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WOODRATS COLLECTING HOUSE BUILDING MATERIALS: CENTRAL PLACE FORAGING FOR NON-FOOD ITEMS

by

MARK ALAN MCGINLEY

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Christopher C. Smith
Major Professor

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The adaptive value of behavior has been a major area of interest to evolutionary ecologists. Foraging behavior has been intensively studied due to the relative ease of quantifying the behavior and its importance to the animal. Optimal foraging theory (see Pyke et al 1977;Krebs 1978 for review) suggests that animals can increase their fitness by maximizing the net rate of intake of some essential resource per unit time.

Orians and Pearson (1979) and Schoener (1979) have examined the special case of central place foragers, who forage by leaving from and returning to a central place. The authors examined the size-distance relationship of food chosen by central place foragers. Schoener predicts that if pursuit or provisioning time is independent of prey size, the optimal prey size increases with distance from the central place. However, if provisioning time increases with prey size, the opposite situation might occur and smaller sizes become favored with distance. He also predicts that animals should forage more selectively farther from the central place. Tests of these predictions (Davidson 1978;Smith et al 1979; Jenkins 1980;Killeen et al 1980) have dealt exclusively with animals foraging for food.

Many species act as central place collectors of non-food items. Many birds collect nest building materials (Welty 1981), bowerbirds collect objects to be used in mating displays (Guilliard 1963), and some mammals, such as beavers (Grinnell et al 1937), muskrats (Errington 1963), and woodrats (Linsdale and Tevis 1951;Rainey 1956;Finley 1958) build houses with the collected material. The collection of non-food items has been studied (Bonaccorso and Brown 1972;Olsen 1973;Wallace 1978 and references therein), but not in terms of foraging theory.

Schoener (1971) lists the 3 steps necessary to solve optimization problems: 1) choosing a currency, 2) choosing the appropriate cost-benefit functions, 3) solving for the optimum. Previous investigations of optimal foraging theory have used energy and/or nutrients as the currency measuring benefit to the animal (Pyke et al 1977). The energetic or nutrient value of a food item can be measured empirically by calorimetry or nutrient analysis. These are not appropriate currencies for studying animals collecting non-food items. I propose that an appropriate currency to measure the positive effect of collecting a non-food item can be called 'value'. The size-value relationship is unknown for animals collecting non-food items, and the value of a stick can not be measured empirically as the energetic and nutrient value can. I will propose a method of determining the size-value relationship for non-food items collected by animals. Once the currencies and the cost-benefit relationships have been determined,the same optimization procedures used to make predictions about optimal diets (e.g. Pulliam 1974;Charnov 1976) can be used to make predictions about which non-food items should be collected.

Eastern woodrats (Neotoma floridana) are medium sized, nocturnal rodents who collect sticks and other objects as house building materials (Rainey 1956;Wiley 1980). The house, which is inhabited by only one woodrat at a time,provides many benefits to the woodrats including protection from predators, protection from the weather, and a safe food storage site (Brown 1968;Vaughan and Schwartz 1980). The woodrats range out from their houses to retrieve sticks, and are thus acting as central place collectors. They therefore offer the opportunity to examine central place foraging for non-food items. This paper will examine the procedure necessary to determine the stick size-value relationship and discuss how the collection of non-food items relates to other areas of interest in optimal foraging theory.

The Model

Optimal foraging models (e.g. Schoener 1971;1979) express the profitability (value/time) of a prey type as-

$$\frac{e}{t} = \frac{Cu - Cp - Ch}{Tp + Th} \qquad (3)$$

where e=energy, t=time, Cu= utilizable calories, Cp= pursuit and provisioning calories, Ch=handling and swallowing calories, Tp= pursuit and provisioning time, and Th= handling and swallowing time.

Sticks collected by woodrats as house building materials have no utilizable caloric value, so equation (1) can not be used. The profitability of a stick collected by a woodrat for house building can be defined as-

$$\frac{V-C}{T} = \frac{\text{Value of Stick} - \text{Cost of Collecting Stick.}}{\text{Time Spent Collecting Stick}} \qquad (2)$$

The major cost of collecting a stick will be the cost of returning the stick to the house. The energetic cost of collecting a stick depends on the stick size and the distance that the stick is carried. The cost of carrying a stick (C) is assumed to increase linearly with distance (D) and exponentially with stick size (SS). The relationship is assumed to be -

$$C = aDe^{bSS} \qquad (3)$$

where a and b are constants (Fig. 1). An exponential relationship between cost and load size has been found for horses pulling loads of different sizes (Brody 1945), so this does not seem to be an unreasonable assumption.

The relationship between the time spent collecting a stick (T) and stick size and distance is assumed to be-

$$T = jDe^{kSS} \quad (4)$$

where j and k are constants.

Each stick returned by a woodrat to its house presumably adds to the value of the house. Different sized sticks may provide different values to the woodrats. The actual relationship between stick size and value is unknown, but depending on the circumstances, any of the 5 following stick size-value relationships could be possible.

1) If all sticks were worth the same to the animals,the value of a stick would be independent of stick size (Fig. 2).

2) If the most important function of the house was protection from the weather, and small sticks were able to pack together tighter and make the house more weatherproof, small sticks would be more valuable than large sticks (Fig. 3).

3) If the most important function from the house was protection from predators, and if large sticks made the house stronger and more predator resistant, large sticks would be more valuable than small sticks (Fig. 4).

4) If middle sized sticks were able to serve both functions at the same time, middle sized sticks would be more valuable than either large or small sticks (Fig. 5).

5) If middle sized sticks were unable to adequately able to serve either function, middle sized sticks would be less valuable than either large or small sticks (Fig. 6).

Profitability ((V-C)/T) vs. distance curves can be simulated for each of the 5 relationships between stick size and value (Figs. 2-6). These show the relationship between profitability and distance for 5 different stick sizes, where stick size 1 is the smallest and stick size 5 is the largest. The profitability of all stick sizes decreases with distance from the house. The cost of carrying stick size 5, the largest stick, is so large that it only provides a positive profitability to the woodrat when the carrying distance equals zero.

These curves can be used to look for consistent trends which allow the formulation of qualitative predictions about the animal's behavior if that behavior is occuring adaptively. If there is a minimum profitability below which the woodrats will not collect, the range of acceptable sized sticks becomes smaller as the woodrats forage farther from the house, regardless of the stick size-value relationship (Figs. 2-6). Which sticks will be collected by the woodrats depends on the abundance of more profitable sticks. If the woodrats were presented with a distribution of sticks where the number of sticks above the minimum profitability value is less than they would collect in a certain period of time, it should be possible to force the woodrats to collect all acceptable sticks while leaving those with a profitability below the minimum value.

The models presented here predict that, regardless of the relationship between stick size and benefit, the number of stick sizes chosen should decrease with increasing distance from the house. Woodrats offer an opportunity to test this prediction due to the large number of sticks that they will collect in a night under laboratory conditions. Bonaccorso and Brown (1972) found that Neotoma lepida would collect up to 359 pieces of house building material per night. I have also found that Neotoma floridana show a high stick collection rate in the lab. Therefore, I predict that the woodrats will collect sticks from fewer size categories as they forage farther from the house.

Methods

The experiments were carried out in pens housed in a barn at Konza Prarie Research Natural Area near Manhattan Kansas from March 27 to June 1, 1982. The pens (6.9 by 11.4 meters) were divided into thirds by 2 partitions with 1 meter wide openings to increase the foraging path length (Fig. 7). The pens contained a support structure made up of overlapping 2 by 4s weighing greater than 2.5 kgs., and dry grass for nest building material (position X in Fig. 7). Woodrats, which had been kept in holding containers to allow them to adjust to captivity, were released into separate pens at position X which became the home site in every case. Food and water were supplied ad lib at position FW in Figure 7. The six animals used in this experiment were all adults weighing over 275 grams.

To determine the appropriate stick sizes to use in this experiment, woodrat houses were examined on Konza Prarie. These houses contained sticks ranging size from .1 gram to greater than 400 grams (Fig. 8). The sticks used in this experiment were divided into 10 size categories-

1) 0-.9 grams
2) 1-4.9 grams
3) 5-9.9 grams
4) 10-19.9 grams
5) 20-34.9 grams
6) 35-49.9 grams
7) 50-74.9 grams
8) 75-99.9 grams
9) 100-199.9 grams
10) greater than 200 grams.

These categories were chosen becaue they appeared to be noticeably different in size from each other (Weber-Fetchner law, Granit 1955). The weight of a stick was chosen as the measure of stick size due to the great variability in stick shape and the corresponding difficulty of determining a meaningful measure of stick length. The minimum linear distance from end to end correlates significantly with stick weight ($r = .54$, $p < .001$). To avoid including unusually long or short sticks in the experiment only sticks within 2 standard deviations of the mean stick length for each size category found in the field were used.

The woodrats were presented with sticks at 3 treatment distances- 5, 10, and 15 meters from the nest site. Sticks were presented at only one distance at a time and for 2 consecutive nights at each distance. The order of the treatments was determined randomly prior to the experiment and the design was stratified so that all possible combinations of treatment orders were used.

Fifty sticks, 5 of each size categoty, were placed at the appropriate treatment distance. The sticks were place 6-9 cms. apart so the woodrat could have access to all of the sticks. The woodrat was allowed to collect sticks overnight and begin to build a house. The next morning the pens were checked, the size of the collected sticks recorded, and the collected sticks were replaced at the experimental distance by a stick from the same size category. The woodrat was allowed to collect from the same distance for a second night and add to its house. The size of sticks collected was recorded and all sticks were removed from both the house and the treatment distance. Fifty sticks were placed at the next experimental distance and the process was repeated until a woodrat had moved sticks for 2 nights at all 3 distances.

Sticks were considered collected by the woodrats only if they were returned to the house. If no sticks were moved by the woodrats overnight it was not considered a sample period, and the sticks were left in the same position until some sticks were moved. It was possible for a woodrat to be scored as collecting no sticks if it moved sticks to some other part of the pen and none to the house site.

To insure that each experimental period began with the removal of sticks from the woodrat's house, sticks were placed randomly throughout the pen prior to the initiation of the experiment. The woodrat was allowed to build a house for one night. These sticks were removed from the house and the pen and the experimental procedure was begun.

Results

The number of sticks of each size category chosen by the 6 experimental animals is summarized in Table 1. The distribution of stick sizes chosen at the 3 experimental distances is shown in Figure 9. The number of sticks collected as house building material ranged from 0-49 out of 50 possible.

The woodrats chose sticks from fewer size categories with increasing distance from the house site (Table 2)(Friedman's test $Q=7.05$, $p<.03$), thereby supporting the prediction of the models.

The models not only predicted that the number of size categories chosen should decrease with distance, but also made predictions about the variance in stick size chosen. Four out of the 5 general models (Figs 2-5) predict that the variance in stick size chosen should decrease with distance. The other model (Fig. 6) predicts that over some distances variance will increase. This possible stick size-value relationship will be rejected for other reasons later, so the prediction of decreasing variance will be tested. Since the range of possible variances decreases as the number of sticks chosen increases, analyses based on variance estimates were not used. Non-parametric tests of variance (Siegel-Tukey) were used instead.

The variance in stick size chosen by the woodrats decreased with increasing distance from the house (Kruskal-Wallis test, using Siegel-Tukey ranking of data aligned by subtracting the mean for each group, KW=5.97, p=.0504)(Fig. 9). Significant differences in variance were found for individual animals between 5 and 15 meters (Table 3). Three out of the 6 woodrats collected sticks with a smaller variance at 15 meters than at 5 meters. These 6 independent experiments were combined (Lehman 1975, p. 132) to show that the woodrats collected sticks more selectively at 15 meters ($Z=12.6$, $p<.0001$).

The woodrats collected more sticks 5 meters from the house than they did at 15 meters (Wilcoxin signed-rank test Vs=0, p=.0156)(Table 4), which is consistent with the idea that the woodrats are collecting all of the sticks above the minimum profitability value since the models predict that fewer sticks should lie above that value at 15 meters.

The number of sticks chosen the first night was not significantly different from the number chosen the second night. (Wilcoxin signed-rank test Va=3, p=.078)(Table 4). The woodrats chose more of the largest stick (size category 10) on the first night (21) than they chose on the second night (11)(Wilcoxin signed-rank test Vs=0, p=.031). There was no difference in the number of the smallest stick sizes (size categories 1 and 2) between nights (Wilcoxin signed-rank test Vs=5, p=.31), so this difference was not due to the avoidance of extreme sized sticks on the second night. There was no difference in the variance of stick size chosen between nights (Siegel-Tukey test $p>.4$).

The woodrats were not collecting sticks randomly (χ^2 test, $p<.001$). The woodrats preferred middle sized sticks over both large and small sticks. The woodrats collected significantly more of the middle sized sticks (size categories 4-8) than large (size categories 9 and 10) and small (size categories 1-3) sticks (Wilcoxin signed-rank test $p < .0001$).

The woodrats collected significtly more of the preferred stick sizes (categories 4-8) at 5 meters than they did at 15 meters (Wilcoxin signed-rank test Vs 0, p .0156), so the decrease in the number of sticks chosen with distance is not only due to the avoidance of unacceptable sticks.

The order of presentation of the treatments did not significantly affect either the number of sticks chosen (Friedman's test $Q=1.30$, $p > .15$) or the selectivity of the animals. There was no significant difference in the number of size categories chose (Friedman's test $Q=.082$, $p > .15$) or in the variance (Siegel-Tukey test $p > .38$).

Determining the Size-Value Relationship

Previous investigations of optimal foraging theory have examined animals foraging for food, and thus have used energy and/or nutrients as the currency of benefit to the forager. It would be inappropriate to measure the value of a non-food item collected by an animal in these currencies. An animal presumably gains some value from any item that it collects. Nest building materials collected by birds should benefit them by protecting the adults, young,and eggs from predators and the weather, thus increasing both adult and offspring survival. Male bowerbirds can increase their reproductive success by collecting non-food items used to attract females. Woodrats who build houses should have increased survival rates and lower costs of thermoregulation. Increased survival and energetic efficiency should increase the fitness of the woodrats, which is the ultimate measure of benefit of any item collected by an animal. Individuals who are unable to build a suitable house in a short period of time should suffer higher mortality than more efficient builders. Choosing the most profitable stick should be a very important part of the efficient building process.

Even though the value of collecting non-food items probably differs between species, and is unknown in most cases, some size-value relationship must exist in all cases. Since the size-value relationship is unknown it is impossible to predict the optimal strategy for the animal, but it is possible to make qualitative predictions about how the animals should behave if they are behaving adaptively. The models presented here predict that, regardless of the stick size-value relationship, the woodrats should collect more selectively when farther from the house if they are foraging adaptively, and not taking sticks below a minimum profitability value. Since 'value' could be used to make predictions about collecting behavior, it seems that it can be used as a currency in foraging models.

The prediction of increased selectivity, measured both by a decrease in the number of stick sizes chosen and a decrease in the variance of stick size chosen, with increasing distance from the house was supported in this study. Since the woodrats collected more selectively with increasing distance from the house, it suggests that the woodrats are taking the profitability ((V-C)/T) of a stick into account when choosing house building materials. If this is the case, it should be possible to use stick size preference to determine the relationship between stick size and value.

If the animals are foraging adaptively, the preferred stick size should indicate the sticks with the highest profitability. The profitability vs. distance curves (Figs. 2-6) give a qualitative indication of the preferred stick size for each stick size-value relationship. When value is independent of stick size (Fig. 2), value decreases with stick size (Fig. 3), and middle sized sticks are less valuable than the benefit of large or small sticks (Fig. 6) the smallest sticks are preferred at all distances from the house. When value increases with stick size (Fig. 4) or middle sized are more valuable than large or small sticks (Fig. 5) middle sized sticks are favored. The size of the preferred stick size should decrease with distance.

The results of this experiment indicate that middle sized sticks are favored over large or small sticks (Fig. 9), which suggests either that value increases with stick size or that middle sizes are more valuable than either large or small. The most likely stick size-value relationship for woodrats collecting house building materials is that value increases with stick size. Large sticks, which are much too large to be moved by the woodrats, provide such great value to the woodrats by providing support for their houses that the woodrats choose to build their houses around one. Eastern woodrat houses in eastern Kansas are usually built around the the base of trees, stumps, fallen logs, or in crevices in rock ledges (Rainey 1956). In this study the woodrats chose to build around the support structure rather than build a house nearer to the sticks. This allowed them to gain the value of a large object without incurring the cost of moving it.

The relationship between stick size and value may change as house building progresses. Larger sticks might be favored early in the house building period if they provide better support for the house. Smaller sticks might become more valuable later in the house building period if they pack together more tightly into small spaces and make the house more weatherproof. If this were true, the number of large sticks chosen should decrease as house building progresses. Significantly more of the largest sticks (size category 10) were taken on the first night, supporting a changing stick size-value relationship. This study only examined the first 2 nights of house building, so a changing stick size-value relationship could explain the difference in the number of small sticks chosen in this experiment compared to the number of small sticks found in the field (Fig. 8).

Using value as a currency and examining the preferred size of items collected by animals when they are foraging adaptively should be a useful procedure for determining the size-value relationship for non-food items. It is possible to make predictions that allow selection between the 5 general size-value relationships. Thus, this procedure can be applied to any animal collecting non-food items.

Time Minimizers and Value Maximizers

Schoener (1971) defined time minimizers as animals whose fitness is increased when the time taken to obtain their daily metabolic requirement is decreased and energy maximizers as animals whose fitness is increased when net energy is maximized in a given time spent feeding. Time minimizers increase their fitness by undertaking other activities once they have consumed their daily metabolic requirement and energy maximizers increase their fitness by foraging for as long as possible. Hixon (1982) suggests that the strategies be renamed feeding time minimizers and feeding time maximizers. The same distinction should be true for animals collecting non-food items- there should be collecting minimizers and collecting time maximizer.

The same animal may have a different strategy depending on the circumstances. Woodrats may show a shift in strategy as house building progresses. A woodrat without a house, who faces exposure to predators and bad weather, should behave as a collecting time maximizer until it has built a house that can adequately protect it. Until the house is finished any extra time spent working on the house should increase the woodrat's fitness more than engaging in other activities would. Once the house is finished a woodrat continues to make improvements. A woodrat should act as a collecting time minimizer when making additions to the house since they can increase their fitness by devoting their time to other activities such as foraging, storing food, mating behavior, or resting in their house where they are safe from predators.

Nest building in birds may offer other opportunities to study these strategies. Male marsh wrens (Telamatodytes palustrus) build many nests located in courting centers which are used to attract females (Verner 1964). After females have chosen a male they either use one of his next or build one of their own. Females who build one of their own nests should act as collecting time minimizers since once they finish a nest they should increase their fitness more by carrying out other activities. Males who have just initiated building in their courting centers should act as collecting time maximizers since they can increase their fitness, attract more mates, by building more nests. They may change strategies and become collecting time minimizers after they have built a number of nests in their courting centers since they might attract more mates by using the time to sing and display for females.

Third and Fourth Order Selection

In order to understand the effects of increasing distance from the central place on the collecting behavior of an animal it is necessary to understand the different choices that foraging animals make. Johnson (1980) presents an ordering of the selection processes that affect foraging behavior.

First order selection is the selection of a geographic region. Second order selection is the selection of a home range within that region. Third order selection is the selection of a feeding site within that home range, and fourth order selection is the selection of items at that site.

Both third and fourth order selection can be influenced by the distance from the central place. Trends is fourth order selection can be predicted by the models of Orians and Pearson (1979) and Schoener (1979), as well as those presented here. These models all predict that animals should take fewer items when foraging farther from the central place because fewer items lie above the minimum profitability value.

In this study, the number of sticks chosen at 5 meters was significantly greater than the number of sticks collected at 15 meters, therefore supporting this prediction. However, the number of sticks in the preferred size categories chosen at 5 meters was significantly greater than the number chosen at 15 meters. The decrease in the number of sticks chosen with distance is not only due to the omission of unacceptable sized sticks. This is not predicted from any of the models mentioned above.

Andersson (1978) mathematically investigated third order selection by examining the optimal foraging area of central place foragers. Using the assumption that if animals were foraging optimally the marginal cost of additional food will be equal throughout the foraging area, Andersson examined the optimal allocation of foraging effort. Andersson predicts, that for animals foraging in uniform environments, the optimal search time per unit area decreases linearly with distance from the central place. Orians and Pearson predict that search time should increase with distance from the central place. They make the opposite prediction since they do not make the assumption of a uniform environment.

Andersson (1981) tested his prediction with the whinchat Saxicola rubetra, an insectivorous bird. He placed a uniform distribution of mealworms around whinchat nests in the field and watched them forage. The whinchats decreased their search time as they foraged farther from the nest. Andersson also predicted that the whinchats would take more of the available food closer to the nest, and this prediction was also supported in his study. The decrease in the number of mealworms chosen with distance is the result of third order selection only since there was no variability in the food quality within a site.

Fourth order selection could also cause a decrease in the number of items chosen with increasing distance from the central place. All of the central place foraging models predict that the range of acceptable items decreases with distance from the central place. Assuming that the animals randomly discover items, the probability of finding only unacceptable items in a period of searching increases with distance from the central place since more items lie below the minimum profitability value. If animals use a decision rule such as 'continue to forage in an area until the average profitability for a given number of trips drops below a given value and then forage elsewhere', animals will stop foraging sooner in areas where there are more unacceptable items. The marginal capture rate drops to the average for the habitat sooner in an area where there are more low profitability items (Charnov 1976). Animals foraging in this manner would be less likely to find all of the most profitable items even though they would choose proportionally more of the preferred items.

The woodrats in this study had no third order selection since sticks were available at only one distance. The total number and the number of preferred sticks chosen decreased with distance, so this difference was the result of fourth order selection. The Orians and Pearson model predicts that search time should increase with distance in this case. It is possible that the woodrats have evolved in an environment with a roughly uniform resource distribution, and thus have evolved to respond as if they were foraging in a uniform environment and decrease their search time with distance as Andersson predicts.

To accurately understand the choices that an animal makes when foraging it is necessary to understand the interaction of third and fourth order selection. A comprehensive model of foraging behavior needs to include both the optimal allocation of search effort and the profitabilities of the items encountered. These 2 parameters combined with an accurate understanding of the decision rules used when foraging would be extremely useful for gaining a better understanding of feeding and collecting behavior.

Literature Cited

Andersson, M. 1978. Optimal foraging area: allocation of search effort. Theor. Popul. Bio. 13:397-409.

_______ 1981. Central place foraging in the whinchat, Saxicola rubetra. Ecology 62:538-544.

Bonaccorso, F.J. and J.H. Brown. 1972. House construction of the desert woodrat Neotoma lepida lepida. J. Mammal. 53:283-288.

Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Corporation, New York.

Brown, J.H. 1968. Adaptations to environmental temperature in two species of woodrats, Neotoma cinerea and Neotoma albigula. Misc. Publ. Mus. Zool. Univ. Mich. No. 135.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Popul. Bio. 9:129-136.

Davidson, D.W. 1978. Experimental tests of the optimal diet in two social insects. Behav. Ecol. Sociobiol. 4:35-41.

Errington, P.L. 1963. Muskrat populations. Iowa State University Press, Ames.

Finley, R.B. Jr. 1958. The woodrats of Colorado: distribution and ecology. Univ. Kans. Publ., Mus. Nat. Hist. 10:213-552.

Fitch, H.S. and D.G. Rainey. 1956. Ecological observations of the woodrat, Neotoma floridana. Univ. Kans. Publ., Mus. Nat. Hist. 8:499-533.

Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. Fur bearing mammals of California: their natural history, systematic status, and relations to man. University of California Press, Berkely.

Granit, R. 1955. Receptors and sensory perception. Yale University Press, New Haven.

Guilliard, E.T. 1963. The evolution of bowerbirds. Sci. Am. 209:38-46.

Hixon, M.A. 1982. Energy maximizers and time minimizers: theory and reality. Am. Nat. 119:596-599.

Jenkins, S.H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Killeen, P.R., J.P. Smith, and S.J. Hanson. 1981. Central place foraging in Rattus norvegicus. Anim. Behav. 29:64-70.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. in Behavioral Ecology, J.R. Krebs and N.B. Davies Eds., Sinauer Associates, Inc. Sunderland Massachusetts.

Lehman, E.L. 1975. Nonparametrics. Holden-Day Inc., San Francisco.

Linsdale, J.M. and L.P. Tevis Jr. 1951. The dusky-footed woodrat. University of California Press, Berkely and Los Angeles.

Olsen, R.W. 1973. Shelter-site selection in the white-throated woodrat Neotoma albigula. J. Mammal. 54:594-610.

Orians, G.H. and N.E. Pearson, 1979. On the theory of central place foraging. In D. Horn, ed. Analysis of ecological systems. Ohio State University Press, Columbus.

Pulliam, H.R. 1974. On the theory of optimal diets. Am. Nat. 108:59-74.

Pyke, G.H., H.R. Pulliam, E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137-154.

Rainey, D.G. 1956. Eastern woodrat, Neotoma floridana, life history and ecology. Univ. Kans. Publ., Mus. Nat. Hist. 8:535-646.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

_______ 1979. Generality of the size-distance relation in models of optimal feeding. Am. Nat. 114:902-914.

Smith, J.P., J.S. Maybee, and F.M Maybee. 1979. The effects of increasing distance to food and deprivation level on food hoarding in Rattus norvegicus. Behav. Neural. Biol. 27:302-318.

Vaughan, T.A. and S.T. Schwartz. 1980. Behavioral ecology of an insular woodrat. J. Mammal. 61:205-218.

Verner, J. 1964. Evolution of polygyny in the long-billed marsh wren. Evolution 18:252-261.

Wallace, R.J. 1978. Hoarding of inedible objects by albino rats. Behav. Biol. 23:409-414.

Welty, J.C. 1981. Life of Birds. W.B. Saunders Company, Philadelphia.

Wiley, R.W. 1980. Neotoma floridana. Mamm. Spec. 139:1-7.

Table 1. The number of sticks of each size category chosen by each of the animals in this experiment.

Replicate	1	2	3	4	5	6	Total
Stick Size							
1	0	0	0	0	4	11	15
2	5	0	8	1	11	21	46
3	16	6	12	3	24	26	87
4	20	13	21	9	27	29	119
5	22	14	26	8	27	30	127
6	27	19	23	2	24	30	125
7	26	17	23	8	25	30	129
8	26	15	23	4	21	30	119
9	21	12	20	7	13	30	103
10	9	0	8	1	2	12	32
Total	172	96	164	43	178	249	902

Table 2. The number of size categories having at least one stick chosen from them each night by each woodrat.

	5 meters		10 meters		15 meters	
Night	1	2	1	2	1	2
Replicate						
1	9	9	9	8	7	6
2	7	7	7	7	0	5
3	9	9	2	8	6	7
4	6	5	5	5	3	3
5	7	9	9	7	4	8
6	10	10	9	8	10	9
Average	8	8.16	6.83	7.17	5	6.33

Table 3. The results of Siegel-Tukey tests on the distribution of sticks chosen at 5 and 15 meters from the house for each of the six replicates. m=number of sticks chosen at 15 meters, n=number of sticks chosen at 5 meters, and p=significance level.

Replicate	m	n	p
1	38	62	.0793
2	9	45	.0202
3	47	82	.0044
4	8	22	.1540
5	37	70	.5239
6	80	97	.0001
Combined	Ws=132.2	Z= -4.76	p<.0001

Table 4. The number and average category size chosen each night at each distance combined over all replicates.

	5 meters			10 meters			15 meters		
	1st night	2nd night	comb.	1st night	2nd night	comb.	1st night	2nd night	comb.
number chosen	185	192	377	135	170	305	95	125	220
average size	5.94	5.49	5.71	6.03	6.23	6.18	5.88	5.99	5.94

Fig. 1: The hypothesized relationship between the cost of carrying a stick (both in terms of energy and time) and the size of the stick.

Fig. 2: Simulated profitability vs. distance curves for the case when value of a stick is independent of stick size. Curves are simulated for 5 stick sizes, stick size 1 is the smallest and stick size 5 is the largest. The profitability of all stick sizes decreases with distance. Stick size 5 is so large that it only provides a positive profitability when the carrying distance equals zero.

Fig. 3: Simulated profitability vs. distance curves for the case where small sticks are more valuable than large sticks. Curves are simulated for 5 stick sizes, stick size 1 is the smallest and stick size 5 is the largest. The profitability of all stick sizes decreases with distance. Stick size 5 is so large that it only provides a positive profitability when the carrying distance equals zero.

Fig. 4: Simulated profitability vs. distance curves for the case where large sticks are more valuable than small sticks. Curves are simulated for 5 stick sizes, stick size 1 is the smallest and stick size 5 is the largest. The profitability of all sticks decreases with distance. Stick size 5 is so large that it only provides a positive profitability when the carrying distance equals zero.

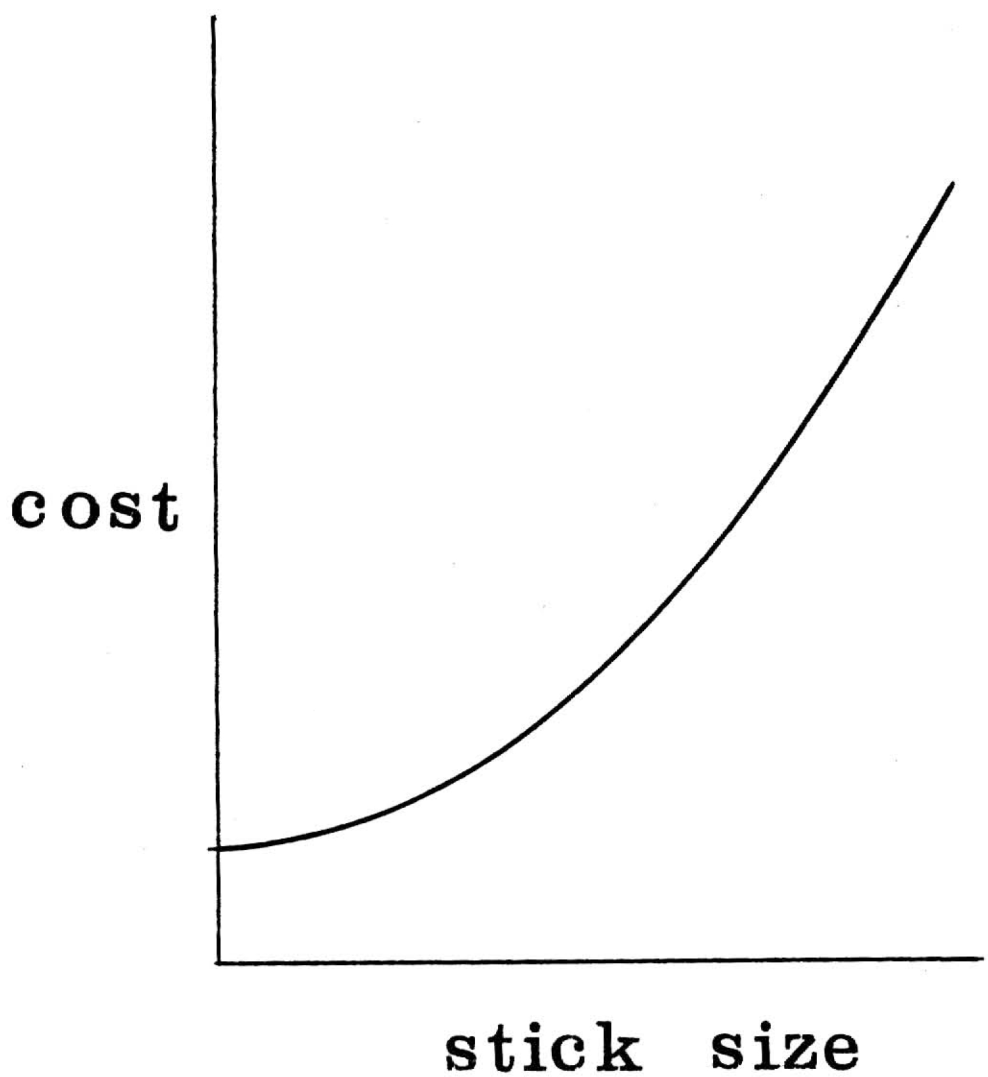
Fig. 5: Simulated profitability vs. distance curves for the case where middle sized sticks are more valuable than large or small sticks. Curves are simulated for 5 stick sizes, stick size 1 is the smallest and stick size 5 is the largest. The profitability of all stick sizes decreases with distance. Stick size 5 is so large that it only provides a positive profitability when the carrying distance equals zero.

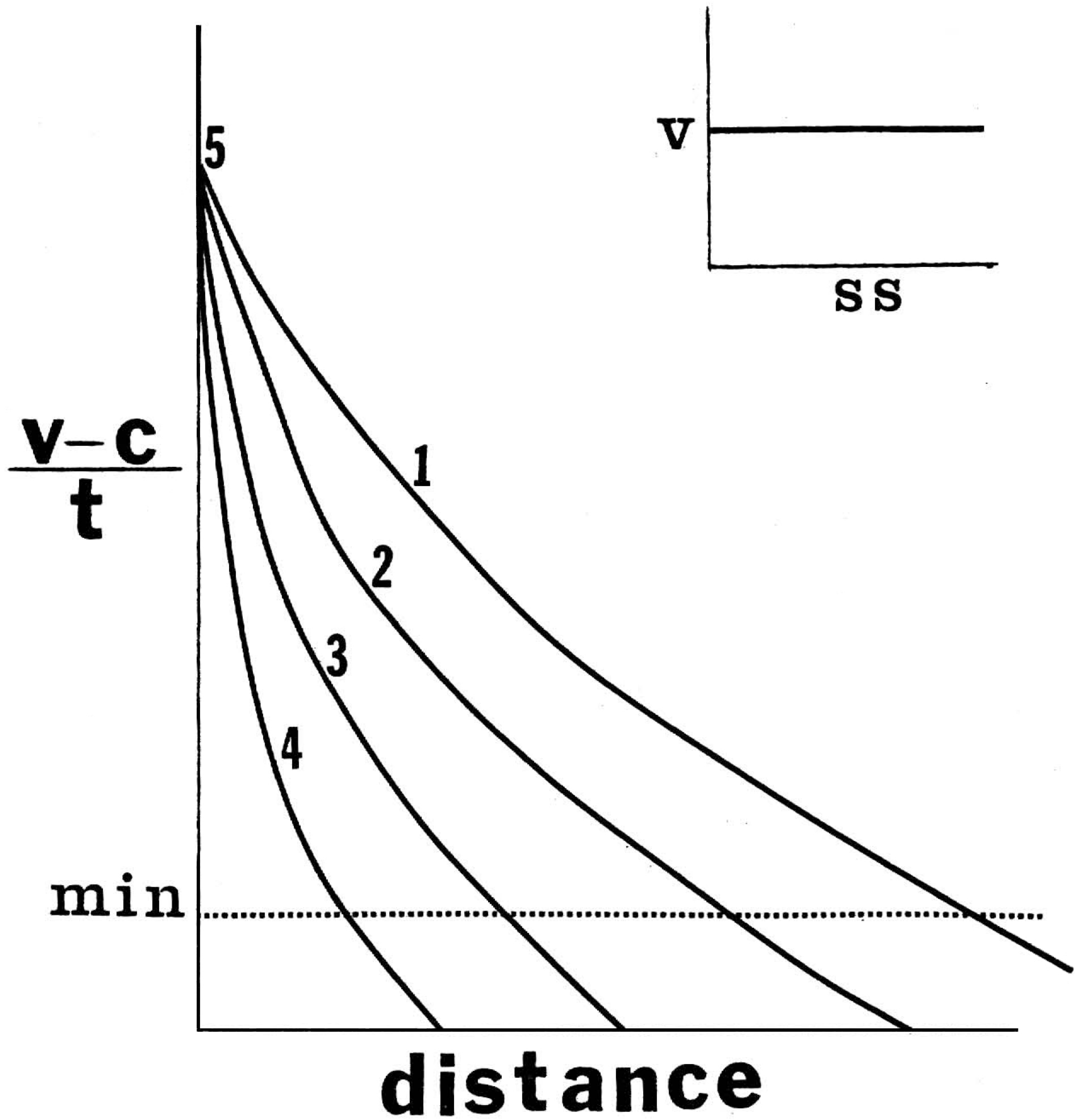
Fig. 6: Simulated profitability vs. distance curves for the case where middle sized sticks are less valuable than large or small sticks. Curves are simulated for 5 stick sizes, stick size 1 is the smallest and stick size 5 is the largest. The profitability of all stick sizes decreases with distance. Stick size 5 is so large that it only provides a positive profitability to the animal when the carrying distance equals zero.

Fig. 7: The experimental pens. Position X represents the house site, fw represents the location of food and water, and the dashed line represents the foraging path of the animals to the 3 treatment distances.

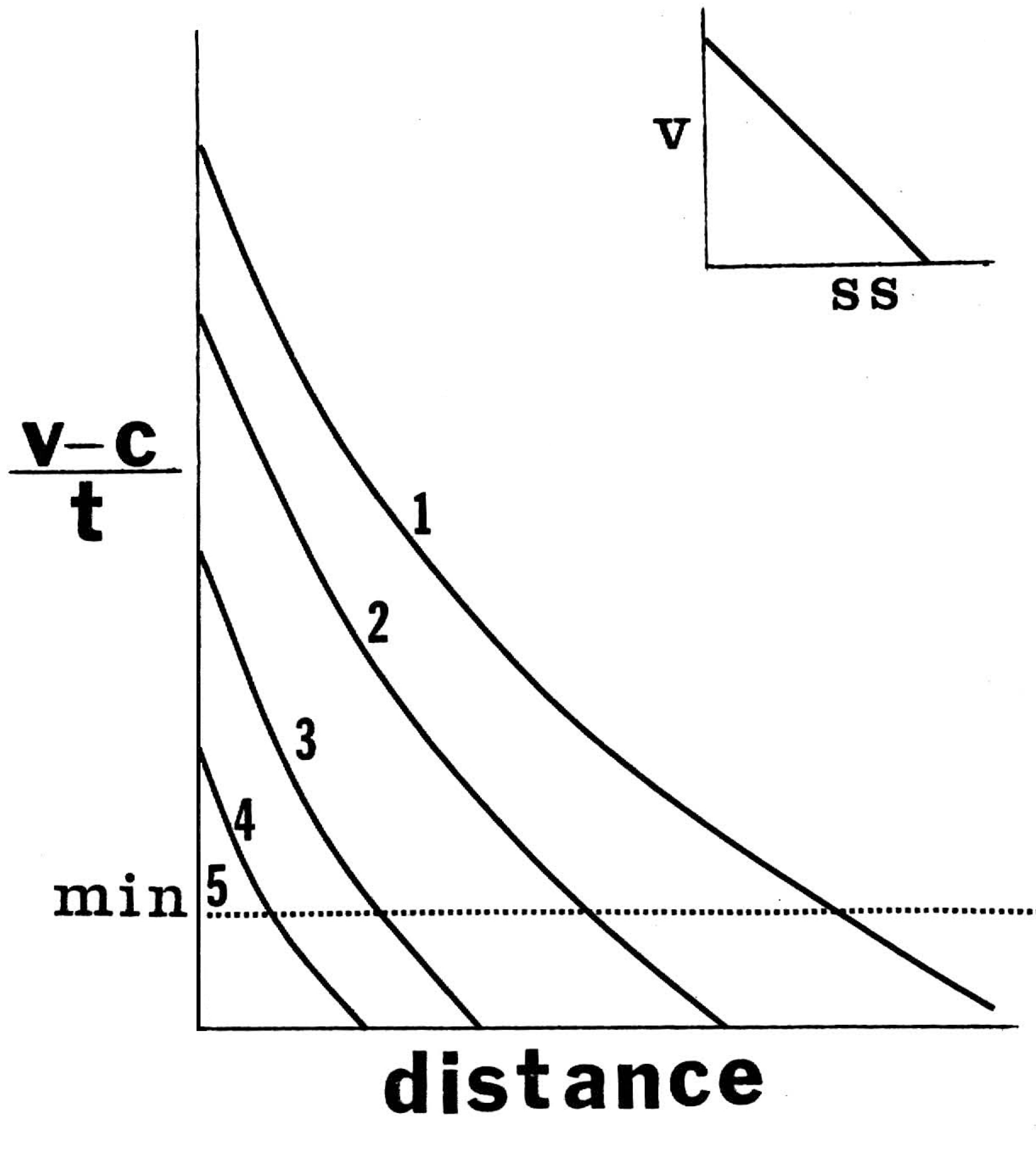
Fig. 8: The distribution of stick sizes from houses sampled in the field.

Fig. 9: The distribution of the number of sticks of each size category chosen at each of the 3 treatment distances. The grey bar represents 5 meters, the open bar represents 10 meters, and the black bar represents 15 meters.


cost
stick size



v
ss
5
1
2
3
4
v–c
t
min
distance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ss
v–c
t
1
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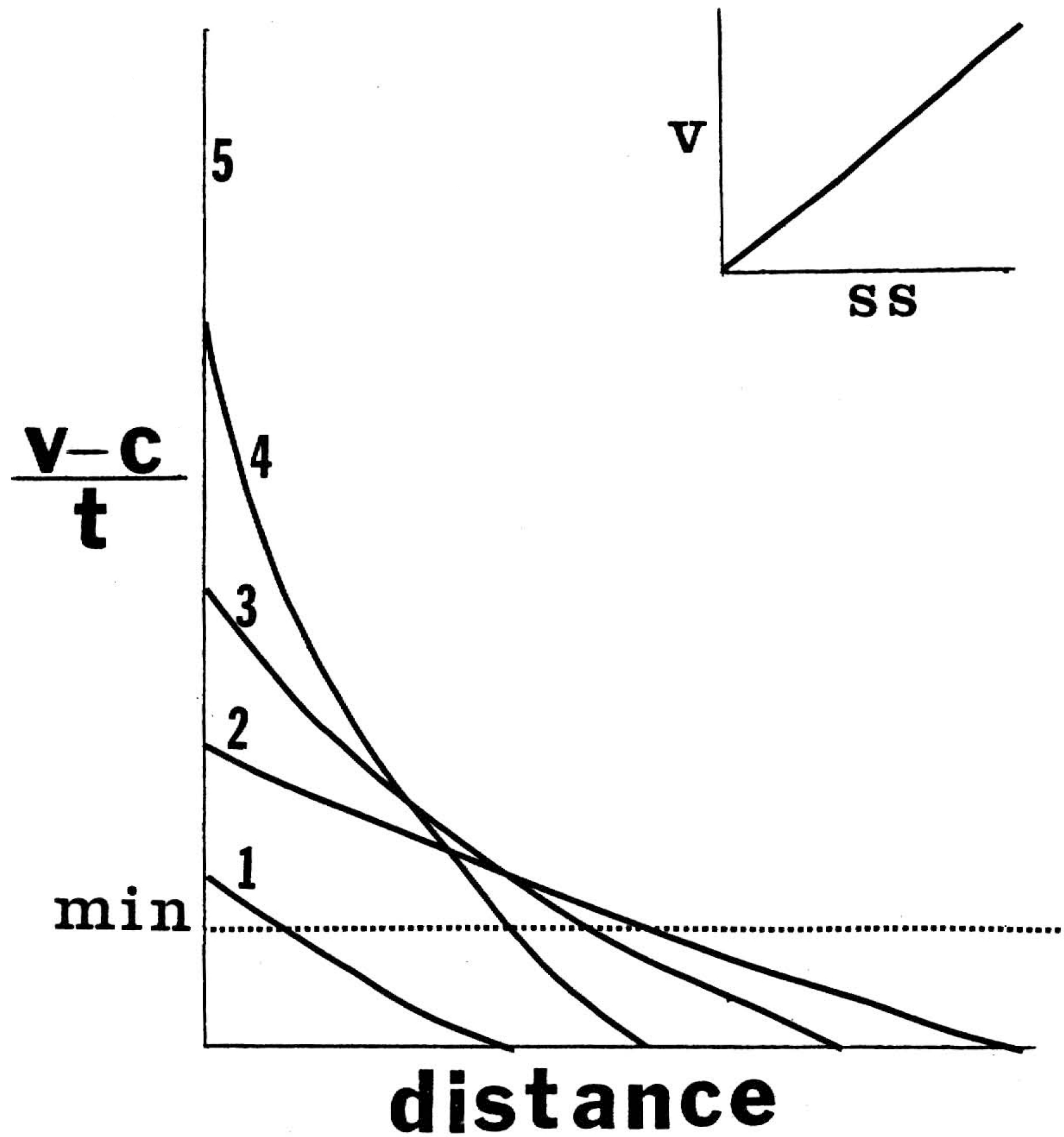
min
distance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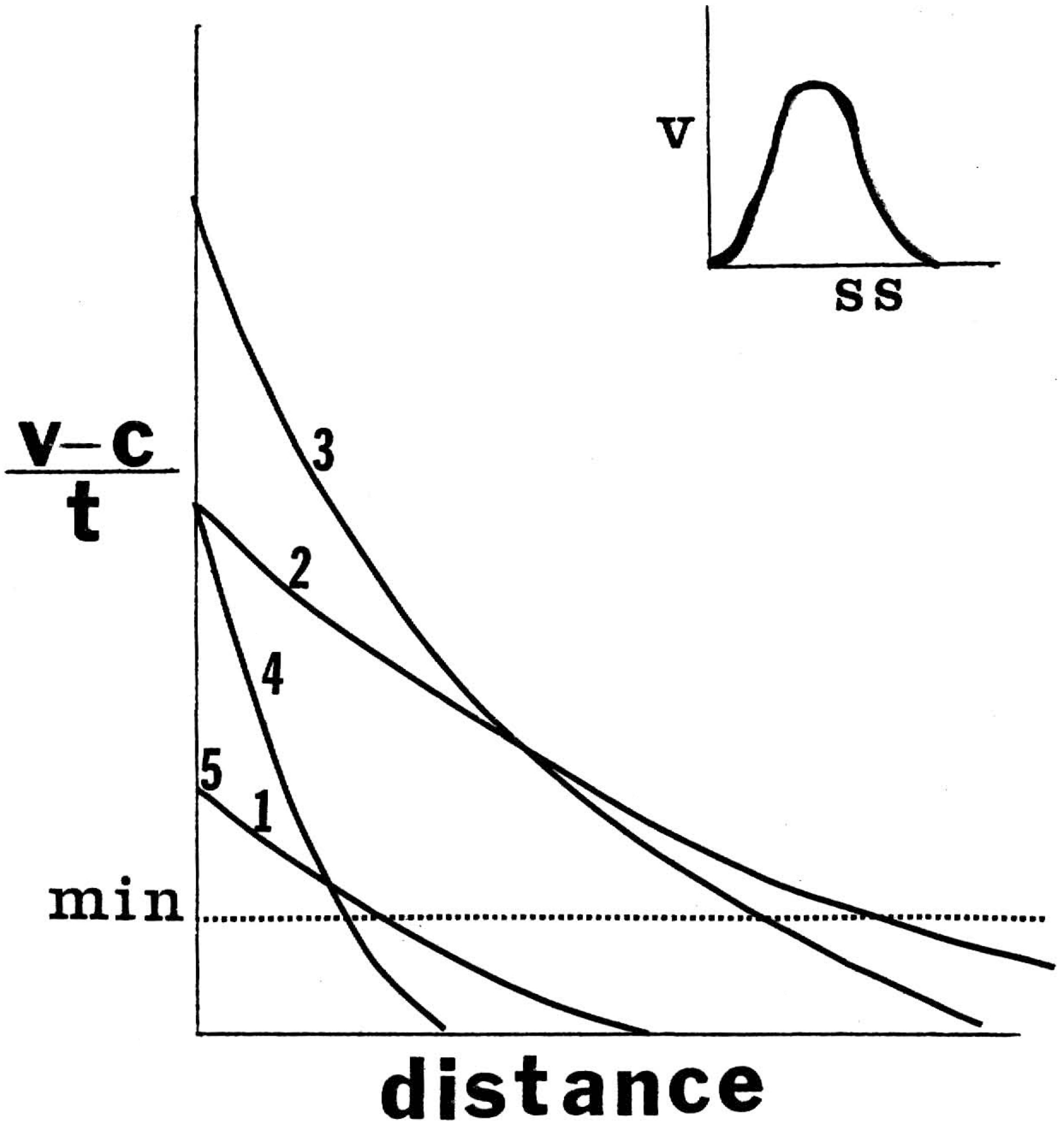
ss
5
4
3
2
1
$\frac{v-c}{t}$
min
distance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5
1
min
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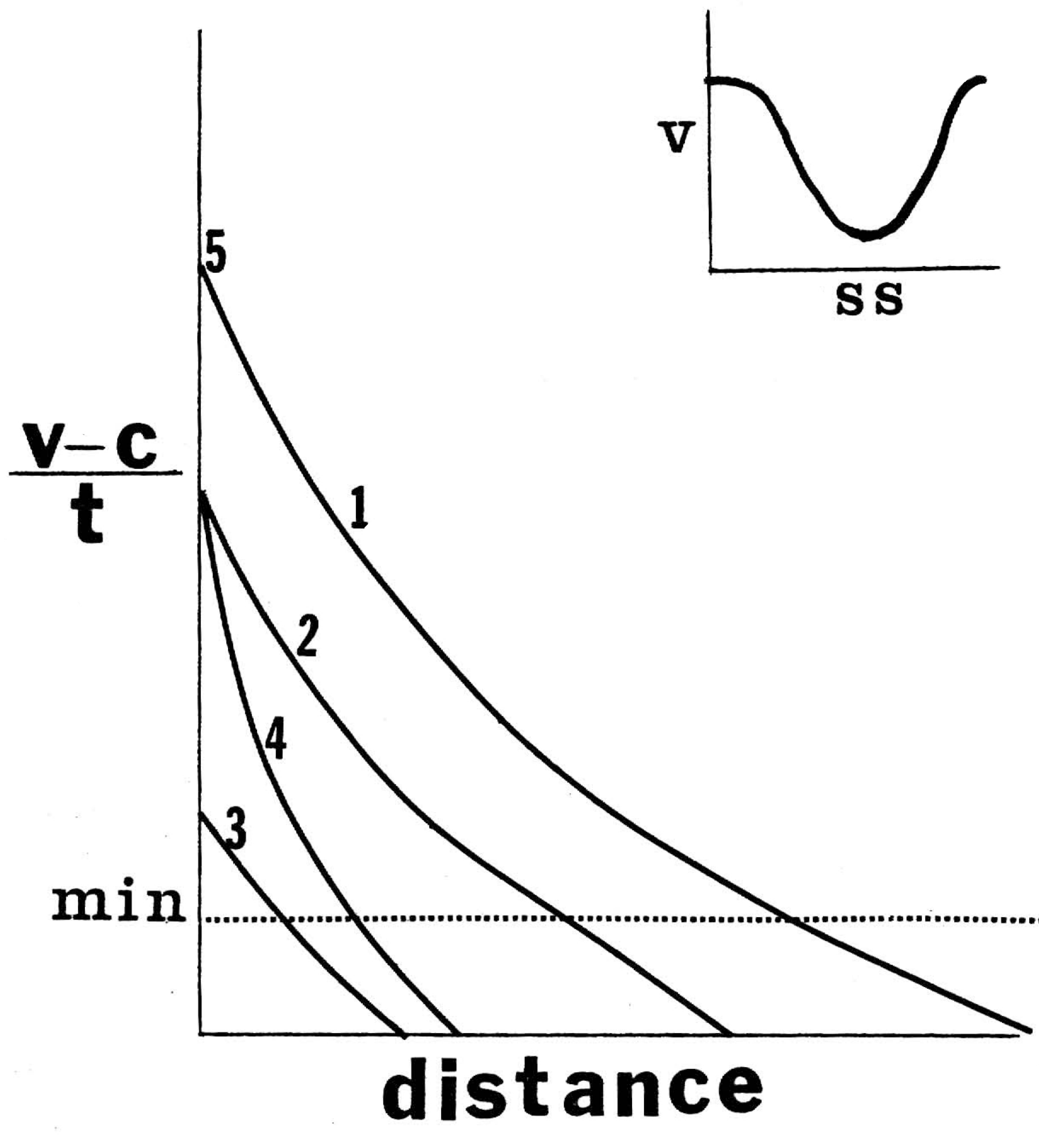
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1
2
4
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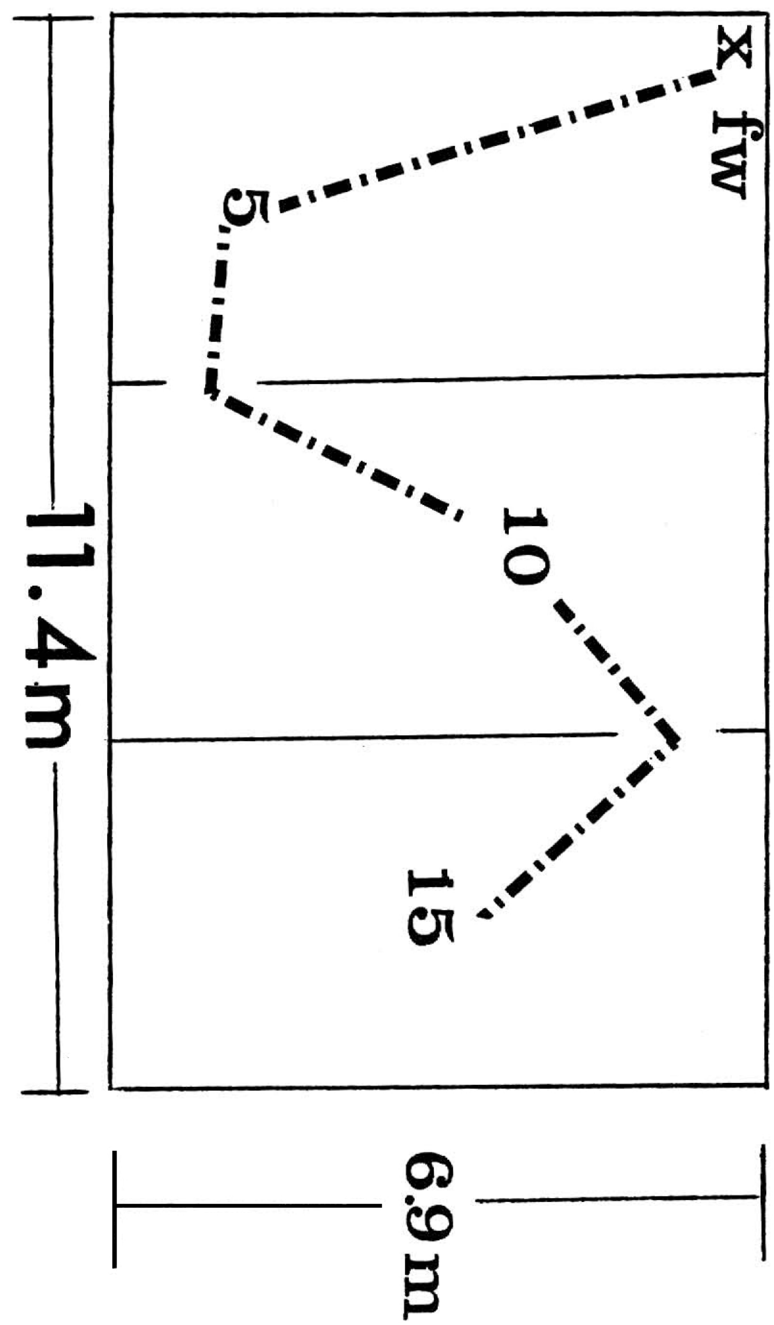
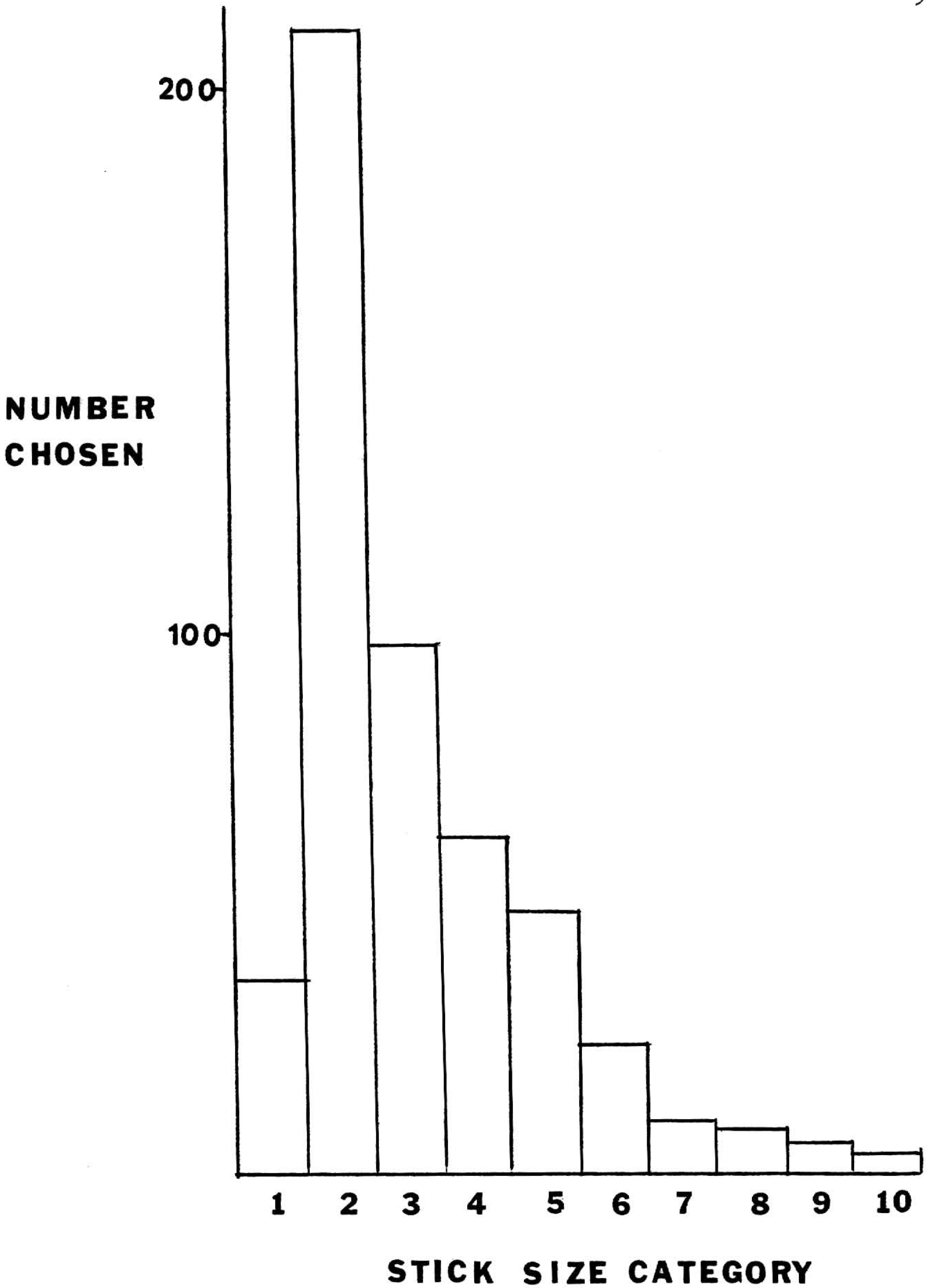
v−c
t
min
distance


x fw
5
10
15
11.4 m
6.9 m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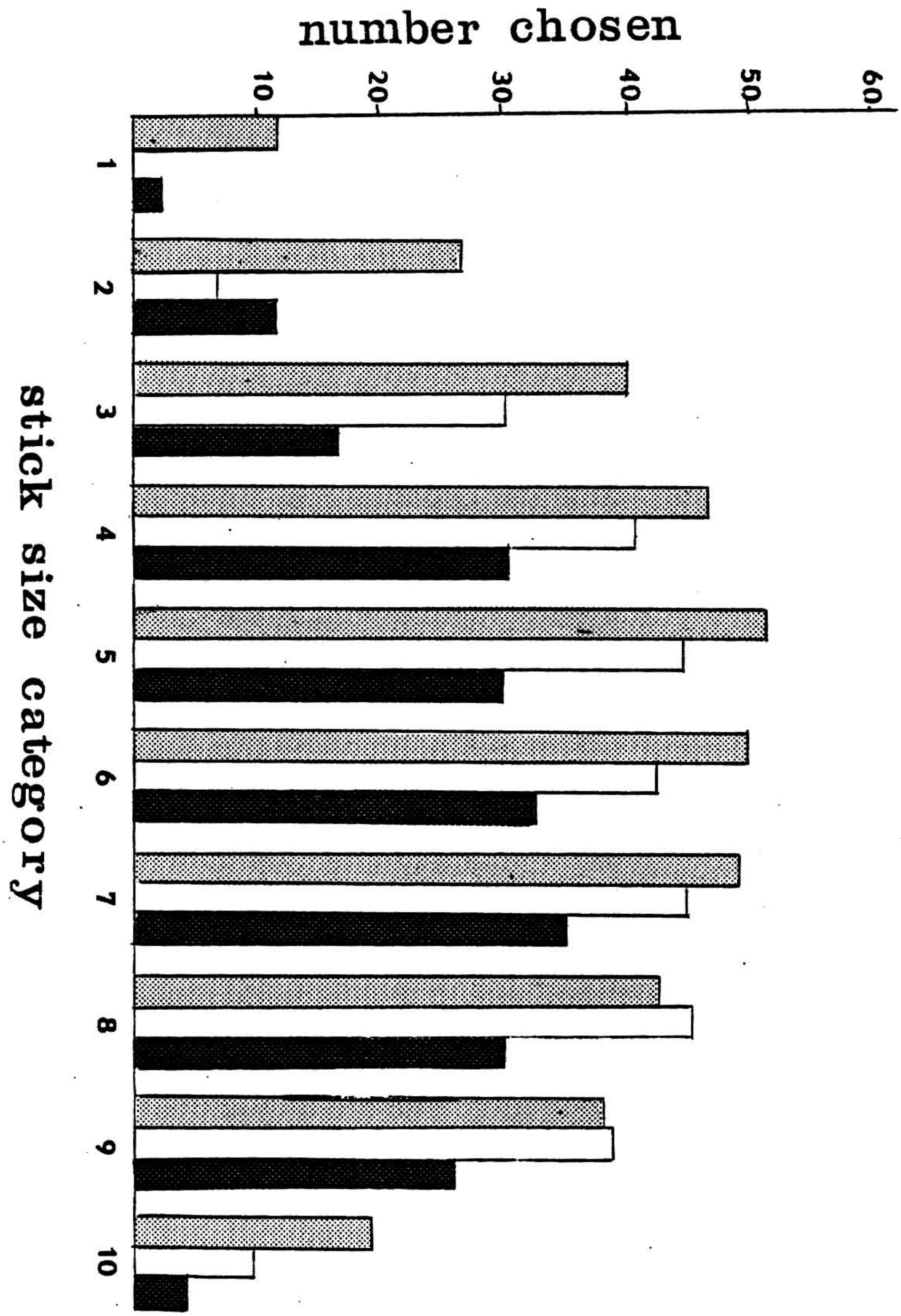
100
NUMBER
CHOSEN
1
2
3
4
5
6
7
8
9
10
STICK SIZE CATEGORY


number chosen
10
20
30
40
50
60
1
2
3
4
5
6
7
8
9
10
stick size category

Appendix

Table 5. The number of sticks chosen each night by each animal used in the experiment.

Replicate 1.

Size category	5 meters		10 meters		15 meters	
	1	2	1	2	1	2
1	0	0	0	0	0	0
2	1	3	1	0	0	0
3	1	4	5	3	3	0
4	2	5	5	5	3	0
5	3	5	5	5	3	1
6	5	5	5	5	2	5
7	3	5	5	5	3	5
8	4	5	5	5	4	3
9	2	5	5	4	2	3
10	2	2	3	1	0	1
Total	23	39	39	33	20	18

Table 5 cont.

Replicate 2.

Size category	5 meters 1	5 meters 2	10 meters 1	10 meters 2	15 meters 1	15 meters 2
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	2	2	1	1	0	0
4	5	1	1	5	0	1
5	5	3	1	5	0	0
6	5	4	2	5	0	3
7	5	2	2	5	0	3
8	5	1	3	5	0	1
9	4	1	1	5	0	1
10	0	0	0	0	0	0
Total	31	14	11	31	0	9

Table 5 cont.

Replicate 3.

Size category	5 meters 1	5 meters 2	10 meters 1	10 meters 2	15 meters 1	15 meters 2
1	0	0	0	0	0	0
2	3	5	0	0	0	0
3	4	5	0	3	0	0
4	5	5	1	4	3	3
5	5	5	2	5	4	5
6	5	5	0	5	5	3
7	5	5	0	5	4	4
8	5	5	0	5	5	3
9	5	4	0	4	2	5
10	5	1	0	1	0	1
Total	42	40	3	32	23	24

Table 5 cont.

Replicate 4.

Size category	5 meters 1	5 meters 2	10 meters 1	10 meters 2	15 meters 1	15 meters 2
1	0	0	0	0	0	0
2	0	0	1	0	0	0
3	0	2	1	0	0	0
4	3	1	0	1	3	1
5	1	5	1	1	0	0
6	1	0	1	0	0	0
7	3	1	2	1	1	0
8	0	0	0	3	0	1
9	2	2	0	1	1	1
10	1	0	0	0	0	0
Total	11	11	6	7	5	3

Table 5. cont.

Replicate 5.

Size category	5 meters 1	5 meters 2	10 meters 1	10 meters 2	15 meters 1	15 meters 2
1	0	4	0	0	0	0
2	0	5	2	0	2	2
3	5	5	5	4	0	5
4	5	5	5	5	2	5
5	5	5	5	5	2	5
6	5	5	5	4	0	5
7	5	5	5	5	1	4
8	3	5	5	5	0	3
9	1	2	4	5	0	1
10	0	0	2	0	0	0
Total	29	41	38	33	7	30

Table 5. cont.

Replicate 6.

Size category	5 meters 1	5 meters 2	10 meters 1	10 meters 2	15 meters 1	15 meters 2
1	5	3	0	0	1	2
2	5	5	2	1	4	4
3	5	5	4	4	3	5
4	5	5	5	4	5	5
5	5	5	5	5	5	5
6	5	5	5	5	5	5
7	5	5	5	5	5	5
8	5	5	5	5	5	5
9	5	5	5	5	5	5
10	4	4	2	0	2	0
Total	49	47	38	34	40	41

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WOODRATS COLLECTING HOUSE BUILDING MATERIALS:
CENTRAL PLACE FORAGING FOR NON-FOOD ITEMS

by

MARK ALAN MCGINLEY

B.A., University of California, Santa Barbara, 1980

AN ABSTRACT OF A MASTER'S THESIS

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requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1982

Abstract

Up to now optimal foraging theory has dealt exclusively with animals foraging for food. The currencies used to measure the benefit of food items, energy and nutrients, are inappropriate measures of the benefit of non-food items collected by animals. This paper proposes that 'value' can be used as a currency for non-food items and presents a procedure for determining the size-value relationship of non-food items. This procedure was used to determine the stick size-value relationship of sticks collected by eastern woodrats.

Eastern woodrats (Neotoma floridana) collect sticks as house building materials. Simulations of profitability ((V-C)/T) vs. distance curves for 5 general stick size-value relationships predict that, regardless of the stick size-value relationship, the number of stick sizes above the minimum profitability value should decrease with increasing distance from the central place. This prediction was supported in a laboratory experiment. The woodrats were also found to forage more selectively (decreased variance) as they collected farther from the house.

Since the woodrats were foraging adaptively, taking only those sticks above the minimum profitability value, it shpuld be possible to use stick size preference to select between the 5 general relationships. It was determined that there is an increasing relationship between stick size and value for woodrats initiating house building. Since it is possible to select between the 5 relationships it should often be possible to use this technique to determine the size-value relationship for any non-food item collected by an animal.