

SCALING PIGEONS' CHOICE OF FEEDS:
BIGGER IS BETTER

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Preferences of hungry pigeons among 10 grains and pellets were analyzed using a Thurstone scaling procedure. The recovered scales were positively correlated with size of the feed. The correlations improved when the Thurstonian assumption of equal-sized discriminial dispersions (Case V) was replaced with the assumption of proportional-sized dispersions (Case VI), as entailed by Weber's law. The correlations weakened when the experiments were conducted with the pigeons close to their free-feeding weights, where the probability of sampling alternative grains increased. In the final experiment, exposure to a large pellet shifted the preferences between two smaller pellets.

Key words: reinforcers, grain, preference, Weber's law, Thurstone, Fechner, scaling, magnitude of reinforcement, quality of reinforcement, foraging, food choice, pigeons

Discriminating nuances in the quality of reinforcers is a major preoccupation of humans. Everything is rated, critics outnumber creators, and books-of-lists top the lists of best selling books. For luxury items such as wines and stereos, marginal utility seems never to decrease, with large premiums paid for differences in quality that require years of training to discriminate.

Despite the importance of quality in human economy, little attention has been paid to it in the learning literature. Many texts merely refer to Elliot's (1928) classic study in which it was found that rats perform better for wet bran than for sunflower seeds, or to Young's (1928) demonstration of rats' preferential discrimination among types of grain. Thereafter, discussion of quality is usually embedded in that of quantity. Many of the extant studies of quality of reinforcers employ sucrose, whose concentration can be conveniently varied over a large range (Young, 1961). Quality is interpreted as quantity of sucrose in a mixture, with preferences generally found to increase with quantity until some ideal point and to decrease thereafter. A review of some of the classic literature on incentive motivation is found in Bolles (1967), with more recent studies of qualitatively different reinforcers to be

found in the literature on behavioral economics (e.g., Lea & Roper, 1977; Rachlin, Kagel & Battalio, 1980) and behavioral ecology (e.g., Krebs & Davies, 1978; Schoener, 1971). Willson (1971) studied seed selection in finches, found idiosyncratic differences among species, and concluded that "preference was decidedly not based on maximizing the number of calories ingested from each kernel" (p. 241). Brown (1969) found "an astonishing amount of individual variation" in pigeons' food choices (p. 118).

Our experiments on preference for various types of reinforcers were pragmatically motivated: We wished to know what to put in the food hoppers in our experimental chambers to maximize the incentive value of reinforcement. Because in such situations pigeons are typically quite hungry and have only brief access to the reinforcer, studies such as Brown's (1969), which measured the amount of each type left after large feedings, were of little utility in addressing that question.

How does one go about measuring preference? Miller (1976) trained animals to respond on concurrent variable-interval schedules and measured preferences among three grains as shifts in bias. But this procedure is more sophisticated and time consuming than necessary for our purposes. The most straightforward approach seems to be to assess preference in the same manner as is normally done with humans: Give the organisms a choice between two or more alternatives and record which is chosen. This is the strategy in all of the experiments that follow. From the results we can infer a rank order of preference among the various feeds, and we can also draw some

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Table 1
Feeds used in Experiments 1, 2, and 3.

Experiment	Symbol	Grain	Weight (mg)
1A	OA	Oats (unhulled)	22
1A, 1B	MT	Millet	6
1B	RI	Rice	18
1A, 1B	WH	Wheat	28
1A	CC	Cracked corn	29
1A, 1B	MI	Milo	25
1A, 3	NP	Noyes pellets	45
1A, 1B	AP	Austrian peas	113
1A, 1B	PC	Popcorn	101
1A, 1B	CP	Canadian peas	141
2	BP	Bioserv pellets	20
2	BP	Bioserv pellets	37
2, 3	BP	Bioserv pellets	45
2, 1B	BP	Bioserv pellets	75
2	BP	Bioserv pellets	94
2	BP	Bioserv pellets	97

inferences about the variables upon which these preferences are based and how they might be scaled.

EXPERIMENT 1A: CHOICE BETWEEN GRAINS METHOD

Subjects

Five adult pigeons, A, B, C, D, and E, were maintained at 85% to 90% of their free-feeding weights. Water and grit were always available.

Apparatus

Pigeons remained in their home cages for all parts of the experiment. Feed cups were 10 cm wide, 6.3 cm deep at the center and rounded at the front corners, and 5 cm high. Paper barriers, 3.8 cm high, divided the interior of the cups into the left and right halves.

Procedure

For 1 week before testing, pigeons were fed a mixture of the grains to be compared. Testing consisted of presenting a feed cup with 10 g of one of the experimental grains in one half of the cup and 10 g of a different grain in the other half. The grains studied are listed in Table 1. The positions (left or right half) and comparison grains were randomized, with the constraint that grains were compared in each position with the other grains for all pigeons. The grains chosen on each of the first 35 pecks

Table 2

Proportion of time row chosen over column in Experiment 1A.

	PC	AP	NP	MI	CC	WH	MT	OA
CP	.55	.70	1.0	1.0				
PC		.80	.90	.79	1.0	.89	1.0	1.0
AP			.90	.85				
NP				.77	.77	.51	1.0	.99
MI					.52	1.0	1.0	1.0
CC						.40	.95	.99
WH							.81	1.0
MT								.55

were recorded; in this experiment the first 10 pecks were discarded (to allow for sampling by the pigeons) and the remaining 25 were taken as measures of preference. The pigeons were allowed to empty both halves of the cup. Trials were conducted once each day, 6 days per week. Pigeons made each comparison twice; for all comparisons in which the preferences were not exclusive, an additional two comparisons were made.

RESULTS

Table 2 shows the average preference for (relative number of pecks at) one grain (rows) over another (columns), averaged over the 5 pigeons. Once a pigeon started eating one of the grains, it almost always continued until all of that grain was consumed. We see that Canadian peas and popcorn were among the most preferred grains (their typical row entries are high), and oats and millet were among the least preferred (their typical column entries are high). Empty cells were not tested.

DISCUSSION

We have answered our original query—peas and popcorn (maize) are strongly preferred—and could stop here. But there is much more information to be found in the pattern of preferences, more than can be absorbed from simply looking at Table 2. How can we distill the information it offers?

One analytic approach is to assume that one or more dimensions underlie preference, and that we can array the different stimuli along these continua to summarize the choices. Scale positions on these dimensions would be fewer in number than the cells of such a matrix, thereby distilling the information it contains into more intuitively acceptable and psycho-

logically meaningful factors. One tactical difficulty might arise: What if preference is not monotonic with the value of a food on the underlying scales? Consider, for example, the dimension of sweetness, and six stimuli with sucrose concentrations of 0.00, 0.05, 0.10, 0.15, and 0.20. If the animals' ideal concentration is 0.12, then we might find the order of preference to be 0.10, 0.15, 0.05, 0.20, and 0.00. The underlying continuum is, as it were, folded over the "ideal," or "bliss" point, with the ranking of stimuli depending on their absolute distance from that point.

How does one get from the recovered preferences to the underlying continua in such cases? This inverse process of analysis is not as easy as generating the above synthetic example. Coombs (1950; see also Torgerson, 1958) pioneered the analyses of such data, calling the process of recovering the underlying continuum a process of *unfolding*. For small or moderate numbers of stimuli, the unfolding can be accomplished by a brute-force computer search. The goal is to find the single continuum such that, when the ideal point is identified, all of the obtained preferences may be accounted for. Thus, in the sucrose example, the preference for the 0.10 solution over the 0.15, but the 0.15 over the 0.05, may be reconciled with unidimensional continuum of sweetness having an ideal point at 0.12. If a second dimension of the stimuli also affects preference, we might find systematic deviations from this primary ranking that can then be reconciled in like manner.

Although some such tactic may be necessary, the original unfolding analysis discards useful information. If Grain A is preferred over Grain B by 55% and over Grain C by 80%, we know more than the simple rank ordering: We know that the organisms strongly prefer A to C but only mildly prefer A to B. We would expect that if the grains were presented in a study such as Miller's (1976), animals would be strongly biased for A over C but almost indifferent between A and B. How might our analysis of the matrix capture those differences? One approach is to represent those degrees of preference by spacing them on the recovered dimensions a distance apart that is proportional to the z scores of their preferences. This is a Thurstonian scaling of the stimuli; combined with the unfolding technique, it is called *probabilistic unfolding*

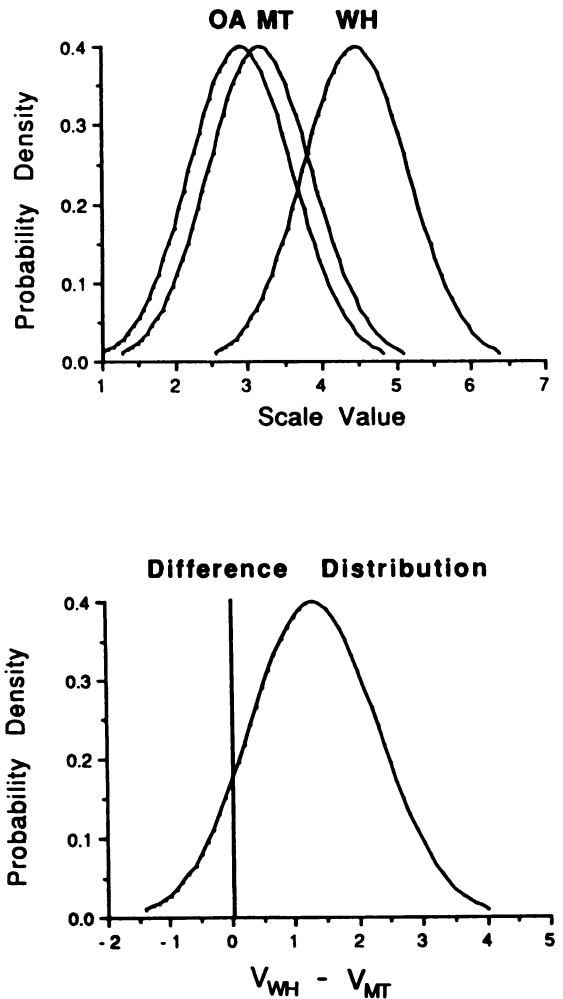


Fig. 1. Hypothetical discrimination dispersions underlying the discriminations among oats (OA), millet (MT), and wheat (WH). The upper curves show the probability that the sample of grain is located over various portions of the value scale; in the bottom curve, the area to the right of 0 gives the probability of preferring wheat over millet.

(Coombs, 1958; Coombs, Dawes, & Tversky, 1970).

For a demonstration of how it works, let us focus on three of the least preferred grains: oats, millet, and wheat. We note that the probability of choosing millet over oats is .55, wheat over millet is .81, and wheat over oats is 1.0. We may arrange these three grains on a continuum such that oats lies close to millet, with greater distance between millet and wheat and the greatest distance between oats and wheat (Figure 1, top). The Gaussian distributions are separated by distances proportional to

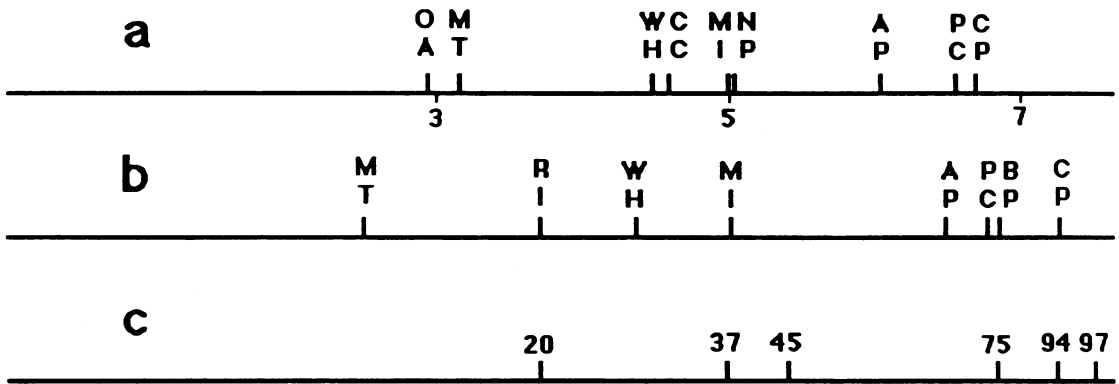


Fig. 2. The psychological scales of value recovered from the Thurstone analysis of data from Experiment 1a (a), Experiment 1b (b), and Experiment 2 (c).

$z(\text{MT}, \text{OA}) = 0.13$, $z(\text{WT}, \text{MT}) = 0.89$, and $z(\text{WH}, \text{OA}) \approx 3$. Thurstone called these hypothetical distributions of sensitivity *discriminational dispersions*. The distributions are interpreted as the probability that the grain will be placed on any particular part of the dimension on any one trial. The substantial overlaps in these distributions indicate that there is substantial variation in the evaluation of the grains, with millet sometimes tasting fairly bad—worse than oats—and sometimes fairly good—better than wheat. The probability that a particular sample of wheat will be preferred over a sample of millet (i.e., be found to the right of it on this hypothetical dimension, so that on that trial $V_{\text{WH}} - V_{\text{MT}} > 0$) is given by the distribution of the difference of the two random variables that generated those distributions. That is also a normal distribution, with a mean equal to the distance between the two relevant dispersions. The standard deviation of the difference distribution depends on the standard deviations of the discriminational dispersions that gave rise to it (and whether the evaluation of the two seeds is independent). In the simplest case (Thurstone's Case V, which is also the case most often invoked in the theory of signal detectability), the variances are assumed to be equal and uncorrelated. The variance of the difference distributions (lower panel) is then equal to the sum of the variances of the dispersions (top panel). The difference distribution for $V_{\text{WH}} - V_{\text{MT}}$ is drawn at the bottom of Figure 1. The area under this curve to the right of zero tells us how frequently wheat will be chosen over millet.

In constructing the Thurstone scale, then,

we first determine the probability of choosing one alternative over the other (say, .81), calculate the z score corresponding to that preference (+0.88), and space the stimuli apart by some multiple of that distance. The finally recovered Thurstonian scale is an interval scale, with an arbitrary origin and scale factor. We have set the value of milo as 5.0 to establish the origin and kept the scale factor as 1.0. These assignments leave all of the information about preference encoded in the differences of the scale values of the grains.

Because there are more entries in the body of the matrix than there are rows to it, the data are overdetermined, providing multiple estimates of the differences. We proceed with the above technique to calculate the z -score differences between the other paired comparisons and construct a scale that respects all measurements. The abscissae of Figure 1 comprise such a scale. In analyzing the current data, our program adjusted the scale positions to minimize the sum of squared deviations between all of the observed preferences and the preferences predicted from the scale values. Note that we work from the measured preferences, not their z scores. For instance, exclusive preference demands an arbitrarily large z score, but a smaller value may be more consistent with the body of the matrix as a whole. Thus, the overall best distance on the scale between wheat and oats is 1.65, underestimating the specific choice between them by 5%.

With only three sets of observations, such data are only weakly constrained. However, the number of possible pairwise comparisons

of N grains increases quickly with N , and for nine grains is $N*(N - 1)/2 = 36$. We did not measure all possible preferences, because the close-to-exclusive preference we expected for some of the cells would add little information to the scaling analysis. The 28 cells we studied are shown in Table 2; those data determined the scaling of the nine grains shown in Figure 2a.

The ideal point is actually a region anywhere within which the scale might be folded and preserve all of the rank order information. For these grains, the unfolding was trivial. The ideal "point" extended from 6.65 to $+\infty$, which indicates that the pigeons' ideal grain was anywhere from a point just to the left of CP to anywhere to the right of it. Therefore, its location was not constrained by these data, nor did it affect their analysis. The correlation between the obtained and recovered preferences is $r = 0.96$; this scaling therefore accounts for 92% of the variance in the average choice data.

The position of the ideal point indicates that the ideal grain should have about as much or more of "quality x " as did CP. Individual pigeons showed deviations from this pattern, but the unaveraged data are not sufficiently precise to determine individual scales with any confidence or to explore correlates of individual animals' ideal points (e.g., there was no significant correlation between beak size or body weight and individual ideal-point values, but the power of such analyses was low). Analysis based on more extensive data may in the future uncover such correlates.

Unfortunately, the above scale is not unique. Thurstonian scaling works only as long as there is significant overlap between the distributions of adjacent stimuli, and this was not always the case with these data. The three most preferred grains were isolated from the rest of the grains, permitting the order of those grains to be permuted: By exchanging the scale values for PC and CP and inserting an ideal point between CP and AP, we can map the present data with accuracy equal to that given by the scale in Figure 2a. Furthermore, the two least preferred grains are separated from the rest with only one meaningful comparison contributing to that distance: the 81% preference for wheat over millet. These weaknesses are rectified in the next experiments.

What was quality x , the physical correlate

of the scale? Why did the pigeons prefer some grains such as popcorn so much and others such as millet so little? There are many differences in the grains and many ways of measuring those differences. There is color, caloric value, size, friability, flavor, and so on. The most obvious correlate of the scale in Figure 2a is size, with millet being the smallest grain (only 6 mg per seed) and CP the largest (140 mg per seed). The correlation between the weight of each seed and its Thurstone value is $r = 0.88$. Experiment 1b was conducted to evaluate more accurately the hypothesis that the physical correlate of Scale 2a was the size of the grain.

EXPERIMENT 1B: ADDITIONAL COMPARISONS

The purpose of this experiment was to replicate some of the above results with new pigeons and a new procedure, while providing more definitive information about certain regions of the scale. To this end, only subsets of the total number of possible comparisons were made, and new grains were introduced to bridge measurements between the more extreme grains and the central part of the scale.

METHOD

Subjects

Four adult pigeons, F, G, H, and I, were maintained at 85% to 90% of their free-feeding weights. Water and grit were always available.

Apparatus

Metal barriers were added to the food cups in place of the paper ones, and each section of the cup was fitted with a hinged metal lid.

Procedure

Sessions were conducted 5 days per week. Subjects were preexposed to mixtures of the comparison grains for a week before testing. Testing consisted of presenting a feed cup with 5 cc of one of the experimental grains in one half of the cup and 5 cc of a different grain in the other half. The grains studied are listed in Table 1. The positions (left or right half) and comparison grains were randomized so that all grains were compared in each position with all other grains for all pigeons. After the pigeon had made its initial choice (pecked at one of

Table 3

Proportion of time row chosen over column in Experiment 1B.

	BP	PC	AP	MI	WH	RI	MT
CP	.65	.70	.80	.98			
BP		.48	.77	1.0			
PC			.58	.98			
AP				.93			
MI					.73	.91	1.0
WH						.73	.95
RI							.88

the grains), it was permitted 5 s to eat and then the lids were closed, terminating that trial. This abbreviated feeding permitted 15 comparisons to be made each day for each pigeon, each comparison involving different grains and spaced approximately 4 min from the previous one.

Each grain was compared with each other a total of 10 times for each pigeon. Grains MT, RI, WH, and MI were compared first, followed by Grains MI, AP, PC, BP, and CP. Because we found in the first experiment that once a choice was made, the pigeons usually (over 90% of the time) stayed with it, in this and all subsequent experiments the first choice determined the recorded preference for that trial. The number of seeds consumed during the feeding episodes was estimated from the weight of the residuum and the known average weight of the seeds.

RESULTS

Table 3 gives the measured preferences (first choices) among grains, averaged over the 4 birds. The recovered Thurstone scale is presented in Figure 2b; once again its origin is fixed with millet at a value of 5.0. The correlation between measured preferences and recovered preferences is $r = 0.99$, with an average deviation of less than 2 percentage points. The larger number of observations per condition made this a more reliable scale than that derived in the first experiment, but one that tells much the same story: The correlation between the scores of the grains in the two experiments is $r = 0.99$, showing that the data set reflect a stable preference structure. Rice falls midway between millet and wheat, as was expected based on its size. The large pellets fall near popcorn. Scale 2b is more spread out than Scale 2a, indicating that, given the fixed unitary variance in the model, these pigeons

made somewhat finer discriminations among the grains.

What is the physical correlate of psychological scale of value? One possibility, suggested by the literature on optimal foraging, is handling speed. The faster an animal can handle a seed, the more it should prefer it. But in neither of these experiments was there a significant correlation between the number of seconds required to consume a seed and the scale value of that seed. That is probably because, although large seeds require more handling time than small ones, they are also more profitable than small ones. If we change the predictor to grams obtained per second of handling, the correlations become larger and statistically significant ($r = 0.83$ and $r = 0.87$, $p < .01$ for Experiments 1a and 1b). But the correlations become somewhat larger still if we ignore handling time altogether and use weight of the seeds as the predictor ($r = 0.88$ and $r = 0.91$, $p < .01$).

DISCUSSION

These results reinforce those found in Experiment 1a. They also raise additional questions: What is the "pure" relation between seed size and preference if we control all other factors? Is there any difference in value between the Noyes pellets and the Bioserv pellets other than that due to the sizes used? Why is it that the scale for Experiment 1b is more spread out, indicating finer discriminations between grains? The first of these questions is addressed in Experiment 2, the second in Experiment 3, and the third in Experiment 4.

EXPERIMENT 2: CHOICE BETWEEN PELLETS OF DIFFERENT SIZES

The correlations between the weights of the seeds and their scale values found in the above experiments were impressive. To isolate this factor more clearly, unconfounded by differences in seed types, the following experiment compared preferences among Bioserv pellets of different sizes.

METHOD

Subjects

Birds F, G, H, and I served as subjects. The apparatus was the same as in the previous experiments.

Procedure

For 3 days prior to testing, subjects received a mixture of all sizes of the Bioserv pellets. Each trial consisted of presentation of the feed cup containing 5 cc of two different but otherwise randomly selected pellet sizes (20, 37, 45, 75, 94, or 97 mg). Subjects were allowed to eat for 5 s, at which point the tops of the cup were closed, ending the trial. Ten trials, each with a different pair comparison, were conducted every day for 15 days, yielding 10 presentations per pair.

RESULTS

There was a clear preference for the larger pellets (Table 4). In Figure 2c the stimuli are spaced according to their recovered scale values, with the scale aligned with that of Experiment 2 at the 75-mg value.

DISCUSSION

This experiment shows that when size is the only difference among foods, it strongly controls pigeons' preference. This is shown in Table 2 and in the regression of the Thurstone scale values on the weight of the pellets, which accounts for 97% of the variance in the scale values. There is, however, a systematic curvilinearity to the regressions, both from this experiment and from the first two experiments. In all cases, the goodness of fit may be improved by a logarithmic transformation of weight. The regressions of value on the common logarithm of the weight of the seeds and pellets are shown in Figure 3. They will be discussed further below.

Were the pigeons reacting to the weight of the feeds or to visual estimates of the weight? We estimated the volumes of the seeds from their linear dimensions and found that the logarithm of the volume predicted the scale values just as well as did the logarithm of the weights of the seeds (the correlations between scale values and either predictor in Experiments 1 and 2 were all above $r = 0.97$).

Although the logarithmic transformation is a familiar one, how may we rationalize its appropriateness in this case? The Thurstone scaling we employed (Case V) forces the underlying discriminial dispersions to be equal: It assumes a constant standard deviation across the continuum. Although this may be reasonable for some qualitative dimensions, it is unreasonable with length and weight, where we should expect Weber's law to hold. That is,

Table 4

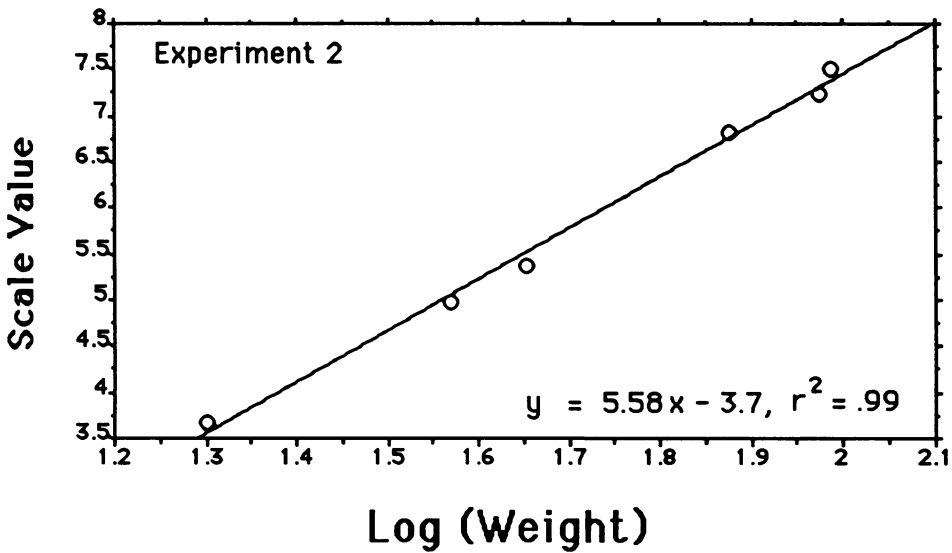
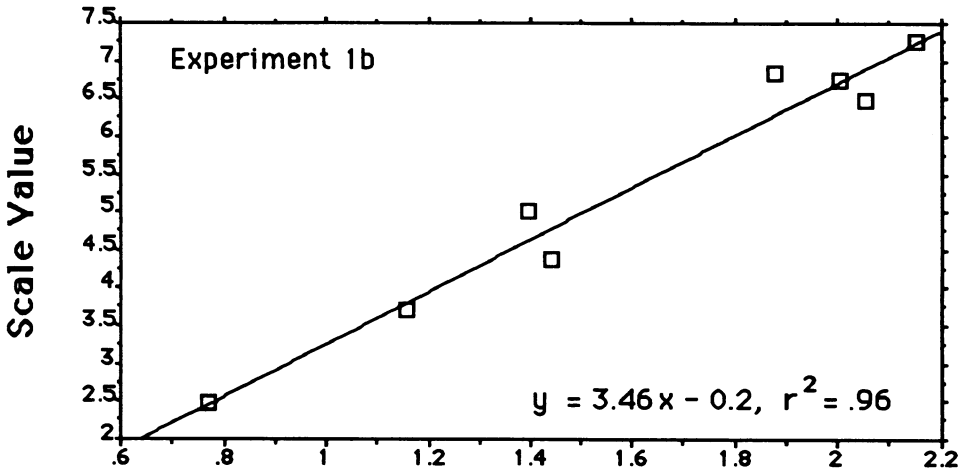
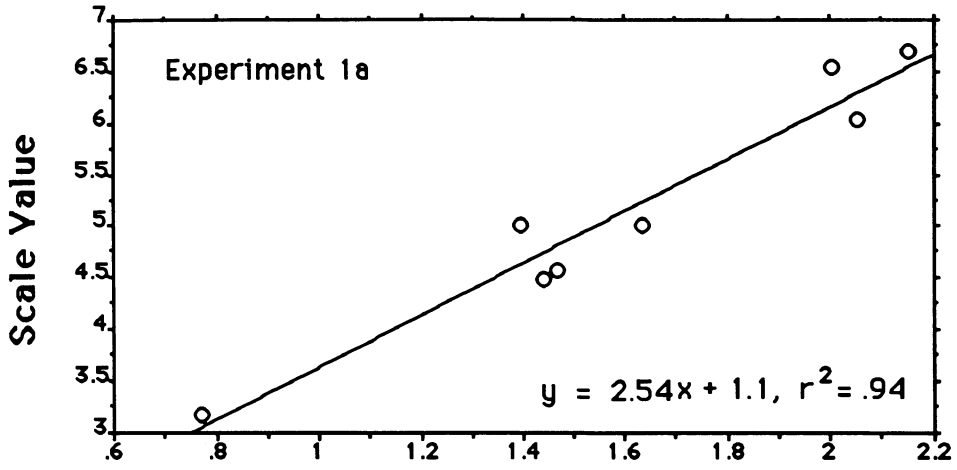
Proportion of time row chosen over column in Experiment 2.

	94	75	45	37	20
97	.59	.78	1.0	.95	1.0
94		.65	1.0	.98	1.0
75			.98	.93	1.0
45				.64	.95
37					.91

the error (standard deviation) of discriminations should increase proportionately with the magnitude of the stimuli. Under the constant variance presumption, however, a fixed difference in scale values would predict the same preference for one grain over the other anywhere along the continuum. In Experiment 2, for instance, a difference of 21 mg between any two grains would predict a difference in value of 1 standard deviation and thus an 84% preference for the larger grain. But if Weber's law is true for that continuum, a fixed difference in scale values would predict less extreme preferences for larger stimuli, because overlap in dispersions would increase proportionately. If Weber's law holds and the analysis does not provide for it (i.e., if it assumes equal variance, as in Thurstone's Case V), then the scaled values would be increasingly compressed with increased magnitude—getting the effects of increased overlap by increasing proximity, rather than by increasing variance. Note that the logarithmic transformation of weight is another way of doing exactly the same thing. That is, it moves the large weights closer together, and by just the right amount.

The simplest explanation of these data are that Weber's law does hold, and we should not use Case V but rather Case VI, in which the standard deviations of the discriminial dispersions are proportional to the magnitude of the stimuli. To test this explanation, the data were rescaled, but with the dispersion (standard deviation) of each stimulus proportional to its weight ($\sigma = 0.27 \times \text{weight}$). This procedure¹ accounted for 92% of the variance

¹ Procedure: Use the Weber fraction to calculate the relevant standard deviations from the weights of the feeds compared. Square and sum the standard deviations to find the variance of the difference scores. Divide the difference of the weights (or volumes) by the square root of the variance to derive the z score. The corresponding probability values predicts the preference for the first feed over the second.



in the matrix of preferences, exactly the same as Case V plus the logarithmic transformation.²

This analysis is accurate, in that it accounts for almost as much variance in the data as is possible using the individual scale values (97%). It is parsimonious, in that it requires one parameter rather than the six directly assigned scale values. It ties the preferences to a physical continuum—size—as measured either by weight or by volume. It conforms to a universal psychophysical law (Weber's law) for prothetic continua such as size. The "Weber constant" found here for weight, $\approx 1/4$, is close to values typically found for such discriminations under less than perfect viewing conditions such as these. This analysis yields Thurstone (Case VI) scales of value that are linear with the size of the seeds. But it is also mathematically consistent with the use of the Case V assumptions and a logarithmic transformations of the scales.

Although the logarithmic scale gives us a convenient and direct estimate of the preferences between two stimuli, it could lead to the erroneous impression that value is a nonlinear function of size (so that two 90-mg pellets seem to be worth more than one 180-mg pellet). Although some research suggests that this may be the case, we cannot draw this inference from these data. These data show that, when we correct for the proportional difficulty in making discriminations (Weber's law) by using Case VI, choice is a linear function of size.

² Procedure: Calculate the common logarithm of the ratio of the weights (or volumes) compared, and divide by the Weber fraction to derive the z score. The corresponding probability value predicts the preference for the first feed over the second. The Weber fraction is the reciprocal of the slopes in Figure 3, multiplied by $\sqrt{2}$. (This last factor converts the estimated dispersions into the standard deviation of the differences, just as we performed the rms of the dispersions in the previous procedure and in Figure 1.) In Experiment 2, where all variables but size were held constant, the z scores were four times the logarithm of size ratios, whereas in the more variable environment of Experiment 1, they were about twice the log ratios.

What then of data showing nonlinearities in preference for feeds of different weights? Shettleworth (1985) found that pigeons preferred 15 20-mg pellets over one 300-mg pellet. Capaldi, Miller, and Alptekin (1989) found that rats preferred multiple pellets whose total weight was 300 mg over a single 300-mg pellet. Shettleworth (1987b) suggested that animals may use rules of thumb, such as "more pellets mean more food"; Capaldi and associates suggested that numerous dimensions control preference, and there might be a bias for animals to perceive an alternative with a large score on one dimension (such as number) to be farther out on another dimension (such as weight per pellet) than is really the case.

How might our analysis deal with these data? One likely possibility is that the ideal point is smaller than 300-mg pellets, which may be too large to handle comfortably. In an ad hoc experiment, we found that 4 pigeons were statistically indifferent between 190-mg and 300-mg pellets over the course of 30 trials. Shettleworth (1987a) found that 3 of 9 pigeons consistently chose 20-mg pellets over 300-mg pellets (even though they preferred 75-mg pellets to 20-mg pellets). Another possibility is that estimates of volume are biased by the amount of feeder space occupied by the grains (i.e., an area measurement): Fifteen small pellets project a larger retinal image than one 300-mg pellet. Young children are unable to conserve volume over variations of constituent dimensions, and pigeons may be no more perceptive.

The choice between these two hypotheses—nonlinearity, based, perhaps, on judgments of two-dimensional size rather than volume or weight, or linearity up to an ideal point somewhere between 125 and 300 mg—will require careful exploration of the choices between large pellets to identify the ideal point and the character of choice behavior around it, and on experiments using seeds of irregular shape (such as lentils and long-grain rice) to remove the confounding effects of weight and linear dimensions. It is of course possible that both

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Fig. 3. The scale values plotted as a function of the common logarithm of the weight of each of the seeds or pellets. No other single physical dimension predicts the scale values, and thus the preferences, better than weight—although volume, as estimated from linear dimensions, does equally well. Note that the scale value for oats was omitted from the regression in the first panel, where its coordinates would be (1.34, 2.94).

factors are operative. Additional experiments could usefully remove the confounding effects of weight and volume by using seeds of different densities. The present experiment gives us a way of correcting for size (i.e., by measuring deviations from the regression on size) that will facilitate the interpretation of such results.

Are deviations from the size dimension systematic, thus indicating the presence of other controlling dimensions, as suggested by Capaldi *et al.* (1989)? By eliminating oats, the correlation between size and value is greatly increased. The oats were of moderate size, but were preferred less than the smallest grain, millet. The oats were not hulled, and that was certainly a factor in the birds' dislike. Milo fell above the 95% confidence interval for the regressions (even with oats excluded), and all of the other grains fell within that interval. There was some suggestion that the pigeons preferred grains with warmer hues (i.e., yellow and red). Given the accuracy in predicting preferences with a single dimension of size and the small number of observations of each comparison, we do not attempt to fit a second dimension to the present data.

Miller (1976) also studied pigeons' preferences among grains. In his experiments he used concurrent variable-interval schedules, and measured how much the matching relation was biased by reinforcing responses on different keys with different grains. He found that wheat was preferred to buckwheat by 1.4 to 1; that is, pigeons would require buckwheat to be delivered with a frequency 1.4 times as often to be indifferent between the alternatives. Buckwheat was preferred over hemp by about 1.1 to 1, and wheat was preferred over hemp by about 1.4 to 1.

We procured samples of each of the seeds and measured their sizes. The average weights were 28 mg (WH), 20 mg (BW), and 14 mg (H). The weights predict the order of preferences that Miller (1976) found. However, our scale predicts more extreme preferences than those he found. This probably occurred for two reasons: Miller's pigeons did not have simultaneous exposure to both feeds, and successive discriminations are never as sensitive as simultaneous ones. Furthermore, under concurrent schedules the longer an animal strives for the preferred alternative, the more likely it is that the nonpreferred one is waiting,

ready to be collected on the alternative operandum. This advantage in immediacy of the nonpreferred outcome will act to buffer extremes of preference.

Regression analysis showed that the slopes of the functions relating weight to value increased from the first to the second experiment, and increased again in the third experiment. These slopes measure the sensitivity of the pigeons to the predictor variable: The reciprocal of the slopes tells us how much we must change weight to get a unit change in preference. We believe that the difference in sensitivity between the first two experiments is due to the smaller number of foods to be discriminated in the second experiment, and that the greatest sensitivity to size in Experiment 2 is due to the homogeneity of the alternatives, with size being the only relevant dimension on which a choice might be based.

Although Figure 1 unambiguously gives us a rank ordering of preferences among seeds and pellets, does it really measure degree of preference? If pigeons always choose the larger of two pellets, Figure 1 reflects the ability to discriminate which is larger, and distances along those scales tell us about relative discriminability, not relative value. This has long been a point of contention concerning Thurstone (and Fechnerian) scaling. Weber's law implies a scale of cumulative discriminability that is linear in the logarithm of the stimulus dimension, as is the case in Figure 3. Fechner took this to be an indication that psychological magnitude grows as a logarithmic function of physical magnitude. In this sense, Figure 2 displays Fechnerian scales of psychological size. In this experiment, however, it should be clear that we are measuring discriminability. Whether an organism prefers one alternative twice as much as another or 200 times as much, an optimal forager should always choose the preferred alternative, and we have no reason to believe that the pigeons did otherwise in these experiments. It is possible, of course, that in close judgments other factors, such as color, would have biased the choice. But all that we have license to conclude is that Figure 2 shows how cumulative discriminability grows with size.

Any attempt to generate a scale of value beyond a Thurstone scale changes the comparisons we ask of an organism. Instead of saying "what do you prefer?" we ask more

complicated questions of the sort "do you prefer 90 mg over 45 mg more or less than you prefer a 5-s delay of reinforcement over a 10-s delay?" The assignment of value must always be made in the context of a comparison scale, which may interact with the continuum we are scaling (Killeen, 1974, 1985); scales of value determined in one context are likely to suffer nonlinear distortions when employed in another. Therefore, Thurstone scales of discriminability may be the most we should aspire to until we have a rich enough understanding of the dimensions of preference and their interactions to derive unidimensional scales as parsimonious axes of a multidimensional preference structure.

EXPERIMENT 3: CHOICE BETWEEN DIFFERENT COMMERCIAL PELLETS

Comparing the scales from Experiments 1 and 2, one brand of commercial pellets seems to have been rated higher than the other, based on indirect inference from their scale values. This experiment therefore focuses on a direct comparison of the Noyes and Bioserv pellets.

METHOD

Subjects and Apparatus

Birds A, B, C, D, and E served as subjects. The apparatus was the same as in the previous experiment.

Procedure

The subjects were exposed to a mixture of 45-mg Noyes and Bioserv pellets for 3 days prior to testing. A trial consisted of the presentation of the food cup containing 5 g of the pellets in each side, with the side for Noyes pellets randomly alternated with the side for Bioserv pellets on every trial. Subjects were allowed to eat for 5 s, at which point the tops of the cup were closed and the trial ended. A total of 16 trials was conducted for each pigeon.

RESULTS AND DISCUSSION

All pigeons chose the Bioserv pellets more often than the Noyes pellets, with the number of times Bioserv was chosen by each being 16, 12, 11, 11, and 9. The binomial test requires 12 or more choices out of 16 to achieve significance (at the .038 level). The aggregate

performance, 59 choices of Bioserv versus 21 choices of Noyes, indicates a general preference for Bioserv. It is not clear on what aspect of the pellets this preference was based; the Bioserv pellets were slightly firmer and slightly lighter and tanner in color. Experiment 1 showed that Noyes pellets were quite acceptable, being preferred over wheat and being comparable to milo, two grains occasionally used as primary reinforcers by investigators. On the same scale, the current results would place Bioserv pellets halfway between milo and Austrian peas.

EXPERIMENT 4: SEEDS OR MOUTHFULS?

The amounts of grain provided in these tests barely covered the bottoms of the food cups, thus inducing the animals to eat only one seed per peck. (The number of pecks required to consume 5 cc of millet approximately equaled the number of seeds typically found in 5 cc of that grain.) In this experiment we filled the cups almost full of 20-mg BP and 45-mg BP. By taking more than one pellet per peck, the animals could achieve an equivalent feeding rate with each size pellet. If they did so, it should erode the large preference found in Experiment 2 for the larger size (95%).

METHOD

Pigeons F, G, H, and I were given 20 choices on each of 2 days between the 20-mg and 45-mg Bioserv pellets, and were permitted to eat for 5 s after each choice.

RESULTS

The pigeons chose the larger pellets 157 times out of the 160 opportunities. Thus, the opportunity to consume more pellets per peck had no effect on the near-exclusive preference for the larger pellets. Of course, we do not know that they *did* consume more than one pellet per peck, nor do we know whether the prior training established habitual preferences. On the other hand, the natural foraging conditions under which these animals evolved would probably make it unlikely that they would be able to fill their beaks with seeds, and might contribute instead to the instinctive choice of larger over smaller seeds as an optimal eating strategy.

EXPERIMENT 5: EFFECT OF HUNGER ON PREFERENCES

The present results seem to be inconsistent with the common observation that when animals are kept at free-feeding weights with ad libitum access to grain, they become "picky" and leave certain grains in the cup uneaten. Some birds leave small grains, but others leave large grains. One published report showed that birds selected grain in the following proportions: corn (maize) 39%, peas 23%, wheat 20%, and kafir 18% (kafir is a small corn, about the size of milo; cited in Roberts, 1962). This ranking is highly correlated with the size of the grains (on the reasonable assumption that the peas were Austrian). However, choices in Experiment 1 for grains sufficiently larger than the alternative were almost always exclusive. Of course, it makes sense to sample the grains to balance nutrients. If this is what the animals typically do, however, it means a shift in feeding strategy: When sufficiently hungry, the bigger the better. When near-adequately fed, other preferences may manifest themselves, or the animals may prefer to sample a range of grains. To examine this issue, we measured preferences for two grains at high and low deprivation levels.

METHOD

Pigeons F, G, H, and I were returned to ad libitum feeding and then reduced in weight until they would approach and eat from the experimental food cups (90% to 95% ad libitum). After each testing session they were given enough Purine Pigeon Chow® to maintain them at that level (about 6 min of access). On each trial they were given a choice between milo and popcorn. Five trials were conducted per day, with 8 s of eating from half-full food cups permitted per trial. The position of the milo and popcorn in the food cups was kept constant. After 10 experimental days, their weights were reduced to 85% of free feeding, and an additional 15 days of trials were conducted. They were then returned to 90% to 95% for an additional 15 days of testing.

RESULTS AND DISCUSSION

There was a strong correlation between body weight and grain preference: When hungry, pigeons consistently chose popcorn; 3 did so exclusively, and 1 did so on 46 of 65 trials. At

or above 90% ad libitum, the pigeons exhibited idiosyncratic preferences, choosing popcorn 100%, 57%, 43%, and 8% of the time. The correlation between percentage of ad libitum body weight and choice of corn was $r = -0.75$. Shettleworth (1987a) also found a significant correlation between percentage of ad libitum body weight and the proportion of large items eaten. This reconciles our findings of the domination of food choice by size for very hungry subjects with the selectivity of eating found in less hungry subjects.

EXPERIMENT 6: SAMPLING OR PREFERRING MILO?

When well fed, do the pigeons sample more, or was there a latent preference for milo that was uncovered when the exigency of hunger was abated? How could we test this distinction? If the only difference between two feeds was size, any shift in preference could not be due to flavor, nutritional value, or shape; it might be due to preference for a smaller size when less hungry or to increased sampling when less hungry. Such a test could rule out many plausible alternatives to the sampling hypothesis, such as latent preferences, nutritional balance, and so forth.

METHOD

Pigeons F, G, H, and I were returned to 90% of their ad libitum weights, the highest value at which they would consistently approach the food cups. The food cups contained 5 cc of 97-mg Bioserv pellets on one side and 5 cc of 37-mg Bioserv pellets on the other side. Birds were allowed 8 s of food access per trial. Five trials were conducted per day, with sides randomly alternated. The dependent variable was the relative proportion of first choices of each side of the food cup.

RESULTS AND DISCUSSION

Preference for the 97-mg pellets dropped from 95% (Experiment 2) to 74% ($F = 8.41$, $p < .01$). Because there was nothing else different about the options than size, the decrease in preference for the larger pellets could not have been due to other dimensions, such as flavor or nutritional balance. Behavior of less hungry pigeons is less under the control of the incentive value of food, and random factors come into play to dilute measured preference.

These results must be interpreted with cau-

tion, however. Some time had elapsed between the 95% preference measured in Experiment 2 and the weaker preference measured here. Furthermore, there were fewer different stimuli in this experiment; but, if anything, that should have sharpened preference.

A more important consideration is that, although we have demonstrated that preferences based on other dimensions are not necessary to explain the decrease in exclusivity of preference for larger feeds, we have not shown that they are irrelevant: Where nutritional or flavor or color differences are present they might indeed come into play in determining choice, and might do so especially at lowered deprivation levels.

EXPERIMENT 7: RANGE EFFECTS

Figure 2 shows that the Thurstone scale in Experiment 1b was slightly longer than that in Experiment 1a. This means that the discriminations between grain types were better in Experiment 1b. There could be many reasons for this, including the different subjects, food cups, and procedure. In this experiment we consider a more interesting possibility. In Experiment 1b we tested small subsets of the possible combinations of grains. This scheduling may permit the animals to focus on a small candidate set of grains, and therefore to make the discriminations more rapidly and more accurately. There are both theoretical and experimental justifications for this suspicion. Ecologists have long spoken of "search images," and Blough (1991) has demonstrated that they may be but one instance of sequential priming. Psychophysicists have also found that extending the range of stimuli to be discriminated can severely undermine discriminations that were previously easily made. In this experiment we test the possibility that range-restriction effects are operative in the choice of foods.

METHOD

Subjects F, G, H, and I were maintained at 85% of ad libitum weights. During the course of this experiment they received all of their food during testing. They were given 10 to 15 comparison choices every day, and were permitted to eat for 5 s per exposure. In Part A, they were given the choice between 37-mg and 45-mg BP. In Part B, they were shown a con-

tainer full of 94-mg BP before each choice between 37-mg and 45-mg BP. The container was a round shallow tray with enough pellets in it to almost cover its bottom; for 6 s it was held close to the position the food cups would occupy next. Otherwise the treatment was identical to that of Part A. In Part C, the pigeons were given choices between 37-mg, 45-mg, and 94-mg BP. A total of 20 choices between each pair of grains was given to each pigeon.

RESULTS

Part A

Pigeons chose the 45-mg pellets over the 37-mg pellets 80% of the time, significantly more often than when that choice was embedded in others in Experiment 2 (64%; $F = 5.33$, $p < .05$).

Part B

Upon being shown the larger grain, choice of the 45-mg pellet decreased to 73%.

Part C

When the 94-mg pellet was included in the alternatives, choice of the 45-mg pellet over the 37-mg pellet decreased again to 60%. The 94-mg pellet was chosen over the 45-mg pellet 92% of the time, and over the 37-mg pellet 100% of the time.

The major results in this experiment were statistically significant according to a repeated measures ANOVA, $F(2, 6) = 5.65$, $p < .05$. A Tukey pairwise comparison of the means showed that the only statistically significant difference in preference for 45 mg over 37 mg was between Part A and Part C.

DISCUSSION

The introduction of a stimulus (94-mg BP) that was rarely or never confused with either of the other stimuli had a significantly detrimental effect on the discrimination between those two stimuli. Extending the range degraded the discriminations. Such range effects are ubiquitous in discrimination studies.

It could be argued that the effect was due to the disruption of a search image for the 45-mg pellets. Such images may operate by narrowing the range of stimuli to be discriminated (see, e.g., Alcock, 1989). This hypothesis could be tested by introducing as the third size a pellet that is never preferred and for which no

search image should be formed. If the disruption of preference is merely another instance of the range effect, it should still occur; if the construct of search image is relevant, we may find that only larger pellets disrupt performance.

SUMMARY AND GENERAL DISCUSSION

It appears that we have replicated a common finding in the literature on quality of rewards: Bigger is better. In the first three experiments, the size of feed accounted for most of the variance in the data. Some grains fell off this regression line: Milo was liked a bit more than it should have been given its size, as were popcorn and Bioserv pellets. Unhulled wheat was disliked more than it should have been, as were Austrian peas and wheat. Both weight of the seeds and volume as estimated from the linear dimensions provided equally good predictors of the scale values.

In most cases, the pigeons could handle two to three seeds per second, with millet (3.5 per second) and oats (1.3 per second) falling outside that range. Because these two seeds were about equally disliked, we conclude that handling time per seed was not the major controlling variable in these experiments. A higher correlation was found between grams consumed per second and scale value. But correlations were higher yet when handling speed was taken out of the prediction equations altogether and the weight of the seeds was used as the predictor. Where handling time does come into play is in choosing the unhulled oats from other grains of comparable size: Oats were less preferred than any other grain and also had the longest handling time. The only other obvious factor that might account for some of the residual preferences, when the variance due to size was accounted for, was color: The most preferred feeds had more saturated yellow or red color, and the less preferred feeds had a more desaturated light or dark color.

Although there were many differences between the feeds in the first experiment, the only difference in Experiment 2 was size. The strong control by size found in that experiment validated the inference that size is generally a powerful controlling variable. The elimination

of variables other than size in Experiment 2 permitted evaluation of transformations to find the one that most accurately predicts value from size. As seen in Figure 3, the logarithm of weight (or volume) is an excellent predictor. This relation follows from Weber's law, with ability to discriminate the larger feed a linear function of its measure. From this relation follows a simple rule of thumb: The z score for preference between two seeds is proportional to the logarithm of the ratio of their sizes.

We did not conduct the extended number of trials necessary to get data from individual subjects that would be stable enough to analyze. It is possible that there were reliable idiosyncratic differences among animals that would be worth studying. The average data revealed very strong control by size of grain, as evidenced by the regressions, indicating this to be the primary controlling variable for deprived pigeons.

A direct comparison of Bioserv pellets with Noyes pellets (Experiment 3) showed a slight preference for the former, a preference that validates an earlier inference from the scaling analysis. Because size and shape were identical, the difference must reflect control by hedonic features of the pellets, such as the yellow hue of Bioserv.

The above conclusions must be tempered by recognition that the pigeons were deprived to 80% to 85% of their ad libitum weights, at which point mere sustenance might have been more important than a balanced diet or than exploration of other potential sources of food. Experiment 5 showed that when the pigeons were near their free-feeding weights, the near-absolute preferences for larger grains moderated. This shift need not be attributed to a weaker preference for hedonic attributes of the smaller grain that was "uncovered" when body weight was raised; Experiment 6 showed a similar moderation in the preference for the larger of two otherwise identical pellets when body weight was increased. Instead, it may be that tendency to choose any one particular grain was weakened along with deprivation, and this let incidental stimuli and vagaries of attention increase the variability of choice, leading to increased sampling of the environment.

In the last experiment, discrimination of two medium-sized pellets (37 and 45 mg) was impaired when a large pellet (94 mg) was in-

cluded in the preference tests. The deterioration in choice of the 45-mg pellet was substantial (from 80% to 60%), even though the large pellet was easily discriminated from the medium and small pellets. This finding is consistent with "range-frequency" effects in psychophysical judgments, and shows that these choices of grains are not independent of irrelevant alternatives.

As a footnote to these investigations, we return to the question that motivated the first experiment: What should one put in the hopper of the experimental chamber? We assume that the more preferred incentive would be the better one to use (Mackintosh, 1974; but see Svartdal, 1993). These experiments clearly show that hungry pigeons prefer larger grains; if that were the only consideration, popcorn would be a good choice. However, each grain of popcorn provides four times as much food as a grain of milo. If popcorn is used, it will be necessary to decrease the number of trials per session or the duration of access to the hopper. Either of those maneuvers may undo whatever benefits accrue to the use of a large grain. Furthermore, because comparisons of grains are not being made, differential sensitivity to one grain over another will be blunted. Because of its low price and moderately high acceptability, milo is a good choice as a reinforcer for deprived pigeons. It is low in Vitamin A (Levi, 1957) and should be supplemented with a balanced feed, such as commercially available fortified mixed grains or Purina Pigeon Chow®.

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