionotus* the lowest

TABLE 2.10

Threshold Estimates (Concentration) Based upon Group Data in *Peromyscus*

Threshold	Species	
	P. polionotus	*P. m. bairdi*
AL G1[a]	.125	.500
AL G2[b]	.210	.625

[a] Defined as lowest concentration at which mean sucrose intake exceeded mean water intake.

[b] Defined as concentration for which by interpolation sucrose intake of 75% of the subjects exceeded water intake.

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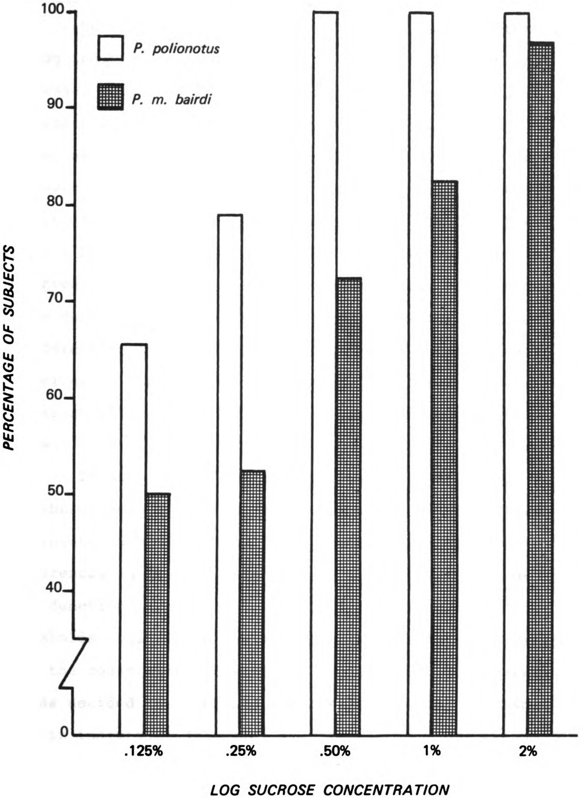
*AL is conventional notation for the absolute threshold in human psychophysical studies, where L stands for the Latin word, "limen" or threshold.

sucrose concentration offered (.125%) resulted in greater intake. For bairdi, however, the threshold estimate was more difficult to define with this criterion. The first increase in intake was observed for .25% sucrose; however, this increase represented a change of only .04 ml which is considerably less than the precision which existed in measuring intake (to nearest 0.1 ml). A more convincing estimate, then, using the current criterion, would be .50% sucrose, for which a mean increase of .3 ml was reliably obtained.

The second threshold estimate (AL G2) reported in Table 2.10 was interpolated directly from data presented in Fig. 2.1 which shows the percentage of subjects consuming more sucrose than water in two test periods for each solution. Again, the lower "threshold" was found for polionotus (.210% vs. .625% for bairdi). Figure 2.1 also reveals that at every concentration offered a higher percentage of polionotus than bairdi consumed more sucrose than water. Moreover, all of the polionotus drank more sucrose from .50% to 2% concentrations inclusive, while some bairdi never consumed more 2% sucrose than water. Thus, not only did bairdi consume less water and sucrose solution (Table 2.6), but fewer bairdi responded more to sucrose than to water at each concentration presented.

Fig. 2.1. Percentage of subjects for which sucrose intake exceeded water intake as a function of concentration.


100
90
80
70
60
50
40
0
PERCENTAGE OF SUBJECTS
P. polionotus
P. m. bairdi
.125%
.25%
.50%
1%
2%
LOG SUCROSE CONCENTRATION

Sucrose Thresholds: Individual Data

Definitions. Underlying all criteria for determining individual thresholds was the assumption that an increase, rather than a decrease, in intake would occur to detectable sucrose concentrations. In other words, it was assumed that sucrose would not be aversive to any individual animal, and, therefore, an indication of their ability to discriminate sucrose from water would be found where a reliable increase in sucrose intake over water occurred. Accordingly, the various threshold definitions to be described are regarded as single-stimulus sucrose "preference" thresholds, even though the subjects were not given an opportunity to demonstrate a "preference" for sucrose to water directly as obtained in two-bottle tests.

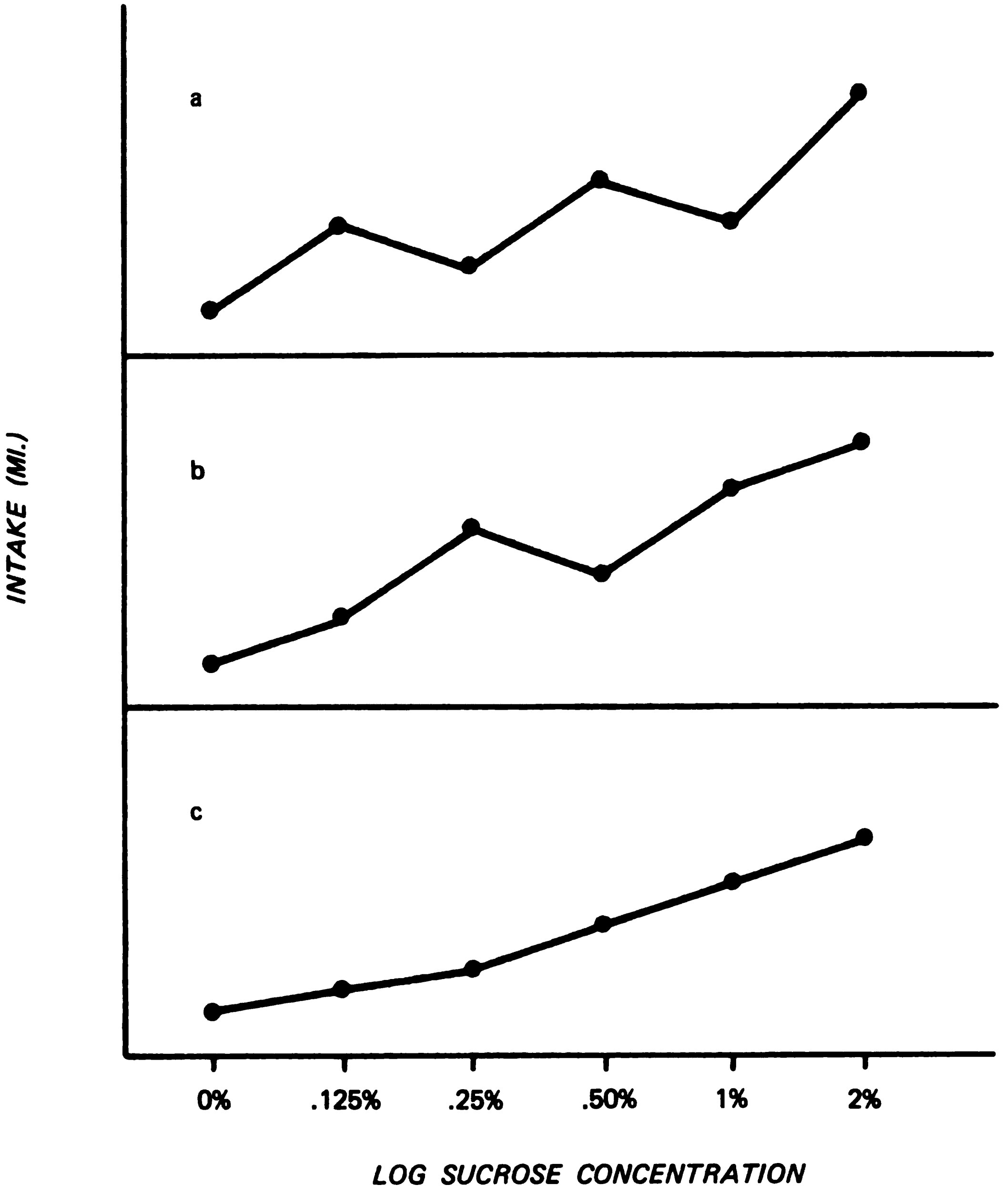
To some extent the criteria used for defining thresholds were suggested from an examination of individual intake curves. As could be expected from the species differences in levels of intake and slopes of their intake functions (Table 2.5), a criterion for defining thresholds could favor one species or the other depending upon the constraints it imposes. Largely for this reason it was decided to determine sucrose "preference" thresholds in individual deer mice by using several criteria. The definition used by Weiner & Stellar (1951) for single-bottle salt thresholds suggested several criteria. An attempt to account for intra-subject variability in fluid intake was a consideration in another definition. Four threshold estimates were obtained on each animal. In the remaining text these threshold estimates will be denoted as AL 1, AL 2, AL 3, and AL 4.

It is recalled that Weiner & Stellar (1951) determined the rat's salt threshold merely by noting the lowest concentration at which mean salt intake exceeded water intake. Because one of the two sucrose thresholds for Peromyscus (GL 1) presented in Table 2.10 was obtained with the Weiner & Stellar (1951) criterion, it was of interest to determine how well the mean threshold value obtained by using this criterion for individual subjects would compare. In other words, to what extent is the group threshold estimate based upon an increase in mean intake of all animals representative of the mean threshold estimate based upon the increase in intake by individual animals?

The Weiner & Stellar (1951) criterion simply suggests that the lowest concentration at which sucrose intake exceeds water intake and continues to exceed water intake at higher concentrations will provide a reasonable measure of the animal's sensitivity for sucrose. This criterion can be satisfied in several different ways, however. That is, individual profiles depicting intake as a function of concentration can be widely different and yet be assigned the same "threshold." Consider the hypothetical examples shown in Fig. 2.2 which illustrate three different intake curves, not atypical of those found in Experiment 1. For purposes of illustration the average water intake is equal in all three cases. Note that in terms of the criterion presently considered, each of the three subjects has the same threshold (.125%), but the slopes and patterns of their curves differ. At .125% individual (a) shows a marked increase in sugar intake over water and intake exceeds water for the remaining concentrations. However, the pattern of intake at higher concentrations fluctuates; at several succeeding concentrations it is less than .125% intake. In the second case, intake for (b) shows a sizeable increase over water at .125% and is less than intake for subsequent concentrations, although the intake for succeeding concentrations fluctuates. The overall slope of the bottom curve (c) is relatively flat, but note that intake for all concentrations exceeds intake for the preceding concentrations; that is, intake increases monotonically for all concentrations above water.

Since the threshold criterion seems to be variably conservative or liberal depending upon the slope and pattern of the individual's intake curve, it is of interest to inquire to what extent threshold estimates based upon criteria customed to each of the three possibilities would

Fig. 2.2. Three hypothetical intake curves illustrating different ways a threshold criterion could be satisfied (explained in text).


INTAKE (Ml.)
a
b
c
0%
.125%
.25%
.50%
1%
2%
LOG SUCROSE CONCENTRATION

agree with one another. They would correlate highly, of course, if the usual pattern was similar to (c); but the agreement would decrease to the extent that patterns (a) and (b) were found. Accordingly, threshold estimates for individual subjects were determined according to the following criteria which impose additional constraints in the order in which they appear:

(AL 1): the lowest concentration from which sucrose intake exceeds water intake and intake from all higher concentrations exceeds water intake.

(AL 2): the lowest concentration from which sucrose intake exceeds water intake and intake from all higher concentrations exceeds intake from that concentration.

(AL 3): the lowest concentration from which sucrose intake exceeds water intake and intake from each higher concentration exceeds intake from immediately preceding concentrations.

These three definitions of thresholds (AL 1, AL 2, and AL 3) do not take into account the relative magnitude of increase in sucrose intake over water. It was suggested previously that a relatively small increase in sucrose intake may represent the animal's ability to discriminate sucrose from water if the difference in intake is a reliable difference. Indeed, for the two-bottle situation it was suggested that the common index of relative sucrose acceptance (sucrose/sucrose + water x 100 = 75) was rather arbitrary; it does not represent the animal's ability to discriminate one of two solutions correctly 75% of the time which would be more consistent with conventional psychophysical definitions. A relative percentage of average intake does not take into account the fact that the variance may differ among animals and various sucrose concentrations. The 75% relative intake measure, then, may be less conservative in situations where there is considerable variability in intake as observed over repeated daily intake measures, and it may be too conservative where less variability is found. In the present study *polionotus* displayed greater intake to all concentrations than *bairdi*; but, while the general slope of the *polionotus* intake curve was steeper, there also was greater variability associated with mean intake at each concentration (Table 2.5). Therefore, although the intake curves were steeper for *polionotus*, smaller but less variable increases in intake for *bairdi* could indicate equal discriminability, but less responsiveness, for sugar than water.

Since threshold estimates AL G1 and AL G2 (Table 2.10) were derived from the pooled data of all subjects and AL 1, AL 2, and AL 3 do not take into account either the intra-subject variability in intake or the relative magnitude of difference in sucrose and water intake, one additional criterion was used for obtaining a sucrose threshold estimate. A difficulty with the individual threshold estimates obtained by adopting the criteria previously described is that their precision is seriously limited by the choice of concentrations, particularly in the upper range. An animal's threshold was necessarily restricted to one of only five discrete concentrations covering a broad range between .125% and 2%. As a result, different levels of discriminability are likely to be represented among a number of animals assigned the same threshold estimate value. In order to overcome this difficulty which was also noted in a previous study (Beck *et al.*, 1965), threshold estimates also were obtained by determining the amount of intake which corresponded to one standard deviation above the average intake of water recorded on six days throughout the experiment. A different criterion was considered which would define the threshold as the concentration which by interpolation exceeds the 95% confidence limit of water intake. However, this criterion was not adopted because it was thought to be too restrictive. Therefore, from the empirical intake functions plotted for each animal, an additional threshold was defined as

(AL 4): the concentration corresponding to intake equal to one standard deviation above the six day water average found by linear interpolation.

Admittedly, the criterion of one standard deviation is arbitrary, but not more so than a .75 relative proportion criterion used in two-bottle studies. However, another way of considering this particular criterion is that the threshold estimate is the concentration for which the difference in average sucrose and water intake is equal to a Z score of +1.00, which corresponds to a cumulative probability of .84 in the normal density curve or an alpha level of .16 for a one-tailed significance test. No difference between the sucrose and water means would correspond to a cumulative probability of .50.

If we consider what this criterion suggests in terms of many repeated measurements of water intake, more than 75% (i.e., 84%) of them presumably will have a value less than one standard deviation above the mean. From this point of view, then, we are designating the sucrose threshold estimate in terms of the intake expected to correspond more than halfway between 50% and 100% of all possible water intake measures for a given individual. Underlying this reasoning are assumptions of normality and equal variance in sucrose and water intake.

Assignment of threshold values above 2%. For some of the *bairdi* subjects the criterion for one or more of the threshold estimates could not be satisfied on the basis of an individual's intake data. That is, the range of concentrations adopted in this study evidently did not embrace the sensitivity or responsiveness of all the animals to sucrose. Therefore, in such cases that a given criterion could not be met, it was decided to assign arbitrarily a value of 3% for that particular threshold estimate. This arbitrary value was used at least once for seven of the 36 bairdi, but not for one of the 29 polionotus.

Threshold estimates. Table 2.11 presents the means, standard deviations, and standard errors of the four threshold estimates expressed as percentage concentration. The species differences were significant for all threshold values (df = 1 & 63; p<.01 for all comparisons). By whatever criterion adopted threshold estimates were lower for polionotus. In fact, the highest mean threshold value obtained for polionotus (.39%) was lower than the lowest bairdi value (.70%). Overall, the difference in mean threshold estimates between species was approximately .50% and higher; for the four criteria used in this study the differences ranged from .47% to

TABLE 2.11

Results of Threshold Estimates (Concentration) Obtained with Different Criteria for Peromyscus.

	Polionotus			Bairdi		
Threshold	Mean	SD	SE	Mean	SD	SE
AL 1	.23	.15	.03	.70	.71	.12
AL 2	.31	.24	.04	.79	.72	.12
AL 3	.39	.37	.07	.92	.71	.12
AL 4	.30	.20	.04	1.03	1.04	.17

.73% sucrose concentration. In general, the variances were proportional to the mean threshold estimates and were larger in all cases for _bairdi_.

The lowest threshold estimates for both species were generally found with the definitions which required noting the concentration at which sucrose intake first exceeded water intake and remained greater at higher concentrations (ALs 1, 2, and 3). And, as expected for these three estimates, the value of the threshold was a function of the number of constraints imposed by the criteria; that is, the definition which required a strictly monotonic intake function (AL 3) resulted in the highest value among these three estimates, while the value based on the criterion imposing the weakest constraint (AL 1) was lowest for both species by ranking.

The intercorrelations among the four threshold values and significance levels are presented in Table 2.12 for _polionotus_ and Table 2.13 for _bairdi_.* The most striking finding from these tables is that for _polionotus_,

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*Because of the dependency among comparisons made from the same sample of subjects, it should be noted that less than one of the ten comparisons would be expected to be significant spuriously at the .05 level (Hays, 1963, p. 576). The values of the coefficients required for significance at the .05 level when testing for the first correlation were $r = .37$ (df = 27) for _polionotus_ and $r = .33$ (df = 34) for _bairdi_. For significance at the .01 level, the corresponding values for _polionotus_ and _bairdi_, respectively, were .47 and .42.

TABLE 2.12

Intercorrelation Matrix of Threshold Estimates for *P. polionotus*

	AL 1	AL 2	AL 3	AL 4
AL 1	--	.56**	.21	.30
AL 2		--	.30	-.05
AL 3			--	.57**
AL 4				--

**p<.01 for first correlation.

TABLE 2.13

Intercorrelation Matrix of Threshold Estimates for *P. m. bairdi*

	AL 1	AL 2	AL 3	AL 4
AL 1	--	.96**	.82**	.55**
AL 2		--	.81**	.65**
AL 3			--	.60**
AL 4				--

**p<.01 for first correlation.

whose individual intake functions were generally steeper in slope and more monotonic than bairdi functions, there was substantially less agreement among the various threshold estimates than for bairdi. Undoubtedly this result was due partially to the differences in variance in each threshold value between species. All of the bairdi intercorrelations were significant, while only three of the ten polionotus comparisons were significantly associated.

In summary, the results presented in Tables 2.11 to 2.13 reveal (1) that bairdi consistently were assigned higher threshold values than polionotus with four different criteria; (2) that the definition which took into account intra-subject variability (AL 4) yielded the highest mean threshold estimate for bairdi, although it agreed well with others for polionotus; and (3) that the agreement among the various threshold estimates determined by their intercorrelations was generally greater for bairdi.

Discussion

The major conclusions drawn from the results of this study are (1) captive P. polionotus ingest more water per day when available ad libitum than captive P. m. bairdi; (2) Polionotus are more responsive to low concentrations of sucrose solutions than bairdi; and

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(3) threshold estimates will vary depending upon the criteria adopted for defining them.

Water Intake

No water intake data have been previously reported for *polionotus*, and data published on *bairdi* intake do not agree well with the results of the present study. Lindeborg (1952) reported an average daily intake of 3.0 ml. for 18.6 gm. *bairdi* maintained on "air-dry" food in a laboratory environment ranging in temperature from 68 to 77 Deg. F. In the present study 16.1 gm. *bairdi* maintained on a dry lab chow diet at similar laboratory temperatures averaged 4.1 ml. daily over six days. Although a statistically significant increase over days was found (Table 2.2), it should be noted that the lowest daily intake recorded (3.8 ml.) was six standard errors greater than the intake reported by Lindeborg. Chew (1965, p. 53) cautions that comparisons of data between laboratories may be uncertain because of the fact that water intake in captive mammals will depend upon a variety of factors, such as temperature and humidity, type of diet, caging conditions, and other environmental considerations.

Attempts have been made previously to identify relationships between habitat and drinking in captivity, but the findings are not very conclusive for explaining the results obtained in the present study. Ross (1930), for example, found a suggestive relationship between a species' presumed region of origin and its drinking in captivity. He found that races of *Peromyscus bairdi*, which occupy a relatively humid habitat, drank more than *Peromyscus eremicus*, which normally inhabit semiarid regions; however, no differences between races within a species were observed. Moreover, Lindeborg (1952), who compared water consumption of 11 races of five species of *Peromyscus*, found some differences with climatic regions, but no differences among species occupying different habitats with the same climate were found.

Even if a reasonably clear relationship between natural habitat and the water consumption of captive animals were to be established, the implications would have to be considered cautiously. For Chew (1965) appropriately points out that the major sources of water in free-living mammals in natural environments is the fluid contained in the food they consume, while captive mammals provided with dry food and water *ad libitum* naturally obtain their water from the drinking bottles. The amount of water consumed and exchanged will depend upon a variety of metabolic and environmental factors. Moreover, the relation of water exchanges in nature to the exchanges on dry food and water in the laboratory has not been established.

Sucrose Intake and Threshold Estimates

The intake curves and threshold data collectively suggest that captive *polionotus* are more responsive to low concentrations of sucrose than captive *bairdi*. *Polionotus* drank significantly more sucrose across the range of concentrations tested than *bairdi*. The slope of the *polionotus* intake curve was steeper than the *bairdi* curve, revealing a greater proportional increase in intake as a function of concentration. Moreover, a larger percentage of *polionotus* consumed more sucrose than water at all concentrations offered. Indeed, the finding that all *polionotus* subjects drank more sucrose than water from concentrations of .50% and above, while less than 100% of the *bairdi* consumed more sucrose at any concentration, strongly corroborates the conclusion that *polionotus* are more responsive than *bairdi* to the presumed palatable properties of sucrose within the range of 0% to 2% concentration.

The single-stimulus procedure did not require the animals to make a choice between alternatives to demonstrate either discriminative ability or a direct preference for any sucrose solution to water. Without a two-bottle test in which the animals are allowed to display a direct choice between water and sucrose solutions, it can only be assumed that the subjects in the pr

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present study would have consumed more sucrose than water from those concentrations for which more sucrose intake was recorded. However, because of the fact that the intakes recorded were highly reliable, and because the differences in threshold estimates were so consistent, it is concluded that the single-stimulus procedure effectively delineated species differences that would be similarly found with a more direct preference procedure. A two-bottle procedure may yield somewhat lower threshold values than were obtained with the one-bottle procedure, but the relative interspecific differences could be expected to remain the same.

Neither the single-bottle nor two-bottle procedure, which depend upon comparing choices or intake of both sucrose and water, would resolve the problem of whether there are interspecific differences in discriminative ability. To resolve the issue a discrimination procedure in which an animal is administered reward or punishment for its choices would be more appropriate for evaluating differences in the capacity to discriminate. Until demonstrated otherwise, then, it can merely be concluded that the responsiveness of *polionotus* and *bairdi* to the palatable properties of sucrose differ; there is no appropriate basis for concluding that *polionotus* and *bairdi* are not equally capable of discriminating sucrose in water.

Group threshold estimates. The most liberal threshold definition for both species, i.e., the one which provided the lowest threshold estimate, was (AL G1), which merely defined the threshold as the lowest concentration at which mean sucrose intake exceeded water intake. It was expected that this criterion, used by Weiner & Stellar (1951) for salt thresholds, would provide the lowest threshold estimate because of the fact that it imposed the fewest constraints on the data. This criterion did not require that sucrose intake exceed water intake by any given amount; therefore, a slight increase in mean intake could result from an increased intake on the part of only a few animals in the group which may be discriminating the sucrose. With so liberal a criterion, therefore, it is interesting that bairdi did not adequately satisfy the criterion at one of the lower concentrations presented.

The second threshold estimate (AL G2) obtained from the group data also yielded values which were lower than any of the four mean threshold values for either species derived from individual intake data. However, this estimate, which incorporated a criterion similar to that used by Burright & Kappauf (1963) and by Beck et al. (1965), agrees well with the least conservative of the other five threshold estimates reported. Thus, for polionotus the .21% value obtained by interpolating the concentration at which 75% of the animals showed an increased intake for sucrose to water (AL G2) corresponds to the .23% estimate which was the average concentration at which sucrose intake first exceeded water intake and intake for subsequent concentrations also exceeded water intake (AL 1). The corresponding values for _bairdi_ were .60% and .70% respectively. Together, these two threshold estimates suggest that approximately 75% of the subjects showed reliable increase in sucrose intake at concentrations of .22% and .65% for _polionotus_ and _bairdi_, respectively. Accordingly because these two estimates substantially agree for each species, it is suggested that (1) .22% and .65% are reasonable sucrose threshold estimates for captive _polionotus_ and _bairdi_ with the single-stimulus procedure used in this study, and, therefore, that (2) determining the lowest concentration at which 75% of the subjects demonstrate increased intake to sucrose over water provides a good approximation of the average concentration at which the subjects reveal a reliable increase in sucrose intake.

Individual threshold estimates. For both species AL 1 and GL 1 provided the lowest "average" threshold values. As expected, though, the mean AL 1 threshold was higher than the GL 1 value for each species. It appears, therefore, that the Weiner & Stellar (1951) criterion adapted either to pooled group data or to individual functions is the most liberal of those considered. As noted above, though, AL 1 and GL 2 yielded similar threshold values with entirely different criteria. And, it was argued, both values are thought to adequately delineate species differences and provide estimates of a representative sucrose "preference" threshold for both species.

Because the individual *polionotus* slopes were generally steeper than *bairdi* slopes, and because the criteria for AL 1, AL 2, and AL 3 are related, it was expected that the agreement among these three threshold values as indicated by intercorrelations would be greater for *polionotus*. However, the intercorrelations were much lower for *polionotus* than *bairdi*. At first it would appear that the extent to which these measures failed to correlate perfectly should be an indication of the lack of monotonicity in individual functions. If all functions were monotonically increasing from the concentration at which sucrose intake first exceeded water intake, then the same value would have been designated for each of the three threshold estimates. However, 66% of the *polionotus* and 61% of the *bairdi* exhibited monotonic intake functions and were assigned the same value for each of the three threshold estimates. Therefore, the lower correlations found for the *polionotus* probably can be attributed to the fact that most of the animals' threshold values were obtained for low concentrations and the variability among thresholds was smaller. To illustrate, only two of the 29 polionotus, but 20 of 36 bairdi, were assigned AL 3 values of 1% or higher. Not a single polionotus was given an AL 1 value greater than .50%, while as many as 13 bairdi failed to satisfy that threshold criterion at a concentration less than 1%. Thus, by taking on a much narrower range of discrete threshold values for AL 1 (.125% to .50% vs. .125% to 3%), the intercorrelations for polionotus were necessarily truncated.

It was found, then, that individual threshold definitions requiring some degree of monotonicity in intake patterns resulted generally in the lowest individual sucrose threshold values. The highest estimate for bairdi were obtained with the threshold definition incorporating intra-subject variability of intake into its criterion. For a variety of reasons, though, it is believed that in the present study the most appropriate definition for determining estimates of single-stimulus sucrose thresholds for individual subjects is AL 4, because it has a statistical basis and it takes into consideration each animal's variability in voluntary intake.

Limitations of threshold criteria. Preliminary data obtained from a pilot study indicated that the 0% to 2% range of concentrations would be adequate for deriving threshold estimates. The range was found to be rather adequate for polionotus, but, unfortunately, it was underestimated for bairdi. Also, by presenting concentrations which increased in logarithmic steps, four of the threshold estimates (GL 1, AL 1, AL 2, and AL 3) were necessarily restricted to one of only six discrete values between .125% and 3% (which was assigned to those animals which did not meet the criterion of 2%). As a result, it appears that the bairdi thresholds were somewhat overestimated compared with polionotus values. The polionotus estimates were undoubtedly more precise because there were smaller differences between successive concentrations within the range in which most polionotus individuals exhibited increased sucrose intake. Two concentrations were offered between 0% and .50%, but none between either .50% and 1% or between 1% and 2%. More than 50% of the bairdi subjects were assigned values with the relatively liberal AL 1 threshold criterion of either 1%, 2%, or 3%. It would be reasonably expected that a number of bairdi would meet the threshold criterion at intermediate concentrations between .50% and 1%, 1% and 2%, and 2% and 3%.

On the other hand, the highest bairdi thresholds were found with AL 4 which interpolated the concentration for which an individual would demonstrate a reliable increase in sucrose intake in comparison with its variability in water intake. The relatively higher and more variable threshold estimate by this criterion may be accounted for in part by the significant increase in water intake over days which may have inflated intra-subject variance, thereby increasing thresholds.

Comparison of deer mice and rat thresholds. Despite the limitations which resulted from the choice of concentrations in this experiment for determining thresholds, by all criteria polionotus were found to exhibit a positive response to sucrose at lower concentrations than bairdi. Collectively, the results of this experiment indicate that polionotus are at least as sensitive generally as the laboratory rat to sucrose, while bairdi evidently have a higher sucrose "preference" threshold. Threshold values for the nondeprived rat have been reported no lower than .32% (Burright & Kappauf, 1963), while the usual threshold value reported is .50% (Richter & Campbell, 1940b). These comparisons assume that two-bottle sucrose "preference" thresholds in Peromyscus would be similar to the single-bottle obtained. Surely the relative magnitude of difference in thresholds between polionotus and bairdi would be expected to remain, although there is reason to expect that the two-bottle estimates may be somewhat lower (Benjamin, 1955).

The relationship of the present data to the postulated survival function of taste is uncertain for several reasons. As Kare (1961) points out, taste acuity would have no survival value for the laboratory rat. If sucrose "preference" thresholds provide a measure of taste acuity in animals, one would expect to find the lower thresholds among *Peromyscus*. However, Maller & Kare (1965) argue that because the laboratory rat has been exposed to different selection factors than its wild ancestor, *Rattus norvegicus*, it is more responsive to the hedonic qualities of taste substances, and exhibits a quantitatively greater preference for sugars. Another consideration, too, is the fact that "preference" thresholds by definition require the animal to demonstrate an increase in intake from taste solutions. As pointed out previously, the concentration of a "preferred" substance which can be initially discriminated from water may differ from the concentration at which a preference to water is initially demonstrated. Comparative studies undertaken to determine the functional value of taste should probably concentrate more on aversive and toxic chemicals.

In summary, the results of Experiment 1 delineated species differences in the voluntary consumption of water and response to low sucrose concentrations. *P. polionotus* consumed less water daily than *P. m. bairdi* and by a variety of criteria were found to have lower sucrose "preference" thresholds than *P. m. bairdi*. It was found that for more precise threshold determinations with the present procedure it would have been advisable to present sucrose concentrations ranging from 0% to 4% in equal steps of .50%. One of the threshold estimates obtained in this experiment will be related to suprathreshold sucrose intake reported in Experiment 2 (Chapter III) in order to provide a test of the usefulness of psychophysical scaling laws for explaining individual differences in sucrose intake behavior (Chapter IV).

Chapter III

SUPRATHRESHOLD SUCROSE INTAKE

The preference for sucrose solutions in rats and other species is widely accepted and well-documented. Sucrose has been found also to be a useful reward substance for instrumental activities. Several studies have been conducted to scale the incentive value of sucrose (Guttman, 1953; Young & Shuford, 1954, 1955). The results from performance and learning studies, ostensibly showing the incentive or reward properties of sucrose, are not necessarily in agreement with the incentive curves demonstrated in intake or preference studies, however.

Sucrose Preference in the Rat

In both single-bottle tests (Owings, Haerer, & Lockard, 1967) and two-bottle sucrose-water tests (Collier & Bolles, 1968; Richter & Campbell, 1940 a,b) functions relating intake of sucrose solutions concentrations typically are inverted-U shaped. Intake is found to be an increasing monotonic function to a peak of about 8% sucrose, beyond which intake declines. Similar shaped functions have been obtained in learning and performance studies in which sucrose was offered as reward; however, the concentration which has been found to provide maximum incentive for performance of instrumental acts is substantially higher. Young & Shuford (1954, 1955), for example, found that runway speed in a 6-ft. maze was an increasing monotonic function of concentration to a maximum of 18%, beyond which speed decreased. Moreover, resistance to extinction varied inversely with the concentration of sucrose offered for reward. Guttman (1953) found comparable results with an operant conditioning technique; response rate increased for concentrations up to 16% before declining, although greater resistance to extinction was observed for a 32% concentration.

These differences in the concentration for which rats will demonstrate maximal intake (8%) and will optimally perform instrumental acts (18%) has led Young (1966) to conclude that "instrumental acts motivated by food reward fail to provide a dependable basis for predicting preference" (p. 83). Accordingly, Young states that the most palatable food (as determined by preference tests) is not necessarily the best incentive for eliciting instrumental activities. His conclusion was based, of course, upon group comparisons from several different studies. It is conceivable that relative preference and instrumental performance for sucrose reward may be found to be positively related in within group comparisons; that is, an animal which displays relatively greater "preference" for sucrose in intake tests may also demonstrate higher response rates or running speeds and greater resistance to extinction for sucrose reward, even though the concentration which elicits maximum performance is higher.

From the wealth of preference and intake data on sucrose in the rat, it is evident that the shape of the function relating sucrose intake to concentration is largely determined by the method used to obtain such incentive curves. Preference curves have been obtained by procedures similar to those used to determine sucrose thresholds. Although there have been variations in the duration of the intake measures, three general methods have been employed: (1) the single-bottle or single-stimulus method, in which a range of concentrations are presented individually to separate groups or to the same subjects in a predetermined (usually random) order; (2) the two-bottle method, in which a sugar solution is paired with either water or another sugar solution; and (3) the multiple-bottle tests, in which three or more concentrations are presented simultaneously.

The different methods yield essentially two different intake functions. The inverted-U shaped curve has been found usually when sucrose solutions are presented singly (Owings *et al.*, 1967; Young & Greene, 1953) or when an animal is given a choice between sucrose and water (Carpenter, 1958; Collier & Bolles, 1968; Hammer, 1967; Richter & Campbell, 1940a,b; Young, 1949; Young & Greene, 1953). However, when sucrose solutions are paired intake is found to be an increasing monotonic function of concentration; the rat generally drinks more from the sweeter solution of the pair, even from concentrations higher than 8% (Campbell, 1958; Young & Greene, 1953).

Owings & Lockard (1968) suggest that the monotonic function may be a transient phenomenon, because they found more reversals in choice for pairs of higher concentrations. The increasing monotonic function has been found also when more than two sucrose solutions have been available simultaneously, e.g., either six (Owings *et al.*, 1967) or eight (Carpenter, 1958). Young & Greene (1953) and Young (1966) have interpreted these differential findings to indicate that results obtained with a single-stimulus procedure do not provide an accurate basis for predicting choice preference, for rats will ingest more of the sweeter of paired concentrations, although less of the sweeter concentration may be consumed when presented singly. Young's conclusion is concerned with the prediction of average intake for independent groups on which either the single-bottle or two-bottle procedure is used.

The extent to which relative difference in intake for a given animal tested by both methods can or cannot be predicted has not been demonstrated.

The disparate results of sucrose "preference" determined from single-bottle and two- (or multiple-) bottle procedures prompted Young & Greene (1953, p. 293) to suggest that the term "preference" should be reserved only for those situations in which an animal is provided with a choice, "for the term 'preference' implies the possibility of choice." Therefore, the single stimulus procedure, first proposed by Beebe-Center _et al_. (1948) as a technique for studying preference is not regarded as "a true preference method because it excludes the possibility of choice" (Young, 1966, p. 61). Young attributes the disparity between the monotonic and inverted-U functions to the absence or presence of an opportunity to display choice behavior. Although there are various explanations which attempt to account for the difference in the shape of the functions beyond merely the opportunity for choice, e.g., postingestional effects (Beck, 1967; Collier & Bolles, 1968; Shuford, 1959), the distinction between preference and intake proposed by Young (1966) is appropriate.

Most of the literature on sucrose preference is based upon domesticated animals of various species (Kare, 1961), particularly the laboratory rat. However, some attention has been given recently to more natural species. Maller & Kare (1965) reported markedly different intake functions to a variety of sweet solutions, including sucrose, for the common laboratory rat and its ancestor, the wild Norway rat. Although both the wild and domesticated rats exhibited qualitatively similar preferences for sugars in 24-hr. intake tests (sugar vs. water), there was a substantially less increase in fluid intake among the wild rats to the sugars. Moreover, the wild rats consumed significantly more food and less water. The authors concluded that "domestication has altered the response of rats to sweet solutions."

Sugar Preference in Deer Mice

The acceptability of sugar solutions for deer mice has been investigated recently by Wagner and his colleagues. In all of his studies Wagner adopted a two-bottle choice procedure in which intake for 2- or 24-hr. was measured. Using glucose solutions primarily, he measured the preference based on intake for pairs of glucose solutions (Wagner & Rowntree, 1966, 1970), for glucose-water pairs (Wagner, 1968a), and for glucose-fructose pairs (Wagner, 1968b). The glucose preferences observed in Peromyscus were generally in agreement with the sugar preferences found with other rodents. The mice preferred glucose to water at all concentrations tested

(Wagner, 1968a), and the sweeter glucose concentration was always preferred to the lesser concentration (Wagner & Rowntree, 1966, 1970), at least among the *Peromyscus* species he studied. Species differences were found in glucose intake and also in relative preference (defined as the difference in intake between the sweeter and less sweet solutions). In these studies *P. m. bairdi* were found to drink the least amount of fluid and also to display the least amount of glucose preference to various hypertonic concentrations. Wagner (1968b) studied individual differences in preference within small samples of several *Peromyscus* species. Noting that few, if any, studies have reported on individual differences in the laboratory rat, Wagner recommended further studies to examine sources of the observed individual differences in deer mice, also.

Intake from highly concentrated solutions of sucrose in paired sucrose tests with *P. m. bairdi* has been investigated by Levine (1969). A model was described in which *bairdi* attempted to mix the solutions available in order to achieve a standard concentration. The model was tested on data from several unpublished experiments. Neither 24-hr. single-bottle nor two-bottle (sucrose vs. water) preference has been reported for deer mice, however.

Methodological Problems and Experiential Effects

The interpretation of comparative taste data is complicated by the fact that widely varying experimental procedures have been used. Virtually all experiments measuring intake from solutions have employed repeated measures designs in which intake to a single concentration presented to independent groups is averaged over several days, or, more commonly, in which intake from several concentrations, each presented separately for several days to each animal, is averaged. With the latter within groups procedure the test periods may be separated by "rest" periods in which water only is presented between presentations of new concentrations in order "to reduce possible carryover effects" (Maller & Kare, 1965); sometimes the concentrations are presented successively without presenting water alone.

Besides differences in experimental design (independent groups or within groups), experiments have differed in the number of repeated measures with either type of design from which average intake is derived (one to four test periods, generally), in the duration of the intake measure (typically, 1-hr., 2-hr., 23-hr., or 24-hr.), and, of course, in the method (single-bottle vs. two-bottle). But, whatever type of design, method, or intake measure is employed, intake in these experiments is commonly derived from averaging repeated measurements on the same individual. If intake is significantly influenced by carryover effects, then attempts to reconcile conclusions among experiments without consideration of the consequences of prior experience poses obvious difficulties.

Wagner has noted various procedural and experiential effects in his experiments on sugar preference in *Peromyscus*. For example, relative preference and glucose intake were found to differ depending upon whether independent groups or within groups designs were used (Wagner & Rowntree, 1966). Moreover, with either method significant Trials and Trials X Concentration effects were obtained for the hypertonic glucose solutions presented for five consecutive days each (Wagner & Rowntree, 1966, 1970). Hammer's (1967) study with rats, employing a Treatment X Subjects design in which six sucrose concentrations ranging from 2% to 32% were presented with water for four consecutive days each, showed that either 30-min. or 24-hr. sucrose intake peaked at 4% rather than the usual 8% concentration.

Other methodological differences among studies have produced results which raise questions about various interpretations of the "preference" curve. For example, Wagner (1968a) found that 2-hr. sugar intake did not predict maximal intake after 24 hr. with deer mice; the sweeter solutions in paired concentrations tests were drunk initially, but intake for the less sweet solutions

increased more over the 24-hr. period. This finding agrees with the results reported by Owings & Lockard (1968) of paired sucrose tests with rats. Over 11 consecutive daily test periods in which intake was measured for either 1-hr. or 23-hr. the frequency of relative preference for the sweeter concentration decreased as a function of concentration and intake duration; moreover, a significant Days X Concentration effect was found, prompting the investigators to conclude that preference for the sweeter of the two concentrations is "a transient phenomenon." It is usually reported that when given a choice between two sucrose solutions of any concentration (including 0% or water, too) animals will "prefer" the sweeter, whether in brief-exposure tests in which intake is uncomplicated by postingestional factors (Young, 1966) or in long-term intake tests in which 24-hr. intake is averaged over several or more days (e.g., Levine, 1968b; Collier & Bolles, 1968).

The experiential effects evidently inherent in repeated measures designs employing relatively long-term intake may be partially explained by adaptation of the taste response. There is evidence to suggest that long-term ingestion of sucrose (and other substances) may modify responsiveness to the taste stimulus, independent of osmotic and caloric postingestional factors (Vance, 1970). Whether this modification in responsiveness is due to an altered response at the receptor level or to changes in central states resulting from receptor adaptation is currently a matter of speculation.

Experiment 2

Because sugars are presumed to be universally acceptable among rodents, it is of interest to determine sucrose preference in rodent species other than the rat. The present experiment was conducted to determine the acceptance of sucrose in *P. m. bairdi* and *P. polionotus* by measuring single-bottle 24-hr. intake from three hypotonic concentrations presumed to be above threshold and within the "preference" limb of intake curves. It was hoped that the intake functions from 2%, 4%, and 8% sucrose would be generally monotonically increasing, for the water intake and threshold data of Experiment 1 (Chapter II) were to be used to determine their explanatory value for individual differences in sucrose intake found in the present experiment (see Chapter IV). It was decided to use a maximum concentration which was less than isotonic (9.3% in the rat) in order to maximize the role of taste factors and to avoid confounding intake level by the introduction of post-ingestional osmotic factors which would be expected to contribute to a decrease in intake.

Method

Subjects

The same 29 P. polionotus and 36 P. m. bairdi which served as subjects in Experiment 1 were used in the present study.

Concentrations

Sucrose solutions of 2%, 4%, and 8% were prepared on a weight/volume (gm./100 ml.) basis in the manner described in the previous experiment. The solutions were stored and refrigerated as described before. Tap water, which was presented in the middle and at the end of this experiment, was also refrigerated.

Because the 24-hr. intake for the concentrations was expected to exceed the capacity of the 25 ml. bottles, 50 ml. bottles were used for measuring intake of the three solutions. In order to assess possible experiential effects of repeated exposure to low concentrations of sucrose in Experiment 1 and of possible additional leakage in the larger 50 ml. bottles, water intake was measured between replications in the 25 ml. bottles, and a 2% concentration was offered as one of the presumed suprathreshold concentrations.

Design

The experiment was designed so that each of the three sucrose concentrations would be presented singly to the subjects in a random order twice. Since there are only six possible combinations of the three solutions presented one at a time, it was decided to assign each possible sequence to an equal number of animals to the extent possible. However, the order of presentation assigned to a given animal was determined randomly for both series. The first and second three-day test periods for the sucrose solutions were separated by one day in which the animals were given tap water. Accordingly, the design of Experiment 2 was similar to Experiment 1, except fewer concentrations were used in the present situation.

Procedure

Testing began for all animals on the first day following the completion of Experiment 1. The animals occupied the same cages and shelf positions as before. Food was available at all times. The daily procedure was essentially identical to that described in Experiment 1. Each day the level of fluid intake was recorded, a new bottle containing a different solution was presented at approximately a 45 degree angle, and the level of the new solution was recorded to the nearest .1 ml. The animals drank from the same tubes which were rinsed in tap water daily. As noted, water was presented between the first and second test sequence in 25 ml. cylinders instead of 50 ml. cylinders.

Results

The means, standard deviations (SD), standard errors (SE), and correlations of 2%, 4%, and 8% two-day intake are presented in Table 3.1. The results are based upon the combined two-day intake from each concentration, while Pearson Product-Moment correlations, which provide estimates of intake reliability, were calculated from the 24-hr. intake recorded on the two separate test days. Table 3.1 shows that intake reliability was reasonably high (the correlations range from .75 to .90).

An analysis of variance on the data is summarized in Table 3.2. In order to establish equal sample sizes for convenience in running the analysis of variance, the same seven _bairdi_ eliminated from the analysis presented in Table 2.3 were also eliminated from the analysis shown in Table 3.2. The analysis reveals that although _polionotus_ consumed more sucrose from each concentration than _bairdi_, the mean difference was not significant statistically ($p>.10$). The Concentration effect was significant, as expected, but the Species X Concentration effect was not, indicating that the average intake patterns were similar for both species; indeed, based on the proportion of the sums of squares due to interaction over the total, virtually none of the variance in sucrose intake for all animals combined could be attributed to the interaction.

TABLE 3.1

Results of Intake from Suprathreshold Sucrose Concentrations by *Peromyscus*

	Concentrations		
	2%	4%	8%
Polionotus			
Mean	11.68	15.31	15.91
SD	4.46	5.91	4.51
SE	.83	1.09	.84
r	.77	.75	.90
Bairdi			
Mean	8.85	12.61	14.42
SD	5.28	6.91	5.02
SE	.88	1.15	.84
r	.87	.79	.89

Note: All correlation coefficients (r) are significant at the .01 level.

TABLE 3.2

Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *Peromyscus*

Source	SS	df	MS	F	eta^2
Between					
Species (Sp)	309.5	1	309.5	1.98	.02
Concentrations (C)	1469.1	2	734.5	52.64**	.11
Sp X C	15.7	2	7.9	.56	.00
Within					
Subjects w/i Sp (S)	8774.8	56	156.7	23.31**	.66
C X S	1562.8	112	14.0	2.08**	.12
Replications	1169.7	174	6.7		.09
Totals	13301.7	347			1.00

Note: Seven *bairdi* were randomly dropped from analysis of variance; *n* = 29 for both species.

$^{**}p<.01$.

The Concentration X Subjects effect was significant, howeever, and the largest portion of the variance (66%) in intake was accounted for by the individual differences in subjects' intake across the three concentrations.

Tables 3.3 and 3.4 reveal that the pooled Concentration X Subjects effect found in Table 3.2 apparently can be attributed mainly to the intake behavior of *bairdi*. The Concentration X Subjects interaction was significant for *bairdi* (Table 3.4), but not for *polionotus* (Table 3.3). For each species the Concentration effect and the Subjects effect were significant, and individual differences accounted for approximately two-thirds of the partitioned variance.

A Concentration X Subjects interaction is of interest, because it indicates that not all individual intake curves were similarly monotonic. Approximately 30% (or 20 of 65) of all of the individual functions were nonmonotonic. For virtually all subjects, however, intake increased from 2% to 4%. Moreover, the overall intake curve of either species was negatively accelerated; the average proportional increase in intake from 4% to 8% was less than from 2% to 4%. Thus, the slope of the average intake curve was not strictly linear across the range of concentrations, and intake was not proportional to the logarithm of the concentration, which the extension of Fechner's law to taste would suggest by assuming

TABLE 3.3

Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *P. polionotus*

Source	SS	df	MS	F	eta^2
Concentrations (C)	608.9	2	304.5	48.08**	.11
Subjects (S)	3854.3	28	137.7	22.94**	.72
C X S	354.6	56	6.3	1.05	.07
Replications	522.5	87	6.0		.10
Totals	5340.3	173			1.00

**p<.01.

TABLE 3.4

Analysis of Variance of Intake from Suprathreshold Sucrose Solutions by *P. m. bairdi*

Source	SS	df	MS	F	eta^2
Concentrations (C)	1164.4	2	582.2	29.66**	.13
Subjects (S)	5684.1	35	162.4	23.33**	.63
C X S	1374.2	70	19.6	2.82**	.15
Replications	751.9	108	7.0		.08
Totals	8974.6	215			.99

**p<.01.

intake was proportional to the sweetness of the solution as explained in Chapter I.

Collectively, the results in Tables 3.1 to 3.4 show that intake increased significantly as a function of concentration for both species, as expected. Although polionotus did not drink significantly more sucrose at any concentration than bairdi, extensive and reliable individual differences were found in subjects' intake from the three concentrations offered. In addition, the Concentration X Subjects effect observed for all subjects combined evidently was influenced mainly by the variation in bairdi intake patterns.

It is noted that 2% intake from the 50 ml. bottles in this experiment exceeded 2% intake from the 25 ml. bottles used in Experiment 1. On the average 2% intake significantly ($p<.01$) increased 1.3 ml. for polionotus and 2.3 ml. for bairdi between Experiments 1 and 2. The increases in intake were representative among individuals of both species, however; 83% of the polionotus and 92% of the bairdi increased their 2% sucrose consumption. Moreover, while the variance in polionotus intake was about the same in either experiment, bairdi variance increased substantially (2.73 ml.). Meanwhile, it should be pointed out that water intake increased negligibly from the end of Experiment 1 through Experiment 2; the average increase from the last two occasions on which water was presented in Experiment 1 to the two presentations in Experiment 2 was only 0.1 ml. for both species. It is recalled that water was presented at all times in 25 ml. bottles.

The inconsistent results of the 2% sucrose intake is revealed also by the finding that the correlation coefficient of average 25 ml. and 50 ml. intake between experiments was merely .54 for <u>bairdi</u> (a significant, but weak association). For <u>polionotus</u>, on the other hand, the correlation was .88. The "test-retest" reliability of either 25 ml. or 50 ml. intake by <u>bairdi</u> in both experiments remained about the same, however (.84 and .87), while the reliability for <u>polionotus</u> decreased from .93 in Experiment 1 to .77 in the present experiment. Thus, although the mean <u>polionotus</u> intake of 2% sucrose increased less between experiments, the reliability of intake dropped somewhat in the second experiment; meanwhile, the much larger increase in 2% <u>bairdi</u> intake was slightly more reliable.

Discussion

The results of this experiment clearly demonstrate that sucrose, at least in concentrations ranging from 2% to 8%, was a palatable substance for both species. On the average, both species more than doubled their total fluid consumption from the sweet solutions compared to amounts of voluntary water intake measured in both

Experiments 1 and 2. Averaged across the three concentrations, though, the ratio of sucrose intake to water intake was slightly greater for bairdi, with 3.1 times as much sucrose consumed compared to a 2.6 ratio for polionotus. The significant Concentration effects (Tables 3.3 and 3.4) reveal that both species found increasing concentrations more palatable, for intake varied directly with sweetness. Thus, in agreement with the results reported for a wide variety of rodents and other mammals (e.g., Carpenter, 1956; Kare, 1961) bairdi and polionotus evidently possess a "sweet tooth" for sucrose.

Contrary to what was expected, however, no significant species differences were found in either intake or in individual intake patterns for these concentrations. Despite the finding that polionotus ingested slightly more sucrose at all concentrations, the proportion of total variance accounted for by species differences in intake was negligible. The results of Experiment 1 showing significant differences in intake at all lower concentrations might have been expected to continue for the higher concentrations. Moreover, surprisingly, no significant Species X Concentration interaction was found. A significant difference was expected at least in the 2% intake of this experiment because of the significant Concentration and Species X Concentration effects found in Experiment 1 (Table 2.7), for which the largest difference in mean intake was found for 2% sucrose. However, on the basis of the results of this experiment showing no significant differences in single-bottle intake, it is concluded that _P_. _polionotus_ and _P_. _m_. _bairdi_ exhibit qualitatively and quantitatively similar acceptance of sucrose solutions ranging from 2% to 8% in concentration.

On the basis of these data it would be expected that similar findings would be obtained from Richter-type (two-bottle) preference tests, also, because of the general correspondence in the shape of preference curves resulting from one-bottle and two-bottle (sucrose and water) tests. Yet, the somewhat proportionally greater increase in sucrose intake over amount of voluntary water intake suggests that _bairdi_ might show a greater relative preference than _polionotus_ for sucrose in two-bottle tests offering sucrose and water alternatives. In paired sucrose tests, however, a greater relative preference for the sweeter solution by _polionotus_ may be expected on the basis of an experiment by Wagner & Rowntree (1970) in which _bairdi_ were found to drink the least amount of other _Peromyscus_, including _polionotus_, from pairs of hypertonic glucose solutions to which they also demonstrated relative indifference.

Satiating Factors in Sucrose Consumption

The solutions used in this experiment were within the range of concentrations which comprise the "preference" limb of the typical inverted-U function obtained for the laboratory rat in experiments employing a range of hypotonic and hypertonic concentrations (e.g., Collier & Bolles, 1968; Hammer, 1967; Owings *et al.*, 1967). The increased preference obtained from single-bottle and two-bottle tests as a function of concentration up to 8% is usually explained by sensory (taste) factors (Pfaffmann, 1961, 1965; Shuford, 1959; Young, 1966). That is, palatability factors are responsible for increasingly greater intake from progressively sweeter solutions. Presumably, the sweeter the solution is the more "preferred" it will be. In motivational terms, differential intake from solutions differing in sweetness represents hedonic responses of proportionally greater intensity (Young, 1966).

For concentrations greater than 8%, various post-ingestional factors supposedly operate to limit intake from sweeter (more concentrated) solutions. Generally, two classes of such satiating effects have been posited: the dehydrating effects of osmotic pressure (Beck, 1967; McCleary, 1953; Mook, 1963; Shuford, 1959) and the tendency of animals to regulate total caloric intake from carbohydrate solutions and other food sources (Collier & Bolles, 1968; Jacobs, 1962).

If taste factors are largely responsible for the increase in intake as a function of concentration for solutions up to 8%, then presumably the major factor preventing the animals from drinking as much of these solutions as perhaps they would like is their inability to consume greater amounts of fluid within a 24-hr. period. Thus, fluid-consumption capacity would be the primary satiating effect limiting intake. Preference functions, then, would be explained by an interaction of taste factors and fluid intake capacity over a designated period (e.g., 24-hr.).

Because the 8% intake by bairdi and polionotus were nearly the same and extrapolation of the average intake functions (Table 3.1) suggests that they would merge at a slightly higher concentration, it appears that the 24-hr. fluid intake capacities of these species may be about the same. If this is the case, then the overall lack of significant species differences in intake and the somewhat (though not significantly) more accelerated bairdi intake function may be explained by differences in voluntary consumption of unflavored solutions (i.e., water) and in ability to discriminate (or the tendency to show initial preference for a sucrose solution). That is, because polionotus normally drank significantly more water than bairdi and exhibited significantly lower thresholds for sucrose, their intake from the sweeter solutions above threshold may have been limited by their inability to ingest increasingly larger amounts of fluid. Meanwhile, the increasing intake by <u>bairdi</u> to these same concentrations may not have represented necessarily a hedonic response of greater intensity to the sweetness of the solutions, but rather a larger capacity than <u>polionotus</u> to ingest increasing amounts of more concentrated solutions up to a limit.

It may not be surprising, actually, that the increase in 4% to 8% intake was proportionally less than the 2% to 4% increase for either species. A 4% solution is sweeter than 2%, and apparently is considerably more palatable. An animal's consumption of 4% solution may be the result of an optimal interaction of its taste response (determining increase in intake) and fluid intake capacity (determining amount of fluid intake). Because 4% sucrose evidently has very strong motivational properties, it is not unlikely that an individual animal's intake would represent an attempt to ingest an amount limited largely by its inability to comfortably consume greater quantities. Intake from the sweeter 8% solution, therefore, may represent some kind of "drinking overshoot." The sweeter taste of the 8% sucrose may offset the tendency of the animal to further limit consumption which at palatable lower concentrations already exceeds the apparent water needs of the animal. For an individual animal, then, intake of an 8% solution may not be proportional to the strength of its hedonic (motivational or incentive) properties, because the animal has ingested virtually as much as it can from a lower (e.g., 4%) concentration. Therefore, for so-called "preference" concentrations, for which intake is presumably affected little by postingestional osmotic pressure and caloric factors, it is suggested that the negatively accelerated intake functions found in the present experiment and in other studies (e.g., Hammer, 1967; Owings *et al.*, 1967) may be accounted for by the sweeter taste of 8% sucrose offsetting a tendency to drink no more than the amount ingested for the highly palatable 4% concentration (or, perhaps, a 5% or 6% concentration, if tested) over a 24-hr. period. If this explanation proves to be reasonable, then it may be surprising that as many as 31% of the *bairdi* and 17% of the *polionotus* exhibited either linear or positively accelerating intake patterns for the three concentrations.

Osmotic dehydration. Because the three concentrations used in this experiment were hypotonic (for the rat, at least), it was assumed that osmotic dehydration would not be a limiting factor in the amount of sucrose consumed. Beck (1967) found that hypotonic sucrose solutions (less than 9.3%) cleared the gastrointestinal tract (stomach and intestine) of the rat rather quickly, while for all concentrations up to 37.5% the amount of ingested fluid recovered at various times following ingestion was inversely proportional to concentration. He concluded that a fixed amount of dehydration apparently was not responsible for stopping drinking, though, and he speculated that the sweeter taste of more hypertonic concentrations may offset its dehydrating properties and result in the rat consuming more than would be otherwise expected. Thus, it appears that palatability factors to some extent may override satiating factors from both low (hypotonic) and high (hypertonic) concentrations.

Caloric constancy. Sucrose as a carbohydrate contains calories, and caloric value has been implicated as a determinant of sugar solution intake. Animals have been found to regulate the number of calories consumed daily from their diets under *ad libitum* conditions (Adolph, 1947), even when carbohydrate solutions are available (Jacobs, 1961, 1962). Because animals evidently decrease dry food intake to compensate for calories obtained from sugar solutions, the caloric value of sucrose and glucose has been postulated as a major satiating factor in the decreasing acceptance of higher, more concentrated, solutions typically found in "preference" studies. The caloric effects of sucrose generally have been considered to be of little consequence with lower concentrations in which increasing intake is thought to be determined mainly by dominating taste factors.

Collier & Bolles (1968) recently suggested that caloric intake is a major determinant of the amount of sucrose an animal will consume from any concentration, even 4% and 8% concentrations. They obtained the usual inverted-U intake function using concentrations ranging from 4% to 64%, and they found that the total calories consumed daily from dry food and sucrose by the rat was generally constant. Moreover, the proportion of total calories consumed from sucrose was relatively fixed and varied as a function of concentration; the proportions from 4%, 8%, and 16%-64% were approximately .10, .20, and .60, respectively. Therefore, the rats evidently demonstrated a tendency to limit their caloric intake by some relatively constant amount from sucrose, even from hypotonic concentrations. A tendency to limit caloric intake would necessarily require limiting fluid intake from a given concentration, of course. The authors conjectured that intake functions in the single-bottle situation, also, would reflect an animal's "tendency to consume a fixed proportion of its total caloric intake from the solutions offered." In addition, they suggested that caloric intake as a determinant of the amount consumed offers an alternative to the usual preference interpretation of fluid intake functions.

Corroborating results for the higher concentrations have been reported by Levine (1968b). He found that independent groups of genetically heterogeneous house mice (*Mus musculus*) offered a variety of sucrose pairs varying in concentrations (from 15% to 60%) consumed a constant amount of sucrose over a four-day period, although the total solution intake decreased with pairs of higher concentrations and the subjects generally consumed a greater amount from the higher of two concentrations. Similar results were found with single-bottle concentrations of 30% and 60%. The total caloric intake from both food and sucrose was not measured, but the constancy of sucrose consumption in grams suggests that mice also may have consumed a fixed proportion of their total calories from sucrose.

While Levine (1968b) suggested that the sucrose constancy hypothesis might break down with concentrations less than 15% because of an inability to ingest vast amounts of liquid, Collier & Bolles (1968) proposed that caloric constancy provides a satiating effect to limit intake of so-called "preference" concentrations, too. In sucrose vs. water tests, or in sucrose only tests, it is clear that the amount (grams) of sucrose solute ingested will increase, because of higher concentrations from which more fluid is usually consumed. However, the tendency to consume a constant, if different, proportion of total caloric intake from 4% and 8% solutions may be merely a coincidental result of, not a determining factor of, how much fluid an animal is able to consume over a 24-hr. period from sucrose solutions. Collier & Bolles (1968) did not demonstrate that caloric regulation was responsible for preventing the animal from drinking more than it would otherwise like to drink from the palatable concentrations. Rather, the proportion of caloric intake itself may have been determined by the animal's tendency to consume so much total fluid within 24-hr. largely on the basis of the sensory properties of sucrose and its inability to ingest greater amounts of liquid. Either interpretation of the results is consistent with their data, and further experimentation would be required to reconcile the different conclusions.

Maller & Kare (1965), contrary to Collier & Bolles (1968), reported that wild and domesticated Norway rats increased their total caloric intake over normal levels during a series of tests with various sugars, all of which were of a single concentration (3.2%). Each sugar solution was presented for four consecutive days followed by four days in which water alone was presented. The increase in caloric intake was smaller by the wild rats (5%) than by the laboratory rats (15%), although the wild rats tended to consume significantly more calories normally. The results suggested "a more precise and careful monitoring of energy intake" by the wild rat.

Few preference curves are based on intake averaged for more than four test periods, and frequently fewer days are involved. In this respect it is interesting to note that the conclusions reached by Collier & Bolles (1968) were based on the results of intake averaged over the last five days of a 40-day testing period in which sucrose solutions and water were presented continuously. In view of possible experiential effects over an extended period the caloric constancy hypothesis based upon such data is questionable on methodological grounds.

Jacobs (1962), who endorses the caloric metering hypothesis, also observed a disruption of caloric intake when glucose solutions were presented initially. Collier & Bolles (1968) even noted that 4% and 8% sucrose intake did not stabilize for nearly two weeks in separate groups of rats. For various reasons, then, a question is raised about the role of the energy properties of sucrose in determining intake and, therefore, in explaining intake curves. It appears that prolonged and repeated experience with sucrose may be required before the reported caloric regulation effects become evident, in the rat at least. In light of the uncertainties over the role of caloric regulation in determining sucrose consumption, it is clear that the sucrose intake behavior of *Peromyscus* would be better understood if both food and sucrose intake had been measured.

Experiential Effects

A Treatment X Subjects design was employed in the present research. Each animal was presented with three different concentrations of sucrose individually without water and with a different concentration presented in a randomly determined order each day. A replication of the procedure was preceded by a single day "rest period" in which water alone was presented. Therefore, for the duration of the experiment the deer mice received these hypotonic concentrations on six of seven days. It would appear that compared to other experiments carryover effects would be minimized, even though no water alternative was available during test periods. The relatively high reliability of intake indicated by the size of correlation coefficients for each concentration (Table 3.1) would seem to support this conclusion.

In light of possible experiential effects, however, the inconsistent results obtained in 2% sucrose intake between Experiments 1 and 2 begs explanation. It is difficult to ascertain whether the discrepancy in results was due to changing the size of the graduated cylinders to accommodate the expected increase in 24-hr. intake, or to carryover effects from Experiment 1. A slight increase in 2% intake from the 50 ml. bottles was anticipated because of the increased volume and air surface area of the larger bottles which could have increased leakage. It was expected that the increase would be minimal and roughly constant for both species, however. While 2% intake increased significantly for both species in Experiment 2, there were differential species effects in both the amount and variability of the intake. For example, the average *bairdi* increase was larger and the variance of intake more than doubled over that of Experiment 1, while the *polionotus* variance was virtually the same.

The drinking tubes used with both the 25 ml. and 50 ml. bottles were the same size. In addition, no difference in normal leakage (in empty cages) was found between the different size cylinders. It is possible, perhaps, that more dripping and leakage would result from the larger bottles with greater licking, but that factor might account for the increased *bairdi* intake and variance only if the 24-hr. *bairdi* drinking patterns differed substantially from *polionotus*, e.g., more frequent, but shorter, drinking periods.

In retrospect, it is clear that the procedure in this study would have been improved by keeping the 25 ml. bottles in both experiments and refilling them when necessary during the 24-hr. period. Originally, though, the use of the 2% concentration in both experiments was thought to provide the control necessary for evaluating the effect of employing different size cylinders for measuring sucrose intake. A differential species change was not anticipated.

Comparative Taste Data

The interpretation and explanation of the present results with *Peromyscus* remains speculative for a number of reasons. Unfortunately, little previous research to invite comparisons has been reported on the sucrose preference behavior of *Peromyscus*. With the exception of Levine's (1969) analysis of paired sucrose choices in *P. m. bairdi*, sucrose preference in *Peromyscus* has not been reported. Wagner and his colleagues have studied the deer mouse's preference for various sugars, but the substances, concentrations, and procedures were considerably different from those used here. Overall, very little comparative taste research has been reported with "natural" animals. While preferences have been tested with a variety of mammalian species (e.g., Carpenter, 1956; Kare & Ficken, 1963), most of the species studied may be regarded as domesticated animals. Clearly, more comparisons such as that of Maller & Kare (1965) with wild and domesticated animals are needed.

While it is asserted that most mammals possess a "sweet tooth," it may be inappropriate to assume that the quantitative differences in relative intake found among many rodent species showing qualitatively similar preferences is merely a matter of degree of preference. Intake from palatable taste substances may be regulated by various underlying mechanisms unrelated to taste factors which may be specific to a particular population of animals. For example, a tendency to ingest a relatively fixed amount of sucrose from single or paired solutions may be a major factor limiting total sucrose intake among certain strains of genetically heterogeneous mice (Levine, 1968b), but the evidence for a proposed caloric constancy determinant in laboratory rats (Collier & Bolles, 1968) is not so convincing, for reasons previously considered.

It would be expected that the water requirements and exchanges for a particular species would have evolved through selection factors to be compatible with the availability of water and the factors causing water expenditure in specific habitats (Chew, 1965). Therefore, species indigenous to different environments would be expected to have different water balance processes. As pointed out in Chapter II, there is some evidence for a suggestive relationship between drinking of captive animals and their presumed region of origin where the amount of water consumed is compared to the relative moistness of the habitat (Fertig & Layne, 1963; Lindeborg, 1952; Ross, 1930). Chew (1965) notes, however, that overall the amounts of water consumed in captivity do not reliably estimate water needs in nature. Moreover, Wagner & Rowntree (1970) found no predictable relationship between presumed water habits and sugar preference and intake among five species of *Peromyscus*. However, Lindeborg (1952) found that the ability of species to maintain weight and survive on reduced rations of water corresponded generally with the judged moistness of their habitats.

Because *P. m. bairdi* and *P. polionotus* were found in this study to differ significantly in voluntary water intake (Experiment 1) but not in amount of sucrose intake from suprathreshold sucrose concentrations (Experiment 2), it appears that sucrose intake did not correspond predictably to apparent water requirements of these two captive species. But, a consideration of only the overall differences and similarities between species does not provide information about the relationship of water intake to sucrose intake for individual animals of either species. Differences in the energy and water regulatory systems of *polionotus* and *bairdi* may be suggested by examining the relationship of the taste and energy characteristics of sucrose to levels of water and sucrose consumption. Correlational analyses may indirectly suggest factors underlying the apparent species interaction with respect to water and sucrose consumption.

Chapter IV

SOURCES OF INDIVIDUAL DIFFERENCES IN SUCROSE INTAKE

The results of Experiment 2 indicate that *Peromyscus*, as many other mammals, respond positively to sucrose solutions. The results also showed that *P. m. bairdi* and *P. polionotus* did not differ significantly in degree of acceptance for concentrations of 2%, 4%, and 8% sucrose. However, the results of Experiment 1, showing significant species differences in voluntary water intake and in apparent sensitivity to low sucrose concentrations, suggested that while there are quantitative species differences in single-bottle intake of supra-threshold sucrose solutions the mechanisms or determinants underlying sucrose intake may differ.

It was concluded that intake was determined largely by an interaction of taste factors and the fluid intake capacities of the *Peromyscus*. The significant *Concentration* effect found for each species for solutions ranging from 2% to 8% (Tables 3.3 and 3.4) showed that intake varied directly with the sweetness of the solution.

However, the proportion of sums of squares for Concentrations indicated that little more than 10% of the total variance in intake was accounted for by differences in concentrations. Most of the variance in intake was accounted for by individual differences. For each species nearly 80% of the total variance in intake was due largely to Subjects effects, showing different levels of intake averaged across the range of concentrations, and to a lesser extent to Concentration X Subjects interactions which reflect the differences found in intake patterns among individuals. Thus, if "taste" factors were mainly responsible for the increasing intake functions found, then it appears that the palatability factors did not override to an appreciable extent whatever other factors were responsible for limiting intake from each concentration. It was suggested that other factors related to the energy characteristics of sucrose (a carbohydrate) may have influenced intake to some extent, also. However, since food (and, therefore, caloric) intake was not measured in this research, there is little empirical basis for supporting speculative conclusions about species' energy regulating mechanisms.

Individual differences commonly are a major source of variation in psychological experiments (Lindquist, 1953). However, to dismiss such differences merely as "random error" may be inappropriate. To a certain extent the idiosyncratic drinking patterns observed among *bairdi* and *polionotus* which did not conform to that of the "average" animal may be attributed to "error" because of possible sequential carryover effects resulting from randomizing the orders in which the solutions were presented. But, if the remaining "error" effects are additive, as assumed in analysis of variance models, then this would suppose that the amount of sucrose ingested from any concentration would be linearly related to its tendency to voluntarily consume so much unflavored fluid (i.e., water) and that the increase in intake for sweeter solutions would be proportionally similar for all subjects.

The assumption about the linearity of effects is rarely examined in experiments. The finding in the present study that the variance associated with mean intake from each suprathreshold concentration of sucrose was substantially greater than the variability in water intake (Tables 2.6 and 3.1) suggests that taste factors were not interacting additively with *ad libitum* water consumption level. This finding partially may be explained by differences in thresholds for sucrose among individual animals. In accordance with psychophysical laws, sucrose intake from a discriminable concentration should be inversely related to threshold value among animals which normally consume equal amounts of water. The variability in sucrose intake and in slopes of individual intake curves among the Peromyscus suggest that differential sensitivity among individual *bairdi* and *polionotus* may have interacted with apparent water need factors in determining the intake from sucrose solutions for these animals.

The extent to which individual differences in sucrose intake from a given concentration may be linearly related to any variable can be determined by correlational procedures. Four such variables were of interest for present purposes, as indicated in Chapter I: (1) voluntary water intake, i.e., the average 24-hr. intake recorded over a total of six days. For obvious reasons the individual levels of water intake would be expected to provide some "explanation" of individual differences in sucrose intake averaged across the three concentrations (i.e., account for the Subjects effects shown in Tables 3.3 and 3.4); (2) age and (3) weight recorded at the onset of the study. Age and weight are normally highly correlated, of course, and in rats fluid intake was found to be an increasing function of age (Goodrick, 1969); and (4) a sucrose threshold estimate. Because of the established role of taste factors (i.e., palatability, "hedonic intensity") in determining sucrose intake, it was of interest to test the explanatory power of psychophysical laws applied to taste behavior. The assumption was that the threshold value should be inversely related to the "hedonic intensity" experienced with a concentration above threshold and be found to influence intake accordingly.

The threshold estimate from Experiment 1 selected for these analyses was AL 4, because it was judged to provide the most representative value among individuals for reasons explained in Chapter II. Briefly, it is recalled that AL 1, which was based upon a more conventional single-stimulus threshold definition (e.g., Weiner & Stellar, 1951), also produced the lowest mean value for both species. However, AL 1 also used the most liberal criterion of the four estimates considered, and for each animal the assigned threshold value was limited to one of only six discrete values (i.e., one of the five concentrations plus 3% which was assigned arbitrarily in some cases). Because these concentrations varied in logarithmic steps up to 2%, it was believed that precision was sacrificed with the AL 1 threshold definition. For these reasons AL 4, which was derived by interpolating the concentration at which sucrose intake would initially exceed an animal's average water intake by a standard deviation, was believed to be a more adequate threshold estimate for explanatory and predictive purposes.

Intercorrelation Matrices

The intercorrelations of water intake, age, weight, threshold value (AL 4) and the three dependent variables, 2%, 4%, and 8% sucrose intake, are presented for polionotus and bairdi in Tables 4.1 and 4.2. The asterisks indicate the level of statistical significance for correlations which differed significantly from zero.* Each table presents 21 intercorrelations resulting from the seven variables. Eight significant correlations were found in the polionotus matrix (Table 4.1) and nine for bairdi (Table 4.2). Because all correlations in each matrix were derived from the same sample, there is a problem of dependency among comparisons. According to Hays (1963, p. 576) more than one correlation in each matrix might be significant by chance alone at the .05 level. However, there is reason to be confident that the significant correlations were not obtained spuriously, because, first, all but two significant correlations in each matrix were significant at the .01 level, and, secondly, the patterns of significant comparisons within each matrix were generally consistent.

Normal water intake was highly correlated with sucrose intake at all three concentrations for polionotus (.65 to .76), but bairdi water consumption was not

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*For polionotus the values of the correlation coefficients required for significance at the .05 and .01 levels (df = 27) were .36 and .46, respectively. Comparable values for bairdi (df = 34) were .33 and .42.

TABLE 4.1

Intercorrelation Matrix of Predictor Variables for Intake of 2%, 4%, and 8% Sucrose Solutions in *P. polionotus*

	H_2O	Age	Wgt	AL 4	2%	4%	8%
H_2O	--	-.25	.39**	.13	.76**	.74**	.65**
Age		--	-.18	-.04	-.14	-.09	-.12
Wgt			--	.01	.26	.25	.23
AL 4				--	-.21	-.28	-.39*
2%					--	.96**	.88**
4%						--	.85**
8%							--

*p<.05.

**p<.01.

TABLE 4.2

Intercorrelation Matrix of Predictor Variables for Intake of 2%, 4%, and 8% Sucrose Solutions in *P. m. bairdi*

	H_2O	Age	Wgt	AL 4	2%	4%	8%
H_2O	--	-.17	.49**	.15	-.29	-.32	.00
Age		--	.00	.06	.00	-.05	-.16
Wgt			--	.29	-.35*	-.37*	-.26
AL 4				--	-.43**	-.54**	-.55**
2%					--	.90**	.55**
4%						--	.51**
8%							--

*p<.05.

**p<.01.

significantly, and somewhat negatively, related to sucrose intake (.00 to -.13). Age proved to be nonsignificantly related to sucrose consumption for either species; in fact, the correlations, unexpectedly, were slightly negative or zero. However, weight correlated significantly and also inversely with two of the three concentrations (2% and 4%) in _bairdi_, indicating that the smaller animal tended to ingest greater amounts of sucrose; yet, _bairdi_ weight and water intake were significantly and positively correlated, indicating that the heavier animal tended to consume larger amounts of water normally. This discrepancy in the relation of weight to fluid intake of water and sucrose by _bairdi_ accounts for the zero or slightly negative correlations found between water intake and sucrose intake. The positive association of weight with water intake was significant for _polionotus_, but not with any of the three sucrose concentrations. All six correlations between threshold value and sucrose intake were in the negative direction, as expected; all three correlations with 2%, 4%, and 8% intake were significant for _bairdi_, but with one possibly spurious exception (8%) the inverse relationships were not significant for _polionotus_.

With respect to the intercorrelations among only the four "explanatory" variables, for both species only weight and water intake were significantly associated. Therefore, with this exception, age, weight, water intake, and threshold value were relatively independent of one another. All comparisons of intake from the three concentrations were found to be significantly intercorrelated at the .01 level for both species, indicating that increases in intake from the sweeter solutions were generally additive among individuals within either species.

The significance of species differences in the correlations obtained with bairdi and polionotus on each explanatory variable with sucrose intake were tested by using the Fisher r to Z transformation procedure described in Hays (1963, p. 532). Significant species differences were found with water intake and weight. The differences in correlation coefficients for water intake and sucrose intake were significant at all three concentrations. Significant differences with weight were found only for 2% and 4% intake. None of the differences between polionotus and bairdi correlations with either age or threshold value and 2%, 4%, and 8% intake were found to be significant at the .05 level, even though AL 4 correlated significantly at all concentrations for bairdi but not for polionotus.

Thus, the results in Tables 4.1 and 4.2 show that despite the finding that no significant species differences were evident for single-stimulus 24-hr. intake of the three suprathreshold sucrose solutions, two variables (water intake and threshold value) appear to be associated with the sucrose intake behavior of *polionotus* and *bairdi* to significantly different degrees. These results suggest that the determining factors underlying sucrose consumption of the *Peromyscus* species may differ, even though the amount of fluid consumed by either species did not differ.

The most striking finding from the intercorrelation matrices (Tables 4.1 and 4.2) was that sucrose intake was found to be highly associated with normal water intake for *polionotus*, while virtually not at all for *bairdi*. The increase in sucrose intake as a function of concentration appears to reflect generally a constant palatability effect among individual *polionotus* with individual differences in sucrose intake determined largely by differences in an individual animal's tendency to ingest a certain amount of fluid in a 24-hr. period. The high intercorrelations for intake among the three sucrose concentrations and water illustrates that individual differences were reliable at all concentrations, i.e., generally the animal which tended to consume the most water also drank the most from each sucrose solution. The virtually nonexistent association of water intake and sucrose intake in *bairdi* and the more variable intercorrelations of sucrose intake among the three concentrations clearly suggests that individual differences in sucrose intake cannot be attributed to differences in voluntary water consumption levels. That taste factors were responsible for differential amounts of sucrose consumption in *bairdi* is suggested indirectly by the strength of the inverse relationship between threshold value and sucrose intake, and, of course, by the lack of a water-sucrose intake relationship.

The coefficient of determination, r^2, when multiplied by 100 gives the percentage of the variance in one variable that is associated with or accounted for by variance in the other variable (Guilford, 1965, p. 379). Conversely, the proportion of variance in one variable not associated with variance in the other is called the coefficient of nondetermination, k^2, which is simply equivalent to $1 - r^2$. In terms of *Peromyscus* sucrose intake, approximately 40%-60% of the variance in sucrose intake by *polionotus* could be accounted for by difference in water intake (i.e., across the three concentrations r^2 varied from .42 to .58). For *bairdi*, AL 4, the variable most highly correlated with sucrose intake, accounted for nearly 20% to 30% of the variance in sucrose intake from the same concentrations. Thus, for *polionotus* and *bairdi*, respectively, approximately 50% and 75% of the variance in intake from the sucrose solutions was left unexplained by the single variables which had the strongest association with sucrose intake.

Multiple Correlation and Multiple Regression

The other "explanatory" variables were correlated with sucrose intake, of course, but to a lesser and generally nonsignificant extent. However, they would be expected to decrease some of the uncertainty over the unexplained variance in sucrose intake to the extent that they are correlated with sucrose intake and also independent of one another. Multiple prediction techniques, i.e., multiple correlation and multiple regression, were used to determine for each concentration (1) the total percentage of variance accounted for by all four variables combined, and (2) the percentage of variance contributed uniquely by each variable. In addition, regression equations were obtained for purposes of determining which variables or combination of variables would be likely to provide best prediction of sucrose intake in cross-validation samples of *bairdi* and *polionotus*.

Separate multiple correlations and regression equations were derived from data obtained from the same subjects within each species. With this kind of procedure there will be dependency among the separate analyses for the three concentrations, because the sampling error associated with intercorrelations of the four "predictor" variables will be the same for each of the three solutions. The use of a random groups design would have eliminated this dependency and provided independent estimates of the parameters for each solution. However, individual differences in intake patterns across concentrations as well as in levels of intake from a single concentration were of interest in the present research. Multivariate analyses of the data obtained from a within subjects design as used here affords an opportunity to explain individual differences in intake "profiles" for the range of concentrations. While the outcome of analyses with data from independent groups may be found to yield similar "profiles," it would not be possible to determine whether intake among the taste solutions would be correlated. Therefore, whether a degree of explanation provided by one or more variables for individual differences to one concentration would hold for other concentrations would be uncertain.

While other multivariate correlation techniques were considered (e.g., factor analysis, cluster analysis), it was thought that multiple regression and correlation would be better suited for present purposes. For both *bairdi* and *polionotus* intake from the three concentrations was highly reliable and intercorrelated significantly. Thus, with other multivariate procedures the dependent variables of 2%, 4%, and 8% intake would probably have been found to "cluster" or to emerge as an orthogonal "factor." This result would have been unsatisfactory, of course, because it was of interest to profile individual differences in intake for each of the solutions. Moreover, multiple regression and correlation were thought to be more familiar, and, therefore, more understandable to most psychologists.

Stepwise regression. The technique of stepwise regression (Darlington, 1968) was used to select which combination of the four variables (water intake, age, weight, and threshold value) would provide the best prediction equation for each concentration. With this technique one variable is selected at a time for regression equations, beginning with the one which is found to be the most valid, i.e., which alone accounts for the largest proportion of the variance. Then, another variable is selected which, when combined with the first, is found to add the most to the multiple correlation and thus provide the best equation with two predictors. Additional variables are selected one at a time in a similar manner. The relationship between multiple correlation and multiple regression is such that the multiple correlation expresses the degree of association between the values predicted by a multiple regression equation and the obtained values (Guilford, 1965, pp. 395-396).

A coefficient of multiple correlation, R, indicates the strength of relationship between one variable (e.g., sucrose intake) and two or more others combined (Guilford, 1965, p. 394). The coefficient of multiple determination, R^2, gives the proportion of variance in the dependent variable which is associated with or predicted by combinations of the predictor variables used in the multiple regression equation (Guilford, 1965, p. 399). Thus, the total proportion of variance in sucrose intake from a given concentration which was accounted for by voluntary water intake, age, weight, and threshold value was determined by the value of R^2 associated with the multiple regression equations which included all four variables.

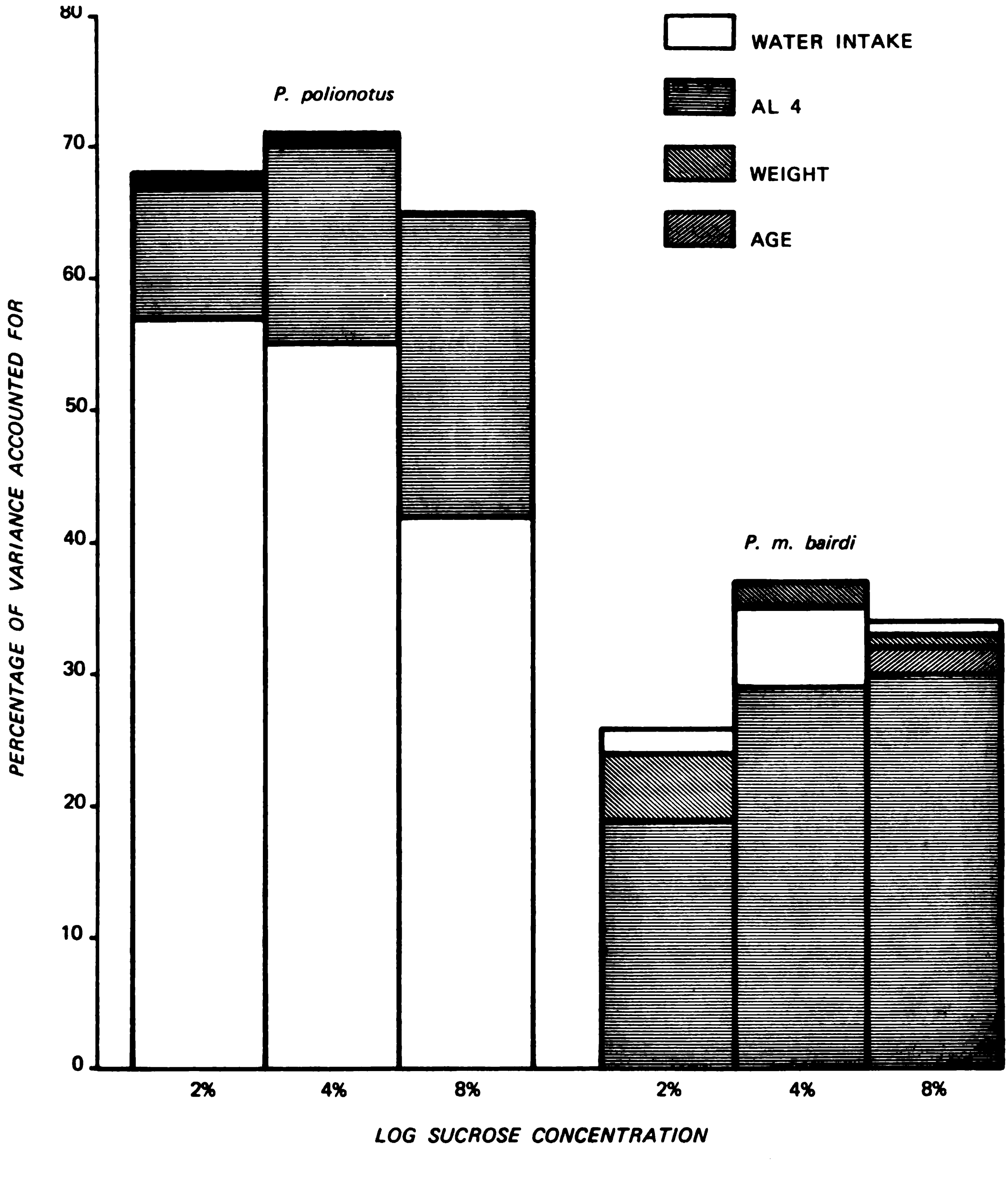
To determine the unique proportion of variance accounted for by each of the four variables in their order of magnitude, the R^2 values for the one-, two-, three-, and four-variable regressions generated by the stepwise regression technique were determined. Then, beginning with r^2, the coefficient of determination for the first variable selected, a subtractive procedure was used to determine how much additional variance was explained by adding one variable at a time in multiple correlations. The difference between values of R^2, then, represented the unique contribution of a single variable to the proportion of the total variance not already accounted for by the other variables.

The percentage of variance in sucrose intake from each concentration (Experiment 2) accounted for by voluntary water intake, age, weight, and threshold value

(Experiment 1) in order of magnitude is presented for both species in Fig. 4.1. Over the three concentrations approximately two-thirds of the variance (65% to 71%) was "explained" by all four variables combined for *polionotus*, while about one-third or less of the individual differences in sucrose intake among *bairdi* was accounted for (26% to 34%). As expected on the basis of the intercorrelation matrices (Tables 4.1 and 4.2) voluntary water intake and threshold value were the variables which alone accounted for the most significant proportion of the variance for *polionotus* and *bairdi*, respectively.

Tests of significance for differences between multiple correlations with variables added (Guilford, 1965, p. 403) showed that the threshold value for *polionotus* explained a significantly greater proportion of the sucrose intake variance than water intake alone at all three concentrations ($df = 1$ & 26; $p<.01$). Age and weight added virtually nothing. For *bairdi* none of the R^2 values with one or more variables added to threshold were significantly larger ($df = 1$ & 33; $p>.05$). Thus, the results show that both water intake and threshold value explained approximately two-thirds of the variability in *polionotus* sucrose intake, while a threshold estimate was the only variable which accounted for a significant, though smaller, proportion of the *bairdi* variance.

Fig. 4.1. Percentage of variance in sucrose intake accounted for by voluntary water intake, threshold value (AL 4), weight, and age in _P_. _polionotus_ and _P_. _m_. _bairdi_ by stepwise regression.


80
70
60
50
40
30
20
10
0
PERCENTAGE OF VARIANCE ACCOUNTED FOR
P. polionotus
P. m. bairdi
WATER INTAKE
AL 4
WEIGHT
AGE
2%
4%
8%
2%
4%
8%
LOG SUCROSE CONCENTRATION

Because thresholds are normally neither of interest nor measured in taste preference experiments, the amount of variability in sucrose intake accounted for only by the other three variables--water intake, age, and weight--which are generally available to the investigator was determined. The results are presented in Tables 4.3 and 4.4. Only water intake for polionotus and weight for bairdi accounted for a significant portion of the variance. The table reveals, as found before, that differences in water intake were responsible for approximately 50% of the polionotus variance in sucrose intake. Differences in bairdi weight accounted for little more than 10% of their intake, and the association was not significant for 8% sucrose.

The results presented in Fig. 4.1 and Tables 4.3 and 4.4 showed that at all three sucrose concentrations single-bottle intake was explained to a larger degree for polionotus than for bairdi. Accordingly, the results indicate that polionotus intake could be predicted better than bairdi intake in cross-validation studies with or without a threshold estimate on each animal. However, these results were based on relatively small samples for correlational purposes; with multiple correlation problems anything less than a sample size of 100 is considered small for purposes of estimating population parameters (Guilford, 1965, p. 400). Thus, the R and R^2 values

TABLE 4.3

Proportion of Variance in 2%, 4%, and 8% Sucrose Intake Accounted for by Water Intake, Age, and Weight for _P. polionotus_ by Using Stepwise Regression

Predictor	Concentration		
	2%	4%	8%
Water	.57**	.55**	.42**
Age	.00	.01	.00
Weight	.00	.00	.00
Totals	.57**	.56**	.42**

Note: Variables are listed in order of importance.

**p<.01.

TABLE 4.4

Proportion of Variance in 2%, 4%, and 8% Sucrose Intake Accounted for by Water Intake, Age, and Weight for _P. m. bairdi_ by Using Stepwise Regression

Predictor	Concentration		
	2%	4%	8%
Weight	.12*	.13*	.07
Water	.02	.03	.01
Age	.00	.01	.03[a]
Totals	.14*	.17*	.11

Note: Variables are listed in order of importance.

[a] Age and Water are ordered inversely for convenience.

*p<.05.

obtained on the present samples of animals would be expected to be somewhat inflated values. For predictive purposes, it is advisable to use the fewest predictor variables necessary, for "the validity of a sample multiple regression equation is very low when the number of predictor variables is large in relation to the number of (animals) in the sample on which the equation was derived" (Darlington, 1968, p. 174).

While the number of possible predictor variables considered in the present study were relatively few, the equations which perhaps best would predict intake of _polionotus_ and _bairdi_ in new samples of animals would incorporate only those variables which were found to account for a significant proportion of the variability. On this basis, then, a multiple regression equation predicting _polionotus_ sucrose intake would incorporate both water intake and threshold value, while a simple linear regression equation using only the threshold estimate for _bairdi_ would be expected to assure prediction with the least error. Accordingly, the regression equations with predicted and obtained values based on the present data for each concentration are presented in Tables 4.5 and 4.6. The linear equations are expressed with raw score coefficients (i.e., not standard score) which indicate the relative importance or weight which should be attached to the value of each predictor variable in order

TABLE 4.5

Prediction with Raw Score Coefficients of
2%, 4%, and 8% Sucrose Mean Intake by
Water Intake (X_1) and AL 4 (X_2)
in *P. polionotus*

Sol.	Equation	Predicted	Obtained	Diff.
2%	$Y = 2.87 + 1.96X_1 - 6.93X_2$	11.65	11.68	.03
4%	$Y = 4.38 + 2.57X_1 - 11.19X_2$	15.26	15.31	.05
8%	$Y = 9.33 + 1.77X_1 - 10.76X_2$	15.91	15.91	.00

Note: $X_1 = 5.54$; $X_2 = .30$.

TABLE 4.6

Prediction with Raw Score Coefficients of
2%, 4%, and 8% Sucrose Mean Intake by
AL 4 (X) in *P. m. bairdi*

Sol.	Equation	Predicted	Obtained	Diff.
2%	$Y = 11.10 - 2.19X$	8.84	8.85	.01
4%	$Y = 16.29 - 3.58X$	12.60	12.61	.01
8%	$Y = 17.14 - 2.64X$	14.42	14.42	.00

Note: $X = 1.03$.

to insure maximum prediction of sucrose intake. Note that the residuals (obtained minus predicted values) for mean intake from each sucrose solutions are very small. The equations, then, fit the "average" case for each concentration with very little error. Least squares regression analyses for these equations and the corresponding R^2 or r^2 values are presented in Tables 4.7 and 4.8.

These four tables collectively show that the linear regression of the mean obtained and predicted values was significant at all concentrations based on the analyses of variance for polionotus (df = 2 & 26; $p<.01$) and bairdi (df = 1 & 34; $p<.01$). However, much more variability in sucrose intake remained unexplained by the linear relationship of these variables for bairdi (70% or more) than for polionotus (35% or less). The proportion of sums of squares due to linear regression over the total (i.e., R^2 or r^2) indicates that the residuals will be generally smaller among individual polionotus than among bairdi. Accordingly, in cross-validation samples better prediction of polionotus intake would be expected on the basis of these data.

A frequency distribution of the residuals (obtained minus predicted values) for intake of individual subjects is shown in Fig. 4.2. Because the sample sizes differed, percentage frequencies are plotted to facilitate comparison. As indicated by the regression analyses

TABLE 4.7

Regression Analyses for Prediction of 2%, 4%, and 8% Sucrose Intake by Water Intake and Threshold Value (AL 4) in *P. polionotus*

Sol.	Source	SS	df	MS	F	R^2
2%	Regression	373.7	2	186.8	26.39**	.67
	Residual	184.1	26	7.1		
	Totals	557.8	28			
4%	Regression	677.6	2	338.8	29.37**	.69
	Residual	299.9	26	11.5		
	Totals	977.5	28			
8%	Regression	370.3	2	185.1	24.20**	.65
	Residual	198.9	26	7.7		
	Totals	569.2	28			

$^{**}p<.01$.

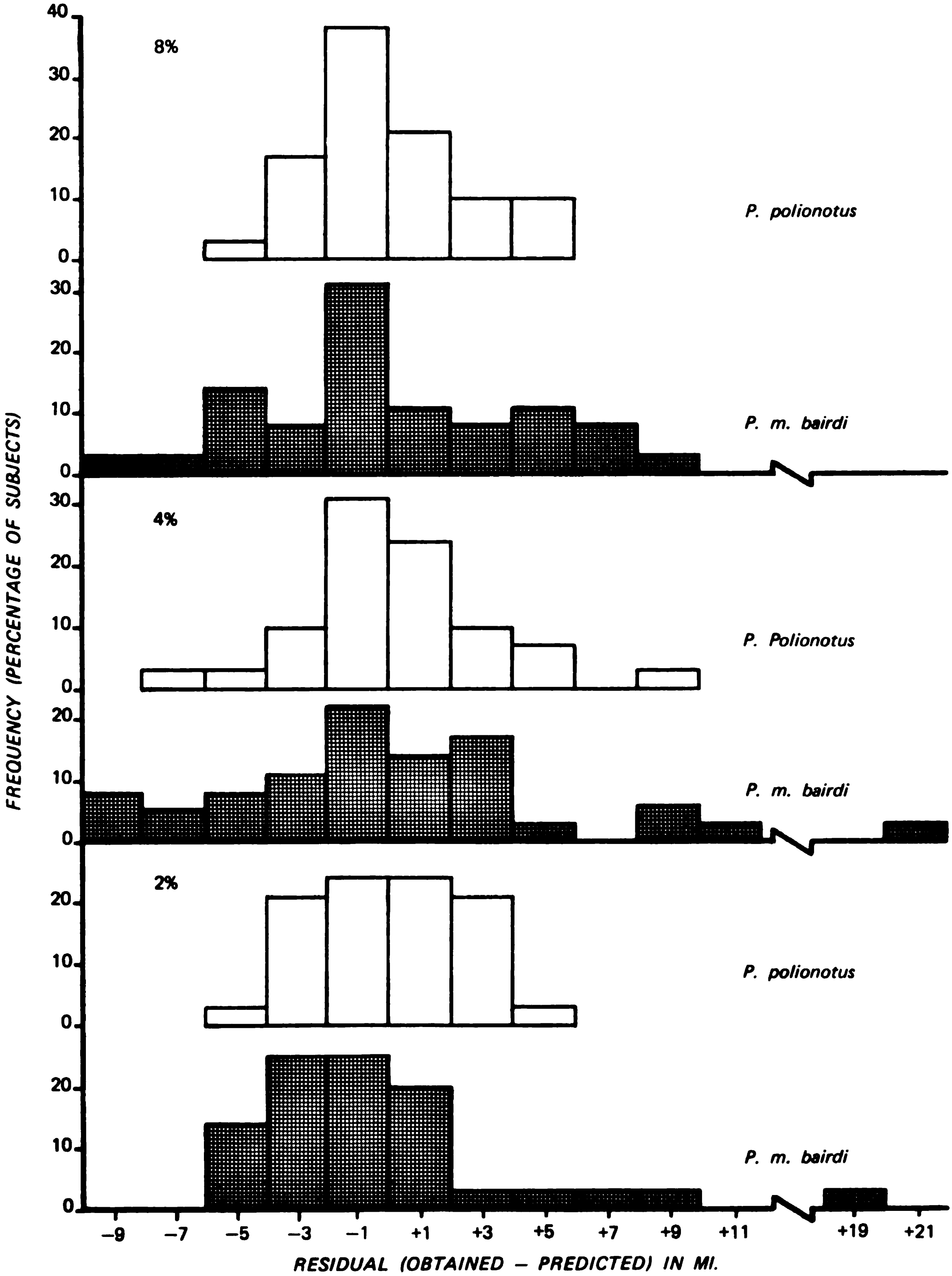
TABLE 4.8

Regression Analyses for Prediction of 2%, 4%, and 8% Sucrose Intake by Threshold Value (AL 4) in *P. m. bairdi*

Sol.	Source	SS	df	MS	F	R^2
2%	Regression	182.0	1	182.0	7.80**	.19
	Residual	792.9	34	23.3		
	Totals	974.9	35			
4%	Regression	485.3	1	485.3	13.92**	.29
	Residual	1185.7	34	34.9		
	Totals	1671.0	35			
8%	Regression	263.4	1	263.4	14.44**	.30
	Residual	620.0	34	18.2		
	Totals	883.4	35			

$^{**}p<.01$.

Fig. 4.2. Distribution of residuals in ml. for *P. m. Bairdi* and *P. polionotus* as a function of concentration.


FREQUENCY (PERCENTAGE OF SUBJECTS)
8%
P. polionotus
P. m. bairdi
4%
P. Polionotus
P. m. bairdi
2%
P. polionotus
P. m. bairdi
40
30
20
10
0
−9
−7
−5
−3
−1
+1
+3
+5
+7
+9
+11
+19
+21
RESIDUAL (OBTAINED − PREDICTED) IN MI.

(Tables 4.7 and 4.8), the residuals for individual *polionotus* were found to be less variable than for *bairdi*. For all concentrations the distribution of *polionotus* residuals have a smaller range. The figure shows, however, that the error in *bairdi* prediction may not be so large as expected merely on the basis of coefficients of determination. For 2% and 4% intake the distributions are considerably skewed, and in each case the intake of a single individual was underestimated by nearly 20 ml. Undoubtedly, were this atypical subject eliminated from the regression analyses for *bairdi* a better least squares regression fit would be found for the data of the remaining 35 animals.

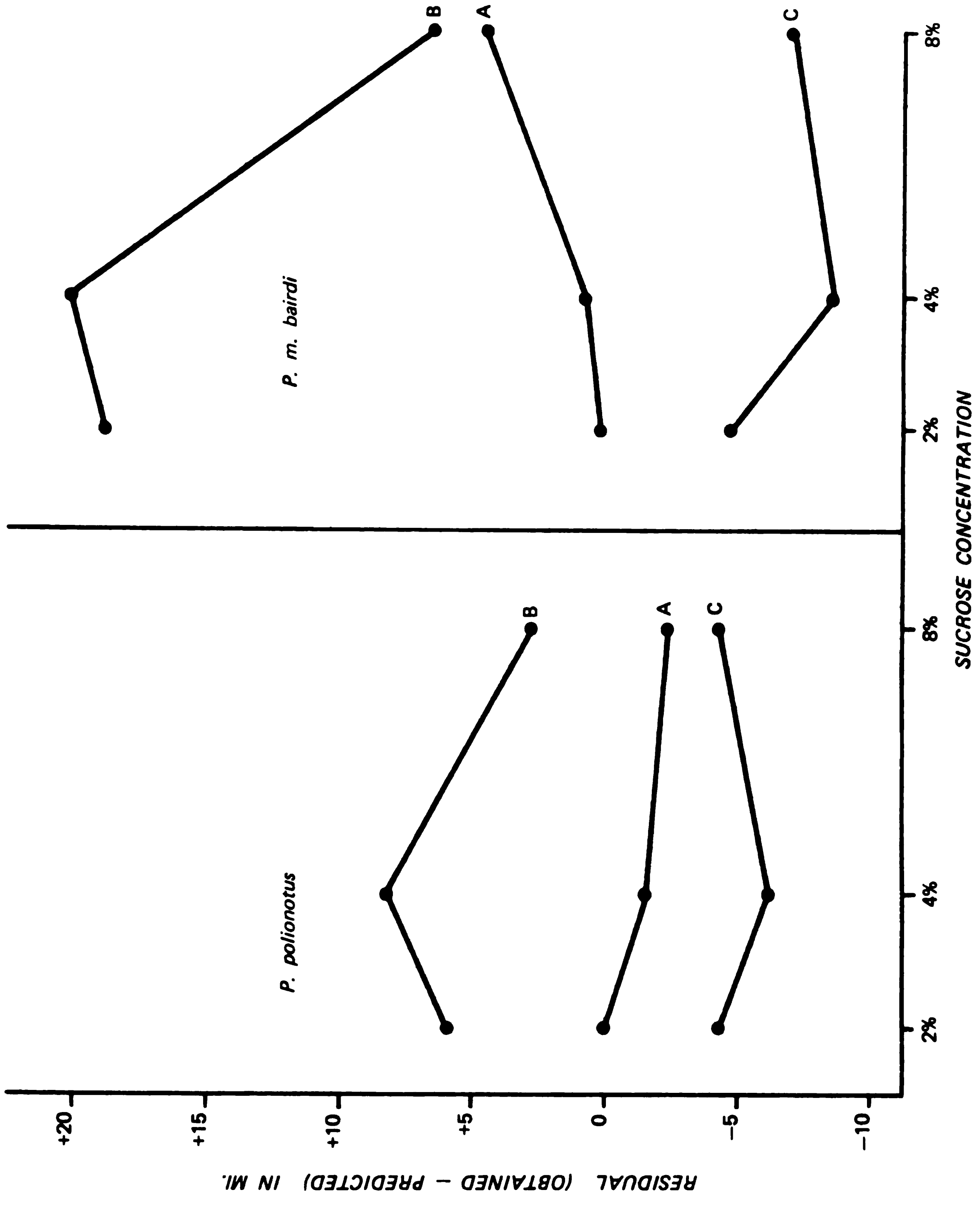
The distributions of residuals (Fig. 4.2) based upon the mean prediction equations generated by the data for each concentration separately (Tables 4.5 and 4.6) do not depict the goodness of fit for an individual animal's intake behavior across the range of concentrations. That is, observed intake may be found to agree with predicted intake better for some concentrations than others among individual animals. For example, virtually errorless prediction for a subject may be found at one concentration, while the observed intake may depart to some extent in either a positive or negative direction for other concentrations.

Figure 4.3 illustrates prediction "profiles" of three individual *bairdi* and *polionotus* to all three concentrations. The subjects selected were those which showed the best fit in predicted and obtained intake (i.e., the smallest absolute residual value) from the 2% sucrose solution and the largest deviation in a positive and a negative direction. The figure shows that relative differences among the three individuals for each species were preserved at higher concentrations, although the predictions for the individual *polionotus* were relatively more stable than for the three *bairdi*. This finding is not so surprising, though, when considering the fact that the intercorrelations of intake from all three concentrations were more stable for *polionotus* and that *bairdi* intake among subjects was found to interact significantly with concentrations.

Interpretations and Limitations

The size of correlation coefficients and, consequently, the validity of regression equations for prediction in cross-validation studies are subject to a number of factors which will have a bearing upon the interpretation of the results. For example, the size of r is dependent upon the variability of the values measured in the samples; the variability, in turn, is related to the conditions under which the measures were

Fig. 4.3. Residuals in ml. as a function of concentration for the three *P. m. bairdi* and *P. polionotus* individuals which demonstrated the smallest (A), the largest positive (B), and the largest negative (C) deviations from predicted 2% sucrose intake.


RESIDUAL (OBTAINED − PREDICTED) IN Ml.
+20
+15
+10
+5
0
−5
−10
SUCROSE CONCENTRATION
2%
4%
8%
2%
4%
8%
P. polionotus
P. m. bairdi
A
B
C
A
B
C

obtained (Guilford, 1965, p. 341). Accordingly, it is appropriate to specify the kind of population represented by the sample of animals from either species to which the conclusions from these experiments may apply. An examination of the relation between size of the intercorrelations of the variables responsible for the multiple correlations and regression equations and the variability in these measures also is desirable.

The samples of polionotus and bairdi were comprised of animals which could be described as mature-young, perhaps. Both the polionotus and bairdi ranged in age from approximately 2 to 5 months of age. Based on the classification scheme for rats used by Goodrick (1969), these deer mice were not immature (1 month), or mature-old (about 1 to 1.5 yr.), or senescent (about 2 yr.). There was no significant difference in the average age of the bairdi (97.4 days) and polionotus (86.1 days). Even though the ranges in age were nearly the same (90 days and 86 days for bairdi and polionotus, respectively), the bairdi were significantly heavier on the average by 2.5 gm. Over the 26-day period of Experiments 1 and 2 neither species gained an appreciable amount of weight (about 1.0 gm. for either species).

For animals of either species within the age and associated weight ranges sampled, there is reason to believe that fluid intake measures recorded in Experiments

1 and 2 provided adequate estimates of both the means and variances which could be expected in cross-validation samples tested by the same procedures. Intake from all solutions was highly reliable for both species, particularly water intake, as indicated by the size of the "test-retest" correlation coefficients on 24-hr. intake during nonconsecutive test periods (Tables 2.6 and 3.1). Moreover, similarly high reliability in intake was found at all concentrations for both species, even though the variability in *polionotus* intake from these concentrations was generally greater than *bairdi* variance.

It is interesting to note how closely related the size of the obtained correlation coefficients were with the means and variability of the measures. The variables significantly correlated with sucrose intake in one species and not in the other also were those with the larger means and variances. For example, the intercorrelation matrices (Tables 4.1 and 4.2) showed that for *bairdi* both weight and threshold value (AL 4) were significantly, and inversely, correlated with sucrose intake, while for *polionotus* only water intake was significantly, and positively, associated with sucrose consumption.

Coincidentally, the species differed significantly in the means for these variables; the *bairdi* weighed more and had a higher threshold, while *polionotus* drank more water. The variances were somewhat proportional to the magnitudes of these means, also, and differed significantly; bairdi variances in weight and threshold value were larger, although polionotus water intake was more variable. The means and variances of age did not differ significantly and were not significantly associated with sucrose intake for either species, although age and water intake were significantly correlated for both species (Tables 4.1 and 4.2). The analyses of the results reveal, then, that the variables found to be differentially associated with intraspecific differences in sucrose intake for polionotus and bairdi were also those for which significant interspecific differences were found in the means and variances. Expected relationships among water intake, age, weight, and threshold value were found in one or the other species, although some other relationships were unexpected and are difficult to explain.

Age, weight, and fluid intake. One peculiar outcome from the multivariate analyses, for example, was the finding that among the mature-young animals tested, bairdi weight was positively correlated with water intake, but inversely related to sucrose intake, to a significant degree (Table 4.2). No ready explanation for the negative relationship is offered. Age and weight were expected to be positively correlated and add little beyond water intake alone in accounting for the consumption of sucrose for either species. It was anticipated that the heavier animal would have the greater apparent water need as indicated by amount of water intake (which the results confirm), and, therefore, that it also would consume more sucrose solution. Undoubtedly, the intercorrelations among age, weight, water and sucrose intake would conform more to the expected if the ages of the animals were more representative of the larger population, i.e., if juveniles and older mice were included in the samples.

The significant differences in the relation of weight to sucrose intake between *polionotus* and *bairdi* suggest that adjusting intake to bodyweight as Wagner & Rowntree (1966, 1970) have done with *Peromyscus* may be inappropriate in some cases. Their procedure was understandable, of course, because in their experiments with a larger variety of *Peromyscus* species they found *P. floridanus* was nearly twice as heavy as *bairdi* and other species, on the average, and that they consumed much larger quantities of sugar solution. However, if the significant negative correlation between weight and sugar intake were to be found in studies with other sugars and with different procedures, then transforming total intake into total intake per 100 gm. bodyweight may introduce a source of error in the results. Thus, intraspecies intake should be positively correlated with weight for such a transformation to be used. The use of a relative preference measure in two-choice preference tests is probably a better method for taking bodyweight into account, although it may require additional transformations for meeting the assumptions of statistical analyses.

Thresholds and Fechner's Law. An inverse relationship between "preference" thresholds and intake from sucrose solutions was expected on the basis of Fechner's psychophysical model applied to taste behavior. Underlying this prediction were assumptions about the relation of intake to stimulus (concentration) and sensation (perceived sweetness or "hedonic intensity") factors as explained in Chapter I. Briefly, more concentrated solutions of a palatable taste substance are assumed to arouse pleasurable subjective experiences having a relatively greater intensity than such reactions to less concentrated solutions (Young, 1959, 1966). These affective processes are viewed as intervening variables (Young, 1959) and merely provided another way of saying that intake (or relative preference) will be somewhat proportional to the concentrations of sucrose solutions, because sweeter solutions arouse greater "hedonic intensities."

On the basis of psychophysical principles and using the motivational assumptions described above, it was expected that individual differences in sucrose intake would be explained partially by differences in "preference" thresholds for sucrose. Where apparent differences are found in levels of near "zero" sweetness sensation (i.e., threshold) among individual animals, it would be predicted that the intensity or magnitude of sweetness experienced for a single concentration above threshold should be relatively greater for the more sensitive individuals. Accordingly, intake should be generally greater at all concentrations for those individuals which demonstrated the lowest threshold for sucrose.

All six simple linear correlations between the threshold estimate and sucrose intake were negative (Tables 4.1 and 4.2), which was in the expected direction. The finding that the threshold value was the single variable most strongly associated with *bairdi* sucrose intake and that it reduced a significant portion of the unexplained variability in *polionotus* intake in combination with water intake provides indirect support for the application of this psychophysical model applied to sucrose intake behavior. Moreover, the generally high intercorrelations among 2%, 4%, and 8% sucrose intake, particularly for *polionotus* (for which r ranged from .85 to .95), indicate that the degree of explanatory value provided by thresholds generally held up well across the range of concentrations for individuals.

On the basis of short-term choice preference data (Young & Greene, 1953) and long-term (23-hr.) single-bottle intake data (Owings *et al.*, 1967), a logarithmic function for average intake which would depict the relationship between intake and stimulus concentration described by Fechner's psychophysical law was anticipated. While both species consumed increasingly larger amounts of fluid from sweeter (more concentrated) solutions, average sucrose intake did not increase in quantities logarithmically proportional to concentration. Instead, intake from suprathreshold solutions was a somewhat negatively accelerated function of concentration. Moreover, for bairdi, particularly, individual intake patterns differed as indicated by a significant interaction between concentration and subjects for intake (Table 3.4). Therefore, neither the average nor individual intake functions conformed particularly well with the direct translation of Fechner's psychophysical scaling law into intake. As suggested previously, an interaction of taste and fluid capacity factors provide an explanation for the smaller increase in intake for higher concentrations. Young (1959) argues that postingestional factors would influence long-term intake, which is the reason for his using brief-exposure tests with which he found a logarithmic relationship between preference and sweetness (Young & Greene, 1953).

Whether the relationship of intake (or some other measure of preference) for a taste substance in rodents is found to be a logarithmic function (Fechner's law) or possibly some form of a power function (Stevens' law) is not a crucial issue for present purposes. Of more immediate interest is the fact that a relationship suggested by psychophysical scaling laws between thresholds and response to stimuli above thresholds was found to be useful for explaining individual differences in sucrose intake to a significant degree among two species of *Peromyscus*. With different species or with different preference measures (e.g., 1-hr. single-bottle intake, or two-bottle relative preference) a more linear and perhaps logarithmic relationship with concentration may be found.

In the present study the intensity of the individual's taste response to sweetness was measured indirectly only by absolute amounts of sucrose intake. To the extent that levels of water and sucrose intake are not independent the relationship between threshold value and magnitude of response to sweetness will be obscured by this apparent tendency among individuals to consume proportionally similar amounts of flavored and unflavored solutions. With *polionotus*, for which there was a highly significant correlation between water and sucrose intake, the degree of association between thresholds and sucrose intake was found to be considerably weaker than with *bairdi*. Therefore, when one considers this limitation imposed by using an absolute intake measure of sucrose acceptance for solutions differing in sweetness, the

degree of explanation provided by thresholds as derived from psychophysical laws is even more respectable.

The roles of water and energy regulation. It was argued that osmotic properties and caloric "metering" played a limited role, if any, in determining intake from the sucrose solutions in this study (Chapter III). While taste (palatability) factors clearly influenced sucrose intake, the results of the multivariate analyses suggest that the mechanisms regulating sucrose intake in *Peromyscus* operate differentially in *P*. *polionotus* and *P*. *m*. *bairdi*. The finding that neither species showed any appreciable weight gain during the duration of the experiments and the indication that level of water intake was a major satiating factor of *polionotus* sucrose intake suggest the possibility that these two species possess different metabolic and water regulatory mechanisms.

The negligible weight gain found in either species over the 26-day period in which Experiments 1 and 2 were conducted was interesting in light of the fact that during six of the last seven days before they were weighed the animals ingested more than 2.5 times the normal amount of fluid intake from sucrose solutions. During these test periods no water alternative was available, and, therefore, the only source of water was the carbohydrate solution which also contained calories. Food intake was not measured in this study, so it was not possible to determine the extent to which total caloric intake may have increased.

Previous findings on wild Norway rats (Maller & Kare, 1965) would suggest that Peromyscus did not increase caloric intake substantially during testing periods compared to normal caloric intake from a lab chow and water diet. If these animals did tend to eat less of the dry lab chow to compensate for the sucrose calories consumed during test periods, then they would have demonstrated an ability to regulate their energy intake more effectively than laboratory rats and monkeys apparently do over relatively short test durations (Maller & Kare, 1965; Maller & Hamilton, 1968). Evidently, then, both species were able to maintain weight balance through efficient energy metabolism, while ingesting more than 2.5 times their voluntary water intake levels from the only fluid available which was flavored with a palatable and caloric substance.

Energy metabolism and water regulatory processes may have interacted differentially in polionotus and bairdi, however, to determine total intake from the different sucrose solutions. To illustrate, a smaller proportional increase to sucrose solutions was found by polionotus which normally consume significantly more water than bairdi. The proportionally larger bairdi increase in sucrose intake across the three concentrations compared to polionotus means that bairdi consumed more calories as well as fluid. Since it is unlikely that animals would repeatedly ingest more fluid than they could comfortably accommodate, and therefore exchange over successive 24-hr. periods, the results of this study suggest that bairdi may have the capacity to exchange hypotonic fluids more rapidly than polionotus. Such an ability by bairdi to ingest and to eliminate greater quantities of fluid than polionotus would explain the proportionally greater increase in suprathreshold sucrose intake by bairdi which eliminated species differences expected merely on the basis of normal water consumption and thresholds.

It is difficult to determine from the data of the present study whether taste factors were more important for bairdi than polionotus in determining their proportionally greater intake of sucrose solutions, or whether a different fluid regulatory system prevented polionotus from consuming as much of the sucrose as they might otherwise tend to do. Either conclusion would be consistent with the data, because no provisions were made in the design of this study to separate taste and fluid capacity factors. But, whatever was responsible for determining 24-hr. intake for these Peromyscus, the results clearly suggest that the quantitatively similar curves of single-bottle sucrose intake for 2%, 4%, and 8%

concentrations were "explained" to different degrees and by different underlying variables.

Implications and Further Research

If interspecific comparisons of *Peromyscus* sucrose intake were limited only to the amounts consumed from 2%, 4%, and 8% sucrose solutions, it would be concluded that *P. m. bairdi* and *P. polionotus* do not differ in their acceptance of sucrose. However, while no interspecific differences were found in the quantitative measurement of sucrose acceptance, the correlational analyses of the collective data from Experiments 1 and 2 indicated that taste and satiety factors operated differently in these species to determine levels of intake. Thus, differences in the behavior of *Peromyscus* to taste solutions were found which would be otherwise obscured if only the amount of intake were considered.

Whether similar findings would be obtained with these deer mice if two-bottle preference tests for sucrose and water were conducted remains to be seen. Regardless, the different conclusions concerning the taste behavior of *P. m. bairdi* and *P. polionotus* for sucrose point to the usefulness of multivariate procedures for comparative studies of taste behavior. For whether species differences in acceptance of sucrose (or other taste substances) are found or not, firm conclusions about degrees of preference among species may be undermined by inappropriate assumptions about the role of "taste" and satiety factors in determining relatively long-term intake. As noted previously, the palatability factors and osmotic-postingestional factors commonly used to explain preference functions do not satisfactorily account for the various curves obtained with different procedures.

Quantitative differences in relative preference between domestic and wild species may be expected if taste is of functional significance as postulated (Kare, 1961; Kare & Fickey, 1963), and if it is assumed that taste behavior measured in the laboratory bears some ecological validity to the role of taste in the animal's natural habitat. As Maller & Kare (1965) noted, the selection pressures are different for commercially bred (domestic) and wild animals; "for commercial animals an acute sense of taste would have no apparent survival value." They concluded that domestication may produce an animal more responsive to the sensory or "hedonic" qualities of food (sucrose), while more limited intake by the wild rat (and deer mouse, perhaps) may reflect a more careful monitoring of energy intake.

While the role ascribed to taste for survival is intuitively reasonable, support for the assumption based upon comparative taste data has met with limited success.

Methodological differences may be responsible partially for the many inconsistencies found in the results of comparative studies. Future investigators probably should take into account the possible consequences of averaging repeated measurements when using either between subject or within subject designs for drawing conclusions about quantitative differences in preference among species. In addition, energy intake from standard diets and carbohydrate solutions should be measured in order to determine the nature of the interaction between taste and energy characteristics of carbohydrates as they relate to consummatory behavior in different species. Few studies have examined both of these factors. Energy balance mechanisms and fluid exchange mechanisms which would effect the consumption of carbohydrate solutions may differ between domesticated and natural species, and evidently even among species exposed to similar selection pressures.

Summary of Research Findings

Experiment 1 showed that relatively young *P. polionotus* and *P. m. bairdi* differed significantly in voluntary water intake and in apparent sensitivity to sucrose as indicated by "preference" threshold estimates derived from 24-hr. single-bottle intake of water and sucrose solutions. While the 36 *P. m. bairdi* tested in this study weighed significantly more than the 29

_P_. _polionotus_ on the average (16.1 gm. vs. 13.6 gm.), the _P_. _polionotus_ reliably consumed larger amounts of water and had lower "preference" thresholds for sucrose based on reliable intake from concentrations ranging from 0% to 2%. Moreover, all _P_. _polionotus_ threshold values defined by various criteria with the same set of data were found to be lower than the corresponding _P_. _m_. _bairdi_ values.

In Experiment 2, however, no significant species differences were found in average intake from suprathreshold sucrose solutions of 2%, 4%, and 8%. For both species intake from the three solutions increased significantly as a function of concentration. Based on ratios of the sums of squares, the estimated percentage of variance accounted for by differences in sweetness of the solutions for each species was approximately 10%. The remaining variation was due to individual differences in either levels of intake averaged across the concentrations or in patterns of intake.

Sources of intraspecific differences in consumption from the suprathreshold concentrations were determined by multiple correlation and regression techniques. The major findings by the multivariate analyses were as follows:

1. Individual differences in age, weight, water intake, and "preference" threshold accounted for 65% or more of the variance in _P_. _polionotus_ sucrose intake, while for _P_. _m_. _bairdi_ only 37% or less was explained by these variables.
2. Stepwise regression showed that both water intake and "preference" threshold value in that order explained a significant proportion of the _P_. _polionotus_ variance (virtually all of the 65% and more), while for _P_. _m_. _bairdi_ only the threshold estimate uniquely accounted for a significant percentage of the individual differences (no more than 30%).
3. For neither species did differences in age or weight account for a significant amount of variability in combination with the other two variables (between 0% and 5%), although alone weight was significantly associated with 2% and 4% sucrose intake in _P_. _m_. _bairdi_.

The results of Experiments 1 and 2 collectively suggest that both species showed increased acceptance of sweeter solutions but that taste and satiety factors operated differently in _P_. _m_. _bairdi_ and _P_. _polionotus_ to determine similar levels of intake from suprathreshold sucrose concentrations. The significant inverse relationships between "preference" threshold and sucrose intake

provides indirect support for the psychophysical scaling of sweetness in deer mice suggested by Fechner's law. It is uncertain, however, whether taste factors were more important in determining levels of sucrose intake among *P. m. bairdi*, or whether a lesser ability by *P. polionotus* to exchange fluids was responsible for their proportionally smaller increase in sucrose intake from sweeter solutions. The possible satiating effects of the energy (caloric) properties of sucrose were not determined.

ADDENDUM

During the oral defense of this dissertation it was suggested that the amount of sucrose solute consumed from the three suprathreshold solutions be examined. Subsequently, sucrose intake in grams from the three concentrations was determined by multiplying each animal's fluid intake from the solutions by .02, .04, and .08, respectively. Preliminary analyses revealed that while fluid intake functions for _P_. _polionotus_ and _P_. _m_. _bairdi_ were negatively accelerated, the corresponding increase in solute intake was directly proportional to concentration for both species. The mean gram intake from the 2%, 4%, and 8% solutions, respectively, were .23, .61, and 1.27 for _polionotus_ and .18, .50, and 1.15 for _bairdi_.

Analyses of variance on these data without replications for each species separately showed that the concentration effect was highly significant. An estimated 75% and 67% of the variance in gram intake was accounted for by the differences in the sucrose concentrations for _polionotus_ and _bairdi_, respectively. This finding contrasts with 13% and 14% found with similar analyses of variance performed on the fluid intake data. The different functions obtained from the correlated fluid and gram intake measures raises additional questions about the roles of taste and regulatory factors in determining sucrose "preference."

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APPENDICES

APPENDIX A

DATA FROM EXPERIMENTS 1 AND 2 FOR INDIVIDUAL *P. M. BAIRDI*

TABLE A1

Water Intake for Six Days in Experiment 1 by *P. m. bairdi*

No.	Days							
	1	2	3	4	5	6	Mean	SD
1	4.5	5.3	5.2	5.2	5.1	4.8	5.02	.31
5	3.1	3.4	3.4	3.4	3.2	3.1	3.27	.15
7	2.9	3.2	3.2	3.5	3.3	3.8	3.32	.31
9	4.4	4.6	4.4	4.8	4.6	4.4	4.55	.20
15	4.8	4.6	5.9	5.5	5.7	5.8	5.38	.55
17	3.1	3.2	2.8	3.8	3.2	3.9	3.33	.43
19	3.9	5.2	5.5	4.9	5.3	5.2	5.00	.57
21	3.6	4.1	4.6	4.2	4.3	4.3	4.18	.33
25	4.0	4.6	5.5	5.7	6.8	6.6	5.53	1.09
27	4.7	5.3	5.4	5.0	5.6	5.4	5.23	.33
29	3.9	4.2	4.2	4.4	4.4	5.0	4.35	.37
31	4.5	4.2	4.6	4.2	4.8	3.8	4.35	.36
33	3.0	3.0	3.1	2.9	2.6	3.0	2.93	.18
35	4.0	4.3	4.8	4.6	5.2	5.2	4.68	.48
37	3.0	2.9	2.6	3.0	2.6	2.7	2.80	.19
39	3.8	3.2	3.6	3.2	3.5	3.2	3.42	.26
41	3.3	3.1	3.1	3.0	3.2	3.2	3.15	.10
43	3.4	3.6	3.4	3.3	4.1	4.4	3.70	.45
45	4.3	3.4	4.0	3.8	3.5	3.8	3.80	.33
47	4.9	3.9	5.3	5.4	4.9	5.6	5.00	.61
49	5.7	6.0	6.0	6.3	6.2	7.0	6.20	.44
51	3.1	3.6	3.6	3.7	3.6	3.6	3.53	.22
53	3.3	2.3	3.1	2.8	3.6	2.9	3.00	.45
55	3.3	3.2	3.8	4.1	4.4	4.7	3.92	.60
57	4.0	5.1	4.6	4.7	5.2	4.8	4.73	.43
59	3.0	3.2	2.9	3.0	3.0	3.1	3.03	.10
61	4.8	3.5	3.8	3.7	3.7	4.1	3.93	.47
63	2.9	3.6	2.9	3.6	2.6	3.5	3.18	.44
65	2.8	3.5	3.6	4.3	4.9	4.8	3.98	.82
67	3.0	3.2	4.0	4.1	3.8	3.4	3.58	.45
69	4.3	4.8	4.9	4.8	5.2	5.2	4.87	.33
71	3.8	5.1	4.2	4.9	4.3	5.6	4.65	.67
73	4.2	4.8	5.0	4.8	4.4	5.3	4.75	.40
75	3.2	3.3	3.6	3.8	4.2	4.2	3.72	.43
77	4.2	4.5	4.4	5.1	4.7	4.7	4.60	.31
79	3.2	4.4	3.9	4.2	4.6	4.8	4.18	.57

TABLE A2

Intake from Threshold Test Solutions during First and Second Presentations in Experiment 1 by *P. m. bairdi*

No.	1st Presentation					
	.000%	.125%	.250%	.500%	1%	2%
1	5.2	4.8	5.1	4.7	5.8	7.8
5	3.4	3.5	3.9	6.2	11.1	14.1
7	3.2	3.6	3.3	4.2	4.6	8.2
9	4.4	4.1	4.5	4.6	5.4	5.3
15	5.9	5.3	5.9	5.5	5.8	10.8
17	2.8	2.9	3.2	3.8	4.7	7.7
19	5.5	5.2	5.1	5.3	6.1	5.1
21	4.6	4.5	4.5	4.6	4.7	4.6
25	5.5	5.6	4.9	5.6	5.8	5.8
27	5.4	5.0	5.1	5.3	5.4	5.8
29	4.2	4.6	4.1	4.4	5.2	7.6
31	4.6	4.3	4.3	4.4	4.3	4.6
33	3.1	3.0	2.8	2.6	2.9	3.2
35	4.8	4.6	4.4	4.3	4.6	5.0
37	2.6	2.4	2.5	2.6	2.6	2.7
39	3.6	3.5	3.4	3.8	3.4	3.4
41	3.1	3.4	3.4	3.7	3.5	5.2
43	3.4	3.6	3.9	3.6	4.3	4.7
45	4.0	4.2	4.1	4.0	5.0	5.3
47	5.3	5.4	5.1	5.2	6.3	6.7
49	6.0	6.1	6.1	6.8	6.3	7.0
51	3.6	3.8	4.0	4.4	6.7	12.2
53	3.1	3.1	3.4	3.7	5.3	4.6
55	3.8	3.8	3.4	4.2	6.1	6.4
57	4.6	5.0	4.7	4.9	5.2	5.8
59	2.9	2.8	3.8	3.3	4.0	4.0
61	3.8	3.6	3.8	4.2	4.6	4.6
63	2.9	3.3	3.9	3.4	5.8	12.9
65	3.6	3.5	3.6	4.4	7.7	6.8
67	4.0	3.5	3.7	3.5	4.0	7.4
69	4.9	4.8	5.4	4.6	5.1	5.8
71	4.2	4.8	4.7	4.8	4.8	5.1
73	5.0	4.8	4.7	5.2	4.8	5.7
75	3.6	3.8	3.3	3.7	3.5	4.4
77	4.4	4.6	5.0	5.1	4.4	5.1
79	3.9	4.3	3.9	3.8	4.9	4.4

TABLE A2--Continued

No.	2nd Presentation					
	.000%	.125%	.250%	.500%	1%	2%
1	5.1	5.0	5.5	5.3	5.5	8.2
5	3.2	3.3	3.5	6.0	9.6	13.6
7	3.3	3.5	2.7	3.6	4.1	5.6
9	4.6	4.4	4.6	4.8	5.1	5.8
15	5.7	5.4	5.6	6.0	6.1	7.9
17	3.2	3.8	3.5	3.4	4.2	5.6
19	5.3	5.2	5.7	5.1	5.9	6.4
21	4.3	4.7	4.7	4.4	4.6	4.6
25	6.8	5.8	6.2	5.8	6.3	6.5
27	5.6	5.4	5.2	5.4	5.8	5.4
29	4.4	4.4	4.6	4.5	5.2	6.0
31	4.8	4.1	4.6	3.9	4.4	4.4
33	2.6	2.8	3.0	3.0	3.5	3.3
35	5.2	5.0	3.9	5.5	5.2	6.2
37	2.6	3.0	2.7	2.8	2.6	2.7
39	3.5	4.0	3.5	3.4	3.7	3.8
41	3.2	3.7	2.8	3.2	4.5	5.6
43	4.1	3.8	3.8	4.4	5.4	7.2
45	3.5	3.6	3.8	4.1	5.0	5.7
47	4.9	5.6	4.6	6.6	5.3	8.0
49	6.2	6.2	5.9	7.1	6.2	7.5
51	3.6	3.3	3.9	4.6	7.0	15.1
53	3.6	2.8	2.7	3.8	4.3	6.4
55	4.4	4.7	4.8	5.2	5.8	7.4
57	5.2	4.7	4.8	4.6	5.0	6.3
59	3.0	3.2	3.0	4.2	4.6	6.0
61	3.7	3.6	3.8	4.4	3.8	6.0
63	2.6	2.7	3.8	3.8	6.7	12.6
65	4.9	4.5	4.6	4.5	6.9	12.2
67	3.8	4.0	4.2	4.4	5.4	7.5
69	5.2	4.5	5.4	5.6	5.0	5.2
71	4.3	4.8	5.2	6.0	5.1	6.0
73	4.4	4.8	5.1	5.4	5.3	5.4
75	4.2	4.0	3.8	3.3	4.9	5.8
77	4.7	4.4	4.5	5.2	5.3	5.9
79	4.6	4.4	4.8	4.8	4.3	5.0

TABLE A2--Continued

No.	Average					
	.000%	.125%	.250%	.500%	1%	2%
1	5.15	4.90	5.30	5.00	5.65	8.00
5	3.30	3.40	3.70	6.10	10.35	13.85
7	3.25	3.55	3.00	3.90	4.35	6.90
9	4.50	4.25	4.55	4.70	5.25	5.55
15	5.80	5.35	5.75	5.75	5.95	9.35
17	3.00	3.35	3.35	3.60	4.45	6.65
19	5.40	5.20	5.40	5.20	6.00	5.75
21	4.45	4.60	4.60	4.50	4.65	4.60
25	6.15	5.70	5.55	5.70	6.05	6.15
27	5.50	5.20	5.15	5.35	5.60	5.60
29	4.30	4.50	4.35	4.45	5.20	6.80
31	4.70	4.20	4.45	4.15	4.35	4.50
33	2.85	2.90	2.90	2.80	3.20	3.25
35	5.00	4.80	4.15	4.90	4.90	5.60
37	2.60	2.70	2.60	2.70	2.60	2.70
39	3.55	3.75	3.45	3.60	3.55	3.60
41	3.15	3.55	3.10	3.45	4.00	5.40
43	3.75	3.70	3.85	4.00	4.85	5.95
45	3.75	3.90	3.95	4.05	5.00	5.50
47	5.10	5.50	4.85	5.90	5.80	7.35
49	6.10	6.15	6.00	6.95	6.25	7.25
51	3.60	3.55	3.95	4.50	6.85	13.65
53	3.35	2.95	3.05	3.75	4.80	5.50
55	4.10	4.25	4.10	4.70	5.95	6.90
57	4.90	4.85	4.75	4.75	5.10	6.05
59	2.95	3.00	3.40	3.75	4.30	5.00
61	3.75	3.60	3.80	4.30	4.20	5.30
63	2.75	3.00	3.85	3.60	6.25	12.75
65	4.25	4.00	4.10	4.45	7.30	9.50
67	3.90	3.75	3.95	3.95	4.70	7.45
69	5.05	4.65	5.40	5.10	5.05	5.50
71	4.25	4.80	4.95	5.40	4.95	5.55
73	4.70	4.80	4.90	5.30	5.05	5.55
75	3.90	3.90	3.55	3.50	4.20	5.10
77	4.55	4.50	4.75	5.15	4.85	5.50
79	4.25	4.35	4.35	4.30	4.60	4.70

TABLE A3

Age, Weight, Mean 6-Day Water Intake, and Threshold Values for *P. m. bairdi*

No.	Age (days)	Weight (gm.)	Water (ml.)	AL 1	AL 2	AL 3	AL 4
				(percentage concentration)			
1	115	18.0	5.02	1.000	1.000	1.000	.800
5	115	11.5	3.27	.125	.125	.125	.150
7	105	19.0	3.32	.500	.500	.500	.380
9	105	15.0	4.55	.250	.250	.250	.510
15	80	19.0	5.38	1.000	1.000	1.000	1.030
17	80	16.5	3.33	.125	.250	.250	.330
19	94	21.0	5.00	1.000	1.000	2.000	.970
21	97	14.5	4.18	.125	.500	2.000	3.000
25	71	22.5	5.53	1.000	1.000	1.000	3.000
27	71	15.5	5.23	1.000	2.000	2.000	3.000
29	112	16.5	4.35	.125	.250	.250	.620
31	138	17.5	4.35	3.000	3.000	3.000	3.000
33	138	15.5	2.93	1.000	1.000	1.000	.790
35	140	14.5	4.68	2.000	2.000	2.000	1.850
37	124	18.0	2.80	2.000	2.000	2.000	3.000
39	113	16.5	3.42	2.000	2.000	2.000	3.000
41	58	13.0	3.15	.500	.500	.500	.110
43	130	12.0	3.70	.250	.250	.250	.590
45	124	16.0	3.80	.125	.125	.125	.520
47	124	19.5	5.00	.500	1.000	1.000	.440
49	124	20.5	6.20	.500	1.000	1.000	.380
51	104	14.5	3.53	.250	.250	.250	.210
53	145	16.0	3.00	.500	.500	.500	.520
55	109	14.0	3.92	.500	.500	.500	.500
57	109	15.0	4.73	1.000	1.000	1.000	1.150
59	109	13.0	3.03	.125	.125	.125	.135
61	87	13.0	3.93	.250	.250	1.000	.440
63	87	14.0	3.18	.125	.125	.500	.145
65	87	14.5	3.98	.500	.500	.500	.590
67	75	19.0	3.58	.250	.250	.500	.730
69	64	14.5	4.87	2.000	2.000	2.000	.250
71	64	14.5	4.65	.125	.125	1.000	.200
73	77	16.0	4.75	.125	.125	1.000	.350
75	61	17.0	3.72	1.000	1.000	1.000	1.100
77	61	17.5	4.60	.250	.250	1.000	.290
79	61	16.5	4.18	.125	.500	.500	3.000

TABLE A4

Intake from Suprathreshold Sucrose Solutions during First and Second Presentations in Experiment 2 by *P. m. bairdi*

No.	1st Presentation			2nd Presentation			Average		
	2%	4%	8%	2%	4%	8%	2%	4%	8%
1	8.9	13.6	21.0	9.5	19.1	21.4	9.20	16.35	23.20
5	18.0	18.9	14.7	19.9	19.2	16.1	19.95	19.05	15.40
7	10.0	18.6	16.4	5.2	8.2	16.7	7.60	13.40	16.55
9	5.4	7.2	10.5	5.7	7.8	10.7	5.55	7.50	10.60
15	7.2	13.9	16.8	8.7	15.9	24.8	7.95	14.90	20.80
17	6.7	16.0	14.8	6.4	10.6	17.2	6.55	13.30	16.00
19	7.3	6.7	7.2	6.7	9.3	10.9	7.00	8.00	9.05
21	4.5	66	14.5	4.7	5.9	13.2	4.60	6.25	13.85
25	6.9	7.7	7.8	6.9	6.5	7.1	6.90	7.10	7.45
27	6.2	6.9	14.7	5.2	8.7	17.6	5.70	7.80	16.15
29	7.4	10.6	20.2	10.5	15.8	20.5	8.95	13.20	20.35
31	4.7	5.1	4.8	4.6	5.2	5.1	4.65	5.15	4.95
33	3.9	3.8	6.5	5.5	6.9	13.2	4.70	5.35	9.85
35	6.3	9.0	13.6	10.5	14.0	15.3	8.40	11.50	14.45
37	3.0	3.3	3.4	3.4	3.1	4.8	3.20	3.20	4.10
39	4.2	4.8	7.4	4.1	5.9	8.7	4.15	4.35	8.05
41	6.9	18.0	23.0	16.6	31.2	22.5	11.75	24.60	22.75
43	6.9	10.0	14.5	8.1	12.9	17.6	7.50	11.45	16.05
45	5.2	10.6	11.5	7.4	14.9	15.2	6.30	12.75	13.35
47	8.3	9.0	12.6	8.3	12.3	19.1	8.30	10.65	15.85
49	7.6	11.1	13.8	8.3	11.0	17.5	7.95	11.05	15.65
51	13.5	27.4	15.0	6.6	11.7	13.6	10.05	19.55	14.30
53	18.8	21.0	13.5	13.6	26.0	16.9	16.20	23.50	15.20
55	6.5	7.7	13.3	8.6	10.6	14.4	7.55	9.15	13.85
57	5.8	7.1	12.0	7.2	11.9	15.4	6.50	9.50	13.70
59	20.4	24.8	17.1	22.1	28.8	19.9	21.25	26.80	18.50
61	9.0	17.4	13.3	7.9	17.3	20.9	8.45	17.35	17.10
63	14.7	16.2	15.1	18.0	19.7	15.0	16.35	17.95	15.05
65	29.2	36.0	22.8	27.8	32.6	21.3	28.50	34.30	22.05
67	9.4	14.3	15.0	12.1	16.7	19.6	10.75	15.50	17.30
69	6.1	6.2	9.3	5.4	7.4	9.3	5.75	6.80	9.30
71	6.5	12.6	18.5	10.2	15.5	22.2	8.35	14.05	20.35
73	6.0	9.0	12.8	6.0	7.6	15.9	6.00	8.30	14.35
75	5.4	12.5	18.1	7.3	10.5	21.2	6.35	11.50	19.65
77	5.8	5.9	8.0	5.7	6.1	8.6	5.75	6.00	8.30
79	5.2	5.9	5.6	4.6	5.7	6.0	4.90	5.80	5.80

APPENDIX B

DATA FROM EXPERIMENTS 1 AND 2 FOR INDIVIDUAL *P. POLIONOTUS*

TABLE B1

Water Intake for Six Days in Experiment 1 by *P. polionotus*

No.	Days							
	1	2	3	4	5	6	Mean	SD
2	3.6	4.0	4.6	4.9	4.8	5.9	4.63	.80
8	3.6	3.3	3.4	3.8	3.6	4.0	3.62	.26
10	3.6	3.5	3.4	3.7	3.4	3.6	3.53	.12
14	5.8	6.2	7.4	8.2	8.1	9.2	7.48	1.29
16	3.4	3.2	3.9	3.6	3.9	3.8	3.63	.29
18	4.9	5.1	5.2	4.8	4.5	4.5	4.83	.29
20	5.4	5.8	5.3	6.2	6.1	6.0	5.80	.37
22	8.1	8.4	7.1	8.5	7.6	6.4	7.68	.82
24	4.1	4.2	4.1	4.5	4.4	4.4	4.28	.17
28	6.9	7.0	10.2	9.6	10.6	10.3	9.10	1.70
30	3.9	3.9	3.7	4.4	4.5	5.8	4.37	.77
32	5.7	5.8	7.0	7.1	6.4	6.6	6.43	.59
34	5.6	6.0	6.0	6.0	6.0	6.0	5.93	.16
36	4.2	4.0	4.2	3.9	4.3	4.1	4.12	.15
38	4.2	4.0	4.1	4.5	4.3	3.6	4.12	.31
40	3.7	3.5	3.7	4.0	3.9	3.2	3.67	.29
42	3.8	3.6	3.7	3.8	4.7	5.8	4.23	.86
44	4.0	3.8	4.8	5.0	4.3	4.5	4.40	.46
46	5.3	5.9	6.4	6.3	7.6	6.0	6.25	.77
48	4.5	4.2	5.2	6.0	4.9	4.8	4.93	.63
50	4.4	5.1	6.0	6.3	5.2	6.0	5.50	.72
52	4.0	4.0	2.7	3.1	3.3	4.7	3.63	.73
54	7.8	7.3	6.2	8.2	8.3	9.1	7.82	.99
56	5.2	5.3	5.2	6.0	5.7	6.2	5.60	.43
58	4.6	5.2	4.9	5.2	5.4	5.1	5.07	.28
60	4.0	3.4	3.6	4.0	4.1	4.3	3.90	.33
62	8.7	9.3	10.5	8.4	9.4	10.2	9.42	.82
64	7.6	8.8	8.2	8.5	9.1	9.2	8.57	.60
66	6.4	7.1	7.8	8.6	10.4	8.9	8.20	1.42

TABLE B2

Intake from Threshold Test Solutions during First and Second Presentations in Experiment 1 by *P. polionotus*

No.	1st Presentation					
	.000%	.125%	.250%	.500%	1%	2%
2	4.6	4.9	5.7	6.3	9.1	9.9
8	3.4	3.5	4.2	3.7	3.9	4.7
10	3.4	3.8	3.6	4.1	4.8	6.7
14	7.4	9.4	9.0	8.7	15.0	14.5
16	3.9	4.2	4.0	4.5	5.4	7.7
18	5.2	5.0	4.7	5.1	8.5	11.5
20	5.3	5.0	7.2	9.7	11.0	11.6
22	7.1	6.3	7.3	9.0	8.8	9.9
24	4.1	4.2	4.7	4.8	5.6	6.3
28	10.2	9.8	9.4	9.8	12.2	14.2
30	3.7	4.5	4.8	6.4	7.6	11.9
32	7.0	6.9	6.9	8.6	10.0	12.0
34	6.0	6.6	6.0	7.5	11.1	15.2
36	4.2	4.0	4.1	4.9	5.6	5.8
38	4.1	4.2	4.4	5.2	8.4	10.8
40	3.7	4.1	3.6	4.0	4.6	6.2
42	3.7	3.7	4.5	6.0	6.0	8.7
44	4.8	4.3	4.6	5.2	4.7	4.8
46	6.4	7.2	6.1	6.9	9.5	14.0
48	5.2	4.7	5.4	6.6	6.4	9.0
50	6.0	5.2	6.7	6.5	8.4	10.4
52	2.7	3.6	3.1	3.2	3.5	3.6
54	6.2	9.0	6.6	8.6	8.7	11.7
56	5.2	5.7	5.8	6.1	5.6	6.8
58	4.9	5.8	5.5	5.3	5.6	6.7
60	3.6	3.9	3.8	4.1	3.9	4.6
62	10.5	9.9	10.6	11.8	12.8	16.4
64	8.2	8.8	10.2	9.5	15.7	18.4
66	7.8	7.7	9.6	8.8	12.5	14.2

TABLE B2--Continued

No.	2nd Presentation					
	.000%	.125%	.250%	.500%	1%	2%
2	4.8	6.4	6.3	7.8	10.6	13.9
8	3.6	3.8	7.1	4.4	4.8	6.4
10	3.4	3.6	3.6	3.5	4.2	4.8
14	8.1	8.9	10.4	11.3	14.9	18.5
16	3.9	3.6	3.6	4.0	6.4	7.2
18	4.5	4.4	4.5	5.6	5.8	8.9
20	6.1	5.7	6.2	7.9	11.6	11.8
22	7.6	8.3	6.5	8.2	8.0	8.4
24	4.4	4.1	4.5	5.2	6.5	6.2
28	10.6	11.8	12.8	13.9	16.1	17.4
30	4.5	4.4	5.2	6.6	7.3	12.6
32	6.4	6.2	7.2	6.3	11.2	11.3
34	6.0	5.8	6.4	6.7	8.6	16.5
36	4.3	4.6	3.9	5.2	4.7	6.9
38	4.3	4.5	5.8	4.8	7.3	12.2
40	3.9	3.4	3.8	3.8	4.2	4.9
42	4.7	6.1	5.8	7.7	10.1	12.0
44	4.3	5.0	5.2	4.6	5.4	5.0
46	7.6	7.2	7.1	7.7	11.4	14.4
48	4.9	4.8	4.8	5.7	6.0	8.3
50	5.2	6.8	7.4	7.2	9.1	9.2
52	3.3	3.9	4.4	3.9	3.7	4.8
54	8.3	8.7	10.5	9.8	12.2	16.6
56	5.7	5.6	5.7	6.1	7.1	6.2
58	5.4	6.0	6.0	5.8	5.5	7.4
60	4.1	4.3	4.4	4.3	5.2	6.2
62	9.4	9.7	10.4	10.5	15.0	18.0
64	9.1	9.8	10.0	11.1	13.8	19.5
66	10.4	10.4	10.0	10.1	12.8	17.2

TABLE B2--Continued

No.	Average					
	.000%	.125%	.250%	.500%	1%	2%
2	4.70	5.65	6.00	7.05	9.85	11.90
8	3.50	3.65	5.65	4.05	4.35	5.55
10	3.40	3.70	3.60	3.80	4.50	5.75
14	7.75	9.15	9.70	10.00	14.95	16.50
16	3.90	3.90	3.80	4.25	5.90	7.45
18	4.85	4.70	4.60	5.35	7.15	10.20
20	5.70	5.35	6.70	8.80	11.30	11.70
22	7.35	7.30	6.90	8.60	8.40	9.15
24	4.25	4.15	4.60	5.00	6.05	6.25
28	10.40	10.80	11.10	11.85	14.15	15.80
30	4.10	4.45	5.00	6.50	7.45	12.25
32	6.70	6.55	7.05	7.45	10.60	11.65
34	6.00	6.20	6.20	7.10	9.85	15.85
36	4.25	4.30	4.00	5.05	5.15	6.35
38	4.20	4.35	5.10	5.00	7.85	11.50
40	3.80	3.75	3.70	3.90	4.40	5.55
42	4.20	4.90	5.15	6.85	8.05	10.35
44	4.55	4.65	4.90	4.90	5.05	4.90
46	7.00	7.20	6.60	7.30	10.45	14.20
48	5.05	4.75	5.10	6.15	6.20	8.65
50	5.60	6.00	7.05	6.85	8.75	9.80
52	3.00	3.75	3.75	3.55	3.60	4.20
54	7.25	8.85	8.55	9.20	10.45	14.15
56	5.45	5.65	5.75	6.10	6.35	6.50
58	5.15	5.90	5.75	5.55	5.55	7.05
60	3.85	4.10	4.10	4.20	4.55	5.40
62	9.95	9.80	10.50	11.15	13.90	17.20
64	8.65	9.30	10.10	10.30	14.75	18.95
66	9.10	9.05	9.80	9.45	12.65	15.70

TABLE B3

Age, Weight, Mean 6-Day Water Intake, and Threshold Values for *P. polionotus*

No.	Age (days)	Weight (gm.)	Water (ml.)	AL 1	AL 2	AL 3	AL 4
				(percentage concentration)			
2	107	12.5	4.63	.125	.125	.125	.120
8	87	11.0	3.62	.125	.125	.500	.130
10	74	13.5	3.53	.125	.500	.500	.120
14	84	11.5	7.48	.125	.125	.125	.120
16	82	14.0	3.63	.500	.500	.500	.300
18	107	14.0	4.83	.500	.500	.500	.420
20	54	13.0	5.80	.250	.250	.250	.210
22	61	11.5	7.68	.500	1.000	1.000	.350
24	72	13.5	4.28	.250	.250	.250	.200
28	84	13.5	9.10	.125	.125	.125	.550
30	82	13.5	4.37	.125	.125	.125	.220
32	140	14.5	6.43	.250	.250	.250	.390
34	140	14.5	5.93	.125	.125	.250	.120
36	120	13.0	4.12	.500	.500	.500	.320
38	107	12.5	4.12	.125	.125	.500	.150
40	107	11.5	3.67	.500	.500	.500	.420
42	115	13.0	4.23	.125	.125	.125	.210
44	87	13.5	4.40	.125	.125	2.000	1.000
46	87	13.0	6.25	.500	.500	.500	.550
48	75	12.0	4.93	.250	.250	.250	.350
50	84	13.5	5.50	.125	.125	.500	.180
52	84	14.5	3.63	.125	.500	.500	.130
54	81	15.5	7.82	.125	.250	.250	.120
56	81	15.0	5.60	.125	.125	.125	.340
58	54	15.5	5.07	.125	.500	1.000	.110
60	54	13.5	3.90	.125	.125	.125	.450
62	62	15.0	9.42	.250	.250	.250	.350
64	62	16.5	8.57	.125	.125	.125	.130
66	62	16.0	8.20	.250	.250	.250	.630

TABLE B4

Intake from Suprathreshold Sucrose Solutions during First and Second Presentations in Experiment 2 by *P. polionotus*

No.	1st Presentation			2nd Presentation			Average		
	2%	4%	8%	2%	4%	8%	2%	4%	8%
2	14.2	20.0	19.0	10.2	14.1	19.8	12.20	17.05	19.40
8	8.5	13.5	14.0	12.0	14.7	15.2	10.25	14.10	14.60
10	4.9	8.5	12.0	7.7	11.2	14.7	6.30	9.85	13.35
14	20.6	22.9	22.3	18.0	25.2	18.7	19.30	24.05	20.50
16	8.1	10.8	12.4	9.1	10.4	12.0	8.60	10.60	12.20
18	8.7	14.8	13.8	8.2	9.0	11.7	8.45	11.90	12.75
20	15.1	12.1	22.3	15.0	17.0	24.0	15.05	14.55	23.15
22	11.5	15.3	16.6	12.4	15.4	18.2	11.95	15.35	17.40
24	6.8	10.6	16.0	10.0	13.1	15.8	8.40	11.85	15.90
28	17.1	19.8	16.7	11.8	21.3	19.0	14.45	20.55	17.85
30	13.0	15.9	19.5	12.8	20.5	20.8	12.90	18.20	20.15
32	10.6	14.5	19.3	13.5	18.0	17.8	12.05	16.25	18.55
34	12.1	15.6	17.6	14.5	20.9	21.5	13.30	18.25	19.55
36	8.5	9.1	11.2	9.0	10.7	10.4	8.75	9.90	10.80
38	13.3	14.9	13.5	10.1	15.5	15.6	11.70	15.20	14.55
40	4.6	8.0	8.2	6.4	8.7	8.9	5.50	8.35	8.55
42	11.7	15.8	17.2	14.3	15.0	15.8	13.00	15.40	16.50
44	5.9	6.1	7.5	5.8	6.6	7.5	5.85	6.35	7.50
46	13.0	16.0	18.7	21.5	29.0	15.8	17.25	22.50	17.25
48	7.5	9.4	11.5	6.2	10.8	10.6	6.85	10.10	11.05
50	9.0	17.1	14.3	12.1	15.3	18.3	10.55	16.20	16.30
52	5.7	8.4	15.3	15.0	16.8	15.7	10.35	12.60	15.50
54	15.1	26.4	17.8	14.7	17.2	18.1	14.90	21.80	17.95
56	6.8	8.4	9.3	7.5	9.1	13.4	7.15	8.75	11.35
58	6.7	8.6	11.6	10.0	14.2	15.0	8.35	11.40	13.30
60	7.4	9.8	8.9	8.2	11.0	11.0	7.80	10.40	9.95
62	19.8	30.0	27.8	23.1	26.7	25.7	21.45	28.35	26.75
64	22.5	29.2	22.1	22.7	31.9	22.9	22.60	30.55	22.50
66	15.2	16.0	17.5	11.5	11.0	15.1	13.35	13.50	16.30

APPENDIX C

ABSTRACT OF DISSERTATION RESEARCH

[Submitted to American Society of Zoologists for Publication in American Zoologist (November, 1971) and Presentation at Meeting with AAAS at Philadelphia, December 26-31, 1971]

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Sources of intraspecific differences in sucrose intake in *Peromyscus*. (Introduced by J. A. King)

A single stimulus procedure was used to measure 24-hr. intake of water and sucrose solutions in *P. m. bairdi* (n = 36) and *P. polionotus* (n = 29). In Experiment 1 *P. m. bairdi* were found to drink significantly less water than *P. polionotus* and were less responsive to sucrose as indicated by higher "preference" thresholds. However, in Experiment 2 no significant species differences were found in 2%, 4%, and 8% sucrose intake for the same subjects. Intake increased significantly over the range of concentrations, but differences in sweetness accounted for only an estimated 10% of the variance in sucrose consumption by either species.

Multivariate analyses revealed that 65% or more of the variance in *P. polionotus* intake from each of the three concentrations could be explained by differences in voluntary water intake, age, weight, and threshold, while for *P. m. bairdi* 37% or less was accounted for by these variables. Both water intake and threshold in that order explained a significant proportion of the variability in

P. polionotus sucrose intake. Only the threshold was uniquely associated significantly with intake among individual *P. m. bairdi*. A degree of explanatory value by thresholds was anticipated on the basis of psychophysical scaling laws and assumptions about the relation of sucrose intake to stimulus (concentration) and sensory (sweetness and "hedonic intensity") factors. (Supported by Department of Psychology, Michigan State University)

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