

A MODEL FOR SEED-SCATTERHOARDING BY ANIMALS:  
COEVOLUTION OF FOX SQUIRRELS AND BLACK WALNUTS

by

MARTIN ANDRE STAPANIAN

B.A., Ohio State University, 1974

---

A MASTER'S THESIS

submitted in partial fulfillment of the  
requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1976

Approved by:

  
Major Professor

LD  
2668  
T4  
1976  
S74  
C.2  
Document

TABLE OF CONTENTS

11

	<u>Page</u>
List of Tables .....	iii
List of Figures .....	iv
Acknowledgements .....	v
Abstract .....	vi
INTRODUCTION .....	1
DEVELOPING THE MODEL .....	3
METHODS AND MATERIALS .....	6
I. Burial Experiment .....	6
II. Parent Sapling Measurements .....	8
III. Dispersal Observations .....	10
RESULTS .....	12
I. Burial Experiment .....	12
II. Parent Sapling Measurements .....	12
III. Dispersal Observations .....	12
DISCUSSION .....	14
LITERATURE CITED .....	19

	<u>Page</u>
Table 1: Survival of black walnuts buried in replicate samples at 3 internut distances.....	22
Table 2: Burial strategies of 5 squirrels in the cemetery.....	23

	<u>Page</u>
Fig. 1: Curves of probability of escape and benefit.....	24
Fig. 2: Product of escape and Benefit curves against distance.....	25
Fig. 3: Prediction $r^\theta = r^{360\sqrt{\frac{360}{\theta}}}$ .....	26
Fig. 4: Calculation of $\theta$ .....	27
Fig. 5: Dispersal patterns observed.....	28
Fig. 6: Regression of $\text{Log}_{10} R = \theta$ .....	30

This manuscript is dedicated to Christopher C. Smith, my major professor. Without his help and encouragement this research would not have been possible. Joseph Arruda gave valuable suggestions and help in the field. Arthur Dayton provided help with statistics. Michael Johnson and Stephen Fretwell gave valuable criticisms of the models and manuscript. I thank Captain C. Cole and the Wildlife Conservation Office on the Ft. Riley Military Reservation and the maintenance crew of Sunset Cemetery for their cooperation. I am grateful to Gary Naughton and the Extension Forestry of Kansas State University for providing suggestions and walnuts for preliminary studies. Joseph Kotek, Frederick Lindbeck, Claudia Kale and Thomas Porter helped lay out the grids and prepare walnuts.

## INTRODUCTION

Recent work (Janzen, 1969 and 1971a, C. C. Smith, 1970 and 1975, Elliott, 1974 and Fox, 1974) has shed much light on the coevolution of seed plants and seed predators. Much of this research has been directed towards responses by seed predators to anti-predator strategies of plants.

Animals store seeds for future use by two major patterns: (1) larder-hoarding, or storing seeds in a large cache or a very concentrated area in an animal's home range (Shaw, 1934, Hawbecker, 1940, Eisenberg, 1962 and C. C. Smith, 1968), and (2) scatterhoarding, or burying small caches at dispersed sites in an animal's home range (Brown and Yeager, 1945, Morris, 1962 and Smythe, 1969).

The pattern of seed storage employed by an animal seems to be related to its ability to defend caches against interspecific competitors. The number of competitors for a seed may be related to the hardness of the protective structure surrounding the seed. Tamiasciurus has no interspecific competitors for its most abundant food, conifer seeds, because no other community member has the ability to cut the cones and extract the seeds from under the scales. These squirrels store cones in a very large central larder (C. C. Smith, 1968). Squirrels of the genus Sciurus, however, compete with several mammals (Goodrum et. al., 1971) and birds (Hay, 1887 and Kilham, 1958) for relatively thin-shelled acorns. The number of vertebrate competitors that fox (S. niger) and gray squirrels (S. carolinensis) have for thick shelled black walnuts (Juglans nigra) and hickory nuts (Carya spp.) is only one or none (USDA, 1965). Mixed caching strategies apparently will not work for reasons explained later.

The inability to defend caches may stem from (1) a marked size difference between the scatterhoarder and competitors and/or (2) a difference in activity time between the scatterhoarder and competitor species. Desert rodents are all nocturnal and larderhoard (Shaw, 1934, Hawbecker, 1940, Eisenberg, 1962 and Smigel and Rosensweig, 1974). Shaw (1934) and Eisenberg (1962) described

defense of larders by individuals against inter- and intraspecific competitors. Several nocturnal species compete for acorns with gray and fox squirrels, which are diurnal (Goodrum et. al., 1971). Moreover, some have a larger body size than squirrels (i.e., white-tail deer and raccoons). Indeed, Sciurus is unable to defend caches against competitors, and is a scatterhoarder. Several tropical rodents (Morris, 1962 and Smythe, 1969) along with Peromyscus leucopus and Clethrionomys gapperi (Abbott and Quink, 1970) have been found to be unable to effectively defend caches against interspecific competitors and scatterhoard seeds. When given nest boxes that could exclude larger competitors, P. leucopus larderhoarded seeds in the nest box (Howard and Evans, 1961).

Scatterhoarding not only provides a future food source for an animal, it is also a means of seed dispersal for many plants. Stebbins (1971) regards animal dispersal of seeds as more effective than wind dispersal. If a scatterhoarder is unable to eat its entire store of seeds, it aids in the dispersal of the food species (Smythe, 1969). The effect of insect predation on seeds is also reduced by scatterhoarding (Janzen, 1969).

Certain foresters have suggested that nearly all walnut and hickory trees originated from nuts planted by squirrels (Cornwell and Mosby, 1966 and Svirdenko, 1971). Dispersal from the parent tree is important in walnuts because of its intolerance of shade and toxic substances it produces in its root zone (USDA, 1965).

In considering seed scatterhoarding by animals, then, it is important to understand the benefit to both the seed food species and the scatterhoarding animal(s). The purpose of this study is to model seed-scatterhoarding strategies by animals. The model and one prediction of the model are tested with fox squirrels dispersing black walnut seeds.

## DEVELOPING THE MODEL

The model begins with a dichotomy: If the seed storer can defend its caches, it is a larderhoarder. If it cannot, its burial strategy can be considered for the model below.

The size of a cache is often equal to the number of seeds an animal carries to a burial site (Hay, 1887, Balda and Bateman, 1971, Eisenberg, 1962, Reller, 1972 and pers. obs.). In the case of the fox squirrel this would be equal to one acorn or one black walnut.

It may require more energy expenditure by an animal to bury caches farther apart, simply because more time must be spent in locomotion. The maximum energetic benefit a scatterhoarder can receive from a buried cache is the energy of the cache ( $E_{\text{cache}}$ ) minus the energy cost of burying and processing the cache ( $B_0$ ), which is assumed to be constant for all intercache distances. The decrease in benefit to the animal, then, is linearly proportional to distance between caches ( $d$ ) and has a slope  $B_1$  (Fig. 1).  $B_1$  is simply the energy cost of transporting a cache a given distance. Benefit can be represented by the simple equation:  $\text{Benefit} = (E_{\text{cache}} - B_0) - B_1 d$ .

Since the scatterhoarder cannot successfully defend its caches against interspecific competitors, the energy benefit of a buried cache cannot be reaped if the cache does not escape predation by naive competitors. With increasing intercache distance one would expect a sigmoidal increase in probability ( $P$ ) of caches surviving naive discovery by competitors (Fig. 1). A similar relationship was found in carrion eating crows (Croze, 1970). Upon finding a cache, a competitor will form a search image for more caches. The strength of this species-specific search image is the amount of searching time a competitor will spend and distance it will cover searching for more of a particular food once it has been found. The reward (energy of the cache) will determine the search image strength. If caches are buried very close together (Fig. 1,A), they have a small chance of surviving naive predation, and

a small increase in intercache distance will not markedly increase P. (Fig. 1, B). Caches buried at distances beyond the range of a competitor's search image will have a P value of nearly 1.0, and even large increases in d will result in only small increases in P (Fig. 1,C). This probability curve can be derived by direct measurement and will be represented by the equation

$$P = B_2(1 - e^{-B_3 d}). \quad B_2 \text{ and } B_3 \text{ are species specific curve constants.}$$

The optimal scatterhoarding strategy would be to maximize the product of the P and Benefit curves (Fig. 1) as a function of intercache distance. This is shown in Fig. 2 to yield a nearly bell-shaped curve with an intermediate intercache distance being optimum.

Three predictions follow from this model:

1. One prediction is represented in Fig. 3. Let  $\theta$  represent the arc surrounding a source of seeds containing habitat suitable for seed burial by animals. If optimal intercache distance is maintained by members of a scatterhoarding population, the average cache should be taken R units from the source if  $\theta = 360^\circ$ . If  $\theta$  is halved ( $=180^\circ$ ), then R must increase by a factor of  $\sqrt{2}$  in order to maintain that same density of caches. An example of  $\theta = 180^\circ$  may be a seed source next to a large lake. If  $\theta = 120^\circ$  (e.g., seed source on a riverbank where the river makes a  $120^\circ$  bend), the average cache should be  $R\sqrt{3}$  units from the source in order to maintain that constant density. Thus,  $R^\theta = R^{360^\circ} \sqrt{\frac{360}{\theta}}$  for a given number of caches (seeds).

2. The optimal intercache distance should be less for low-energy caches than for high-energy caches. The Benefit line in Fig. 1 would be lowered ( $E_{\text{cache}}$  would be less) and the P curve would be shifted toward the origin, as the strength of the competitor's search image would be less for a smaller reward.

3. If constant intercache distance is maintained, the average cache should be taken farther from the source when more seeds are available. For any

taken  $R\sqrt{2}$  units farther from the source. If  $N$  is tripled,  $R$  should increase by a factor of  $\sqrt{3}$  in order to maintain constant intercache distance. If  $D$  (=density of buried caches) is maintained, then  $R = \sqrt{\frac{N}{\pi D} \frac{360}{\theta}}$ .  $D$  is in terms of caches per unit area ( $=\frac{N}{\pi R^2}$ ). Cache size is assumed constant. A tree which exhibits mast yearing and has its seeds dispersed by scatterhoarders would have its seeds dispersed farther during high mast years if this strategy is employed.

I will now provide a test for the model and the first prediction.

## METHODS AND MATERIALS

### I. Burial experiment:

The field sites for the burial experiment were located in 2 woodlots on the Ft. Riley Military Reservation .8 km. south of Keats, Riley County, Kansas. Five study grids were located in a woodlot on the west bank of Wildcat Creek. Along the western edge of this woodlot were a milo field and a pasture which was burned every other year. The sixth study grid was in a woodlot on the opposite bank of Wildcat Creek. A milo field was on the eastern side of this woodlot. The vegetation of these plain woodlands of the Kansas Flint Hills is described by Barker (1969). Squirrels and their large nocturnal competitors (white-tail deer and raccoons) were seen on the area.

Survival of black walnuts buried at different distances apart was studied. On 18 October 1975 6 grids of 64 burial sites were set out. The burial sites were arranged in columns and rows 8 ft. apart in 2 grids, 15 ft. apart in 2 grids and 30 ft. apart in 2 grids. Five of these grids were arranged in 8 column x 8 row fashion. The grid on the eastern bank of Wildcat Creek, due to the long and narrow shape of the woodlot, had 4 column x 15 rows and 1 column x 4 rows. Three of the 4 productive walnut trees in the woodlots were located in the grid on the western bank of Wildcat Creek where burial sites were 30 ft. apart.

A strip of masking tape was fastened around the circumference of the trunk or convenient branch at breast height of the 2 trees nearest to most burial sites. The burial site number (1-64 in each grid) was inked on the two tapes so that two identical numbers faced each other. When no trees were near a burial site, two sticks were placed in the ground approximately 1 m. from the burial site on opposite sides, and the site numbers were labeled as above at the tips of the sticks. When only one tree was near a burial site, it was taped at breast height, and the burial site number with 2 arrows pointing downward were marked on the tape. All metal that could be detected with a

Sears Jetco metal finder was removed from the burial sites.

In preliminary work on the area, burial sites were marked by tongue depressors stuck into the ground approximately .3 m. from each buried walnut. The squirrels apparently received visual cues for buried walnuts from the tongue depressors, as they removed 790 out of 800 buried walnuts within one week. To eliminate such visual cues in the study, masking tape was fastened at breast height around 159 tree trunks ("bogus trees") outside of the grids in both woodlots.

Walnuts collected in the Manhattan, Kansas area were husked and covered on one half with aluminum foil. A strip of Scotch tape was then attached along the outer perimeter of the foil-walnut interface. Only walnuts unfested by insect larvae were used. Squirrels showed no preference between walnuts wrapped in aluminum and "untreated" walnuts in preliminary work on the study site.

On 25 October 1975 one prepared walnut was buried in each of the 384 burial sites. Walnuts were buried foil side down, 2-4 cm deep to simulate actual squirrel efforts as described by Cahalane (1942) and Allen (1943). The nuts were buried halfway between two trees (or two sticks) bearing the same numbers. Where solitary trees were used to identify burial site locations, walnuts were buried directly below the corresponding number and arrows. Wads of Scotch tape were similarly buried at 145 locations between the "bogus" trees to test for possible olfactory cues squirrels may receive from tape on the walnuts. None of these wads of tape were disturbed by squirrels.

Grids were checked daily for nut predation by searching the ground at each marked burial site with the metal finder. When the presence of foil was not detected at a burial site, that walnut was recorded as "taken". Preliminary work showed this to be quite an effective method, as the instrument was well able to detect smaller bits of metal buried greater than 7 cm. below

the ground. It also appears that the squirrels remove the foil and tape before taking a nut away. These materials were found above ground at all burial sites where predation occurred in preliminary work, and in all but two cases during the actual test.

After each daily check, the numbers of nuts in each grid surviving predation (i.e., 64 - number "taken" up to that point) was recorded. A summation of these daily counts, in nut-day units (1 nut-day = 1 nut surviving 1 day), was made when the experiment was terminated after 31 days (Table 1). One-way analysis of variance (Snedecor and Cochran, 1967) was used to compare survival within and between the 3 internut distances used for burial.

## II. Parent-sapling measurements:

Between 1 June and 9 August 1975 20 isolated, mature walnut-producing trees were found in Riley and Pottawattomie Counties, Kansas. A walnut tree was considered mature if it had a breast height circumference (BHC) greater than 0.5 m. A tree was studied only if (1) it was at least 125 m. from the nearest mature walnut tree and/or (2) it was at an end of linearly positioned mature walnut trees. When trees were multitrunked at breast height, BHC was calculated as that circumference giving an area equal to the summation of the cross-sectional areas of the trunks at breast height.

From maps made of the locations of the 20 parent trees,  $\theta$  (the arc surrounding the parent containing habitat suitable for nut burial) was calculated for each parent tree. Rivers, lakes, rocky cliffs and large, open fields (Allen, 1943) were considered habitat unavailable to squirrels for walnut dispersal. If any such "barrier" was located less than 20 m. from a tree's canopy edge,  $\theta$  was calculated in the following manner (Fig. 4): Along each side of the woodlot bordering a barrier, a line 103 m. long was drawn parallel to the parent so that the perpendicular from the parent bisected this line. I used 103 m. because that was the farthest distance a sapling occurred

from a parent in this study. Each half of the bisected line(s) was again bisected, and lines connecting these bisection points to the parent were drawn.  $\theta$  was then the difference between 360 and the sum of the angles formed by the parent and these points.

Distances and compass directions saplings occurred from the parents were measured. Only saplings beyond 5 m. from the edge of the parents' canopies were used in data analysis. Five meters was estimated as a fair distance a walnut could be dispersed by gravity and rolling. According to USDA (1965), walnuts are dispersed to a limited extent by gravity. For reasons discussed later, it would be disadvantageous to a squirrel to bury nuts under or near the canopy of the source of nuts.

To eliminate as much overlap of parents' seedling shadows as possible, measurements were taken only for saplings not between 2 walnut parent trees when the measured producer was at an end of linearly positioned mature walnut trees.  $\theta$ , however, included all habitat suitable for burial. Linearly positioned trees generally had a small  $\theta$  and were occasionally close together (<25 m. apart), so some saplings measured from end trees may have arisen from seeds of another producer. Thus, R values (average trunk-sapling distance for saplings  $\geq$  5 m. from the canopy edge) may be shorter than that distance the squirrel actually disperses a walnut. Because the model predicts large R values for small  $\theta$ , such measurements would give weaker support for the prediction.

Again, considering only saplings greater than or equal to 5 m. beyond a parent's canopy edge, I looked at several possible relationships between the average trunk-sapling distance (R) and  $\theta$  for each parent. For each producer the R-value and its  $\delta^2$  were calculated. Multiple regressions of the models  $R = \theta + \text{BHC of parent}$  and  $R = \theta + \theta^2$  were run. Single regressions of the models (1)  $R = \theta^2$ , (2)  $R = \log_{10} \theta$ , (3)  $\log_{10} R = \theta$  and (4)  $\log_{10} R = \log_{10} \theta$  were

also computed. In these regressions, R is the dependent variable.

### III. Dispersal Observations:

The site for dispersal observations was the southeast quarter of Sunset Cemetery in Manhattan, Riley County, Kansas. The Cemetery was fairly open, the grass was mown approximately every 10 days during the study by the maintenance crew. Black walnut and Burr oak (Quercus macrocarpa) lined the 4 edges of the cemetery. 1975 was a very high mast year for both species in the area. A casual walk through the entire cemetery resulted in the sighting of 20 squirrels. The squirrels in the cemetery were semi-tame.

From 19 August to 12 September 1975, 6 squirrels were observed in Sunset Cemetery so that they could be identified from the rest of the local squirrel population. Poor trap success in the area prompted use of this identification method. Some individual squirrel characteristics were: (1) Squirrel No. 1 was trapped and hair on the dorsal side of the right shoulder was slipped with scissors, leaving an unmistakable bare spot; (2) No. 2 was a female with hair conspicuously missing from the tail; (3) No. 3 was a very large female having slightly mottled coloration; (4) No. 4 was a very large, very active dominant male. He repeatedly chased away other squirrels and often did acrobatics on the ground; (5) No. 5 was a very small male, possibly born that spring. His tail seemed longer and narrower than the rest; (6) No. 6 had distinct black markings on the muzzle, much darker than any other squirrel. Number 6 concentrated much of his activity as near to No. 4 as the latter would allow. Prior to burial observations the squirrels were often seen eating black walnuts from trees on the cemetery grounds. I removed as many walnuts as possible from these trees to increase the squirrels' interest in the nuts I supplied.

From a common central point (CCP) I sighted the 8 multiples of  $45^{\circ}$  compass readings and placed marker flags at 5 m. intervals along these sighted lines (Fig. 5). A tongue depressor was set into the ground next to each

marker flag. At the CCP I piled 375 black walnuts and observed squirrels eating and burying the nuts. Locations of each squirrel's burial sites, along with the numerical order in which each squirrel buried a nut, were charted on a map made of the site (Fig. 5). Squirrels were identified with a pair of 7x35 binoculars. Walnuts were removed from the CCP and flags were removed from the sighted lines after each observation session. Before the walnuts were replaced at the CCP, the flags were replaced next to the tongue depressors at the beginning of each session. Squirrels were observed from 21 September to 24 October 1975 (160 total hours). If the identity of a nut-burying squirrel was unknown or undetectable a "?" was logged on the map at that location.

For each nut buried, the distance to the nearest nut buried by the same squirrel was determined and used in the data analysis.

## RESULTS

### I. Burial experiment:

The survival (S) of walnuts buried in replicate samples at 3 different densities is shown in Table 1. Any nuts removed from a grid were considered lost to an hypothetical squirrel employing that burial strategy. As nuts were buried farther apart, a significant ( $p < .05$ ) increase in survival from predation was seen over the 31-day test (Table 1). Percent of walnuts surviving predation in a grid of 64 ranged from 87.5 (56 survivors) to 4.7 (3 survivors).

There was little variation in this survey within grids of the same inter-cache distance, with a single exception. The 2 grids at intercache distance = 30 ft. had 56 and 29 survivors respectively. The higher survival occurred in the isolated grid on the east side of Wildcat Creek. Three walnut-producing trees were found in the grid with 29 survivors; perhaps influencing squirrel foraging activity.

### II. Parent-sapling measurements:

A fairly high correlation ( $r^2 = .48$ ) between  $\log_{10}R$  and  $\theta$  was found (Fig. 6). The following models yielded lower  $r^2$  coefficients: (1)  $R = \theta$  ( $r^2 = .30$ ), (2)  $R^2 = \theta + \theta^2$  ( $r^2 = .34$ ), (3)  $R = \log_{10}\theta$  ( $r^2 = .36$ ), (4)  $\log_{10}R = \log_{10}\theta$  ( $r^2 = .46$ ). BHC of the 20 parents explained an insignificant ( $r^2 = .04$ ) amount of variation. I found no obvious biological explanation for the correlation differences for the log regressions. Because  $R$  and  $\theta$  were expected to have a curvilinear regression, however, it was expected that the log regressions would have higher correlations than the untransformed regressions. BHC of the 20 parents had an insignificant ( $r^2 = .03$ ) correlation with  $\theta$ .

The F-test value (16.3) of the analysis of variance for  $\log_{10}R = \theta$  was highly significant ( $p < .01$ ).

### III. Dispersal Observations:

No buried nuts were seen removed and eaten or relocated by squirrels

during the study.

Clearly, there is more variation among the  $\delta^2$  of internut distance within squirrels than among mean distances between squirrels (Table 2). A Bartlett's test for equality of variances revealed a significant ( $p < .05$ ) inequality of these within squirrel variances. Thus, use of analysis of variance and other parametric tests (e.g., Dunnett's least square difference) of equality of means is invalid. A test for equality of means for heterogeneous variances (Sokal and Rohlf, 1969) revealed no significant difference between these mean distances.

Interestingly, the grand mean of intercache distances between squirrels was 9.2 m. (32.7 ft.), a distance which approximates that yielding the highest survival in the burial experiment (Table 1).

Squirrel No. 1 buried only one walnut and died. Squirrel No. 4 buried the most (28) during the study period. Average internut distance ranged from 7.8 m. to 16.0 m. (Table 2).

The average walnut was taken 38.1 m. from the CCP and no walnut was buried less than 15 m. from the CCP (Fig. 5). With few exceptions, the squirrels seemed to bury walnuts in a more or less exclusive area of their home ranges.

## DISCUSSION

The type of hoarding is based on a continuum of intercache distance. There is no sharp distinction between scatterhoarding and larderhoarding. To determine where on the continuum a particular dispersal system lies, it is necessary to know intercache distances of individuals in a population of seed storers.

Although the regression for  $\log_{10} R = \theta$  was significant, much variation was still unaccounted for. As mentioned,  $R = \frac{\sqrt{N}}{\pi D} \frac{360}{\theta}$  and some of the variation in the above regression might well be explained if  $N$  could be measured for the 20 parent trees. Measuring the number of saplings is not indicative of a season's nut production, as many parents had different ages of saplings (measured by BHC of saplings). It was thought that a correlation between parent BHC and  $R$  should exist. An older producer, it was reasoned, makes more nuts than a younger one. Findings by USDA (1965) and Naughton (1970), however, seem to indicate that crop size is not directly proportional to age of parent. The most productive years for black walnut are between the ages of 20 and 35 years (Naughton, 1970). The resulting low correlation between BHC of parent and  $r$  seem to support this conclusion. To test the prediction  $\Delta R = \frac{\sqrt{\Delta N}}{\pi D}$  for a given  $\theta$ , populations of squirrels could be given different sized mast crops and then observed burying the nuts. Animal-scattered tree species exhibiting mast yearing should have seeds dispersed farther in high mast years than in low mast years as the number of nuts ( $N$ ) is increased in the former case.

The number of nuts at the CCP may have been greater than that normally available to squirrels for burial in autumn. A period of increased food consumption and lipogenesis occurs in late summer and early fall, a time when walnuts are eaten in large quantities and a large part of a mast crop may be eaten before it is dispersed (Short and Duke, 1971 and pers. obs.). My observations of nut burial in the cemetery occurred after the main period of lipogenesis, which may help explain some of the difference between the  $R$

value for the cemetery (38.1 m.) and for the 2 parents where  $\theta = 360^\circ$  (15.5 and 25.5 m.). The openness of the cemetery may also have added distance to the R value. The burial observations, then may have simulated those of a high mast year.

It is expected that tropical trees having mast every 3-4 years have wind-dispersed seeds (Janzen, 1974). Boreal forests show this same trend (C. C. Smith, 1970 and Mattson, 1971). Temperate hardwoods seem to be exceptional since several of those exhibiting mast yearing have their seeds dispersed by scatterhoarding animals. Individual oaks seldom bear heavy seed crops in consecutive years (Downs, 1944) and black walnuts produce only about 2 large crops every 5 years (Brinkman, 1957).

One important advantage of mast yearing is to reduce the number of seed predators. If a seed producer relies on an animal seed predator for dispersing its seeds, having long intermast periods would be maladaptive. Holding off of mast by 1 or 2 years by animal dispersed plant species may be adaptive for reducing numbers of insect predators and parasites of seeds so that as many seeds as possible escape predation. Janzen (1971a and 1974) observed mast year intervals to be shorter for plants which have their seeds dispersed by animals than by wind.

For these reasons it would be expected that long intermast periods in wind-dispersed species would select for extended diapause in insects which prey on and parasitize these seeds. Support for this prediction was shown by Keen (1958) for western conifers and hardwoods and from Michelbacher and Ortega (1958) and Johnson (1969). By varying intermast length, seed trees can avoid predation by insect species adapted to a set diapause period.

As mentioned, fox squirrels have several vertebrate competitors against which it cannot defend acorn caches, but few or no competitors for black walnuts and hickory nuts. Two questions immediately arise: (1) Why don't

the squirrels scatterhoard acorns and larderhoard walnuts and hickory nuts, and (2) since acorns are lower in caloric reward to the squirrel (Smith and Follmer, 1972) than walnuts and hickory nuts, why don't the squirrels ignore acorns and larderhoard walnuts and hickory nuts when all foods are abundant? The first question is easily answered. If an animal scatterhoards one type of seed and larderhoards the other, it cannot effectively defend its larder against conspecifics when looking for its scattered hoard. A strategy combining scatterhoarding and larderhoarding by an individual would thus be an energy waste. As for the second question, Smith and Follmer (1972) stated that both acorns and walnuts are needed by fox and gray squirrels during times of low food abundance. Data by Allen (1943), Brown and Yeager (1945) and Moore (1957) indicate that both types of food are used heavily from late fall through spring. The high energetic content per gram of walnuts and hickory nuts are especially useful during mating and active periods when a large volume of food in the stomach would be undesirable. Acorns are eaten more rapidly, thus reducing exposure time during inclement weather. The added weight in the stomach from several acorns would not be a hindrance in the nest (Smith and Follmer, 1972). The walnut's thick shell may be adaptive by "forcing" squirrels to use alternative foods during cold weather (thus delaying predation may enable more walnuts to germinate later) as well as serving as protection from insect predation and parasitism.

To budget for losses to competitors, a seed storer should bury more seeds than necessary to satisfy its energy requirement for periods of food shortage. Here abiotic factors (mainly weather) may strongly influence how many buried seeds will germinate. From Kleiber's (1961) formula, a 0.75 kg. squirrel will expend about 5004 kcal (basal) in a 90-day period (about the length of a winter). A walnut contains about 12.7 kcal of food usable to the squirrel (Smith and Follmer, 1972), so this squirrel requires the energy

from about 394 walnut kernels to satisfy just basal metabolic requirements for a 90-day period. According to Seton (1928), fox squirrels are easily capable of scatterhoarding this many black walnuts. These figures are a gross estimate, as metabolism decreases in late autumn and winter (following the period of lipogenesis) and food consumption rates gradually decrease until spring (Short and Duke, 1971). Because periods of food scarcity may be of unpredictable lengths in different habitats (M. C. Smith, 1968), it may be advantageous for scatterhoarders to store as much food as possible.

As mentioned, no walnuts were buried in the cemetery less than 15 m. from the CCP. It may be to a squirrel's advantage not to bury nuts under or near the mast tree's canopy. Seed predators are "density-responsive" in that predatory search may decrease with decreasing density of seeds (Janzen, 1974). The highest seed density often occurs at the source. Dispersal may serve as a means for lowering olfactory cues for seed predators (Janzen, 1969 and Wilson and Janzen, 1972). Those seeds which germinate under or near the canopy of an isolated parent may arise from seeds undetected or rejected by squirrels. Cahalane (1942) found that squirrels recovered 99% of nuts they had buried. Dice (1927) and Seton (1928) stated only a fraction are recovered. Dispersal by scatterhoarding, then is beneficial to both the plant and animal disperser.

The total weight of seed embryo, endosperm and protective structures is of great importance when considering dispersal mechanisms. Clearly, heavy nuts such as black walnuts and acorns cannot be effectively wind-dispersed. Embryo and endosperm size are controlled primarily by abiotic factors (Salisbury, 1942 and Baker, 1972) and have a secondary effect on the distribution of reproductive energy into antipredator defenses (Salisbury, 1942). Seed predators, then, exert selective pressures for these defense mechanisms. Because additional energy put into seed protection will result in fewer number

of seeds produced per season, there is an optimization of seed size and numbers of seeds a parent could produce to maximize individual fitness (Smith and Fretwell, 1974).

There was much more variation within each squirrels burial strategy than between the mean internut distances maintained by the squirrels (Table 3). By varying intercache distances about a mean optimum distance, scatterhoarders may prevent competitors from getting a search image for regularly spaced caches. Maintaining an overall optimum intercache distance in a more or less exclusive part of a scatterhoarder's home range, as the squirrels in the cemetery seemed to do (Fig. 5), would reduce loss of caches to naive competitors.

The results suggest existence of an optimum intercache distance that maximizes net energy benefit to a scatterhoarder.

# LITERATURE CITED

- Abbott, H. G. and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. *Ecol.* 51(2): 271-278.
- Allen, D. L. 1943. Michigan fox squirrel management. Game Div. Publ. Dept. Conserv., Lansing, Mich. No. 100. p 1-404.
- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecol.* 53(6): 997-1110.
- Balda, R. P. and G. C. Bateman. 1971. Flocking and annual cycle of the Pinon jay Gymnorhinus cyanocephalus. *Condor* 73: 387-302.
- Barker, W. T. 1969. The flora of the Kansas Flint Hills. Univ. Kans. Sci. Bull. 48(14): 525-584.
- Brinkman, K. A. 1957. Silvical characteristics of black walnut. Cent. States Forest. Expt. Sta. Misc. Release 22. 15 p.
- Brown, L. G. and L. E. Yeager. 1945. Fox squirrels and gray squirrels in Illinois. Ill. Natur. Hist. Surv. Bull. 23: 449-536.
- Calahane, V. H. 1942. Caching and recovery of food by the western fox squirrel. *J. Wildl. Manage.* 6(4): 338-352.
- Cornwell, G. W. and H. S. Mosby. 1966. The eastern gray squirrel. Virginia Wildl. Conserv. Notes Circ. 1019. 11 p.
- Crane, H. L., C. A. Reed and M. N. Wood. 1937. Nut breeding. U.S. Dep. Agric. Yearbook 1937: 827-889.
- Croze, H. 1970. Searching images in crows. Hildebrandt & Stephan, Berlin, Germany. 86 p.
- Downs, A. A. 1944. Estimating acorn crops for wildlife in the southern appalachians. *J. Wildl. Manage.* 8(4): 339-340.
- Eisenberg, J. F. 1962. Studies on the behavior of Peromyscus maniculatus gambelii and P. californicus parasiticus. *Behavior* 19(3): 177-207.
- Elliott, P. F. 1974. Evolutionary responses of plants to seed-eaters: Pine squirrel predation on lodgepole pine. *Evol.* 28: 221-231.
- Fox, J. F. 1974. Coevolution of white oak and its seed predators. Ph.D. dissertation. Univ. of Chicago. 83 p.
- Goodrum, P. D., V. H. Reid and C. E. Boyd. 1971. Acorn yields, characteristics and management criteria of oaks for wildlife. *J. Wildl. Manage.* 35(3): 520-532.
- Hawbecker, A. C. 1940. The burrowing and feeding habits of Dipodomys venustus. *J. Mammal.* 21(4): 388-396.
- Hay, O. P. 1887. The red-headed woodpecker as a hoarder. *Auk* 4(3): 193-196.
- Howard, W. E. and F. C. Evans. 1961. Seeds stored by prairie deer mice. *J. Mammal.* 42(2): 260-263.

- Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evol.* 23(1): 1-27.
- \_\_\_\_\_. 1970. Herbivores and the number of tree species in tropical forests. *Amer. Natur.* 104: 501-528.
- \_\_\_\_\_. 1971a. Escape of Cassia grandis L. beans from predators in time and space. *Ecol.* 52(6): 964-979.
- \_\_\_\_\_. 1971b. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2: 465-492.
- \_\_\_\_\_. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6(2): 69-103.
- Johnson, W. T. 1969. Plant pests. In *Handbook of North American Nut Trees*. p. 67-156. R. A. Jaynes, Ed. The Northern Nut Growers Assoc. Knoxville, Tenn. 421 p.
- Keen, F. P. 1958. Cone and seed insects of western forest trees. U.S. Dept. Agric. Tech. Bull. 1169. 168 p.
- Kilham, L. 1958. Sealed-in winter stores of red-headed woodpeckers. *Wilson Bull.* 70(2): 107-113.
- Kleiber, M. 1961. The fire of life. John Wiley & Sons, Inc. New York. 454 p.
- Mattson, W. J. 1971. Relationship between cone crop size and cone damage by insects in red pine seed-production areas. *Can. Ent.* 103(4): 617-621.
- Michelbacher, A. E. and J. C. Ortega. 1958. A technical study of insects and related pests attacking walnuts. *Cal. Agric. Expt. Sta. Bull.* 764. 86 p.
- Morris, D. 1962. The behaviour of the green acouchi (Myoprocta pratti) with special reference to scatter hoarding. *Proc. Zool. Soc. London.* 139(4): 701-732.
- Naughton, G. G. 1970. Growth and yield of black walnut plantations. *Kans. State Univ. Exten. Forest.* Manhattan, Kans. 11 p.
- Packard, R. L. 1956. The tree squirrels of Kansas: Ecology and economic importance. *Univ. Kans. Mus. Nat. His. & State Biol. Surv. Kans. Misc. Publ.* 11: 1-67.
- Reller, A. W. 1972. Aspects of behavioral ecology of red-headed and red-bellied woodpeckers. *Am. Midl. Nat.* 88(2): 270-290.
- Salisbury, E. J. 1942. The reproductive capacity of plants. G. Bell and Sons, Ltd. London. 244 p.
- Shaw, W. T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. *J. Mammal.* 15(4): 275-286.
- Short, H. L. and W. B. Duke. 1971. Seasonal food consumption and body weights of captive tree squirrels. *J. Wildl. Manage.* 35(3): 435-439.

- Smigel, B. W. and M. L. Rosenzweig. 1974. Seed selection in Dipodomys merriami and Perognathus penicillatus. Ecol. 55(2): 329-339.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. Ecol. Monogr. 38: 31-63.
- \_\_\_\_\_. 1970. The coevolution of pine squirrels (Tamiasciurus) and conifers. Ecol. Monogr. 40(3): 349-371.
- \_\_\_\_\_. 1975. The coevolution of plants and seed predators. In L. E. Gilbert and P. H. Raven (ed). Coevolution of Animals and Plants. Univ. Texas Press, Austin. pp 53-77.
- \_\_\_\_\_ and D. Follmer. 1972. Food preferences of squirrels. Ecol. 53:82-91.
- \_\_\_\_\_ and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Am. Nat. 108 (962): 499-506.
- Smith, M. C. 1968. Red squirrels and cone failure. J. Wildl. Manage. 32(2): 305-317.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Am. Nat. 104(935): 25-36.
- Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. 6th Ed. Iowa State Univ. Press. Ames, Iowa. 593 p.
- Sokal, R. R. and F. S. Rohlf. 1969. Biometry. W. H. Freeman & Co. San Francisco. 776 p.
- Stebbins, G. L. 1971. Adaptive radiation of reproductive characteristics in angiosperms, II: Seeds and seedlings. Ann. Rev. Ecol. Syst. 2: 237-260.
- Sviridenko, P. A. 1971. [Role of Sciurus vulgaris L. in distribution of walnut.] Vestn. Zool. 1: 87-88. In Russian with English summary.
- U.S.D.A. 1965. Silvics of forest trees of the United States. U.S. Dept. Agric. Handbook 271. 762 p.
- Wilson, D. E. and D. H. Janzen. 1972. Predation on Scheelea palm seeds by bruchid beetles: Seed density and distance from parent palm. Ecol. 53: 954-959.

Table 1: Survival of black walnuts buried in replicate samples at 3 internut distances.

<u>DISTANCE BETWEEN NUTS (FT.)</u>	<u>NO. TAKEN</u>	<u>SURVIVAL (NUT-DAYS)</u>	<u>% SURVIVING</u>
30	8	1945	87.5
	35	1209	45.3
15	50	577	21.8
	53	543	17.2
8	60	323	6.3
	61	209	4.7

$F(2,3) = 10.2$   $P < .05$

Table 2: Burial strategies of 5 squirrels in the cemetery.

<u>SQUIRREL NUMBER</u>	<u>NO. OF NUTS BURIED</u>	<u>MEAN DISTANCE BETWEEN NUTS (M)</u>	<u>S<sup>2</sup></u>
2	15	10.5	25.5
3	19	10.5	251.2
4	28	7.8	104.3
5	7	16.0	61.3
6	9	15.6	134.0

**THIS BOOK  
CONTAINS  
NUMEROUS PAGES  
WITH DIAGRAMS  
THAT ARE CROOKED  
COMPARED TO THE  
REST OF THE  
INFORMATION ON  
THE PAGE.**

**THIS IS AS  
RECEIVED FROM  
CUSTOMER.**

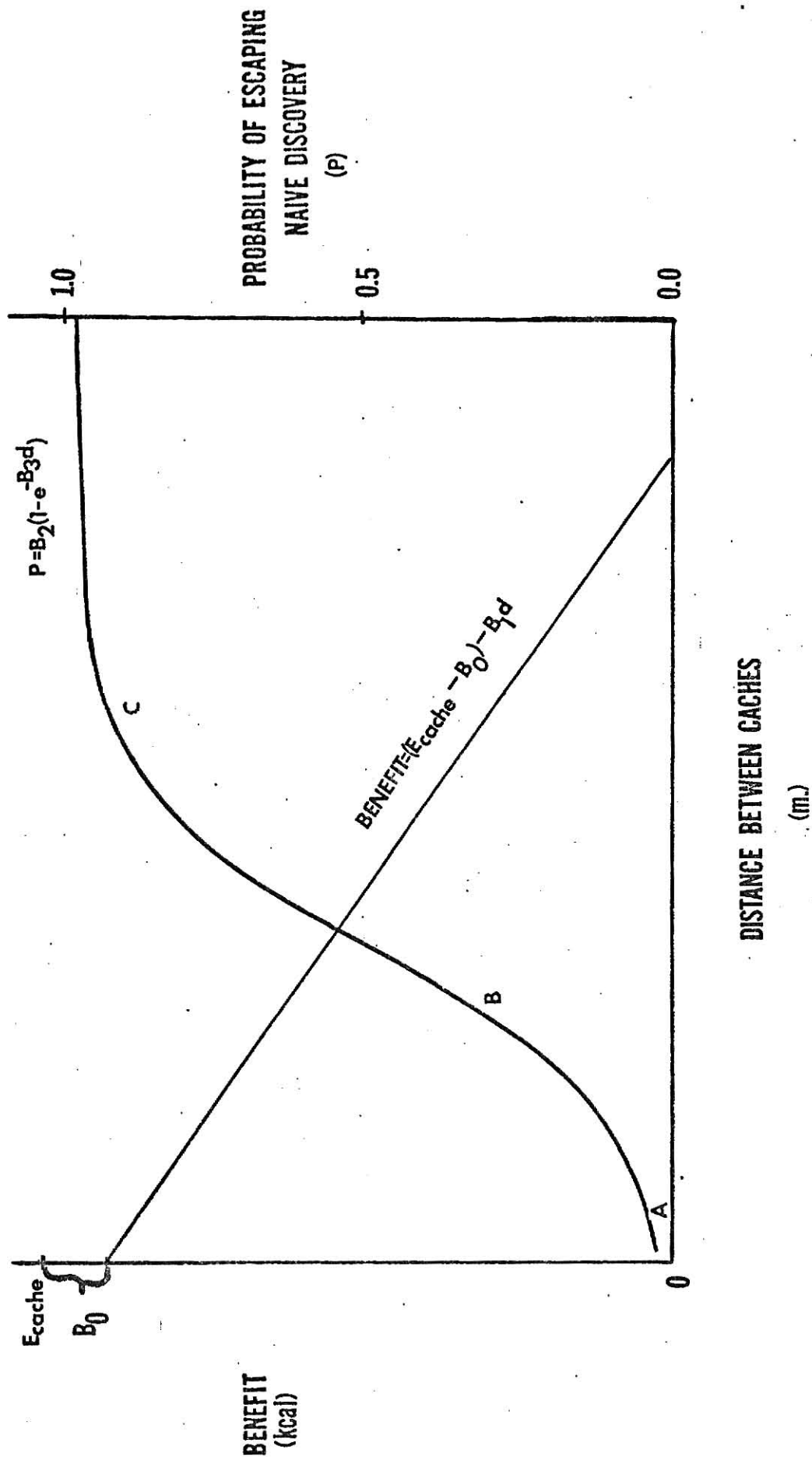


Fig. 1: Because of increased energy expenditure, Benefit will decrease linearly with intercache distance. Probability (P) of a cache surviving naive predation will increase sigmoidally with intercache distance. Areas A, B, and C are discussed in the text.

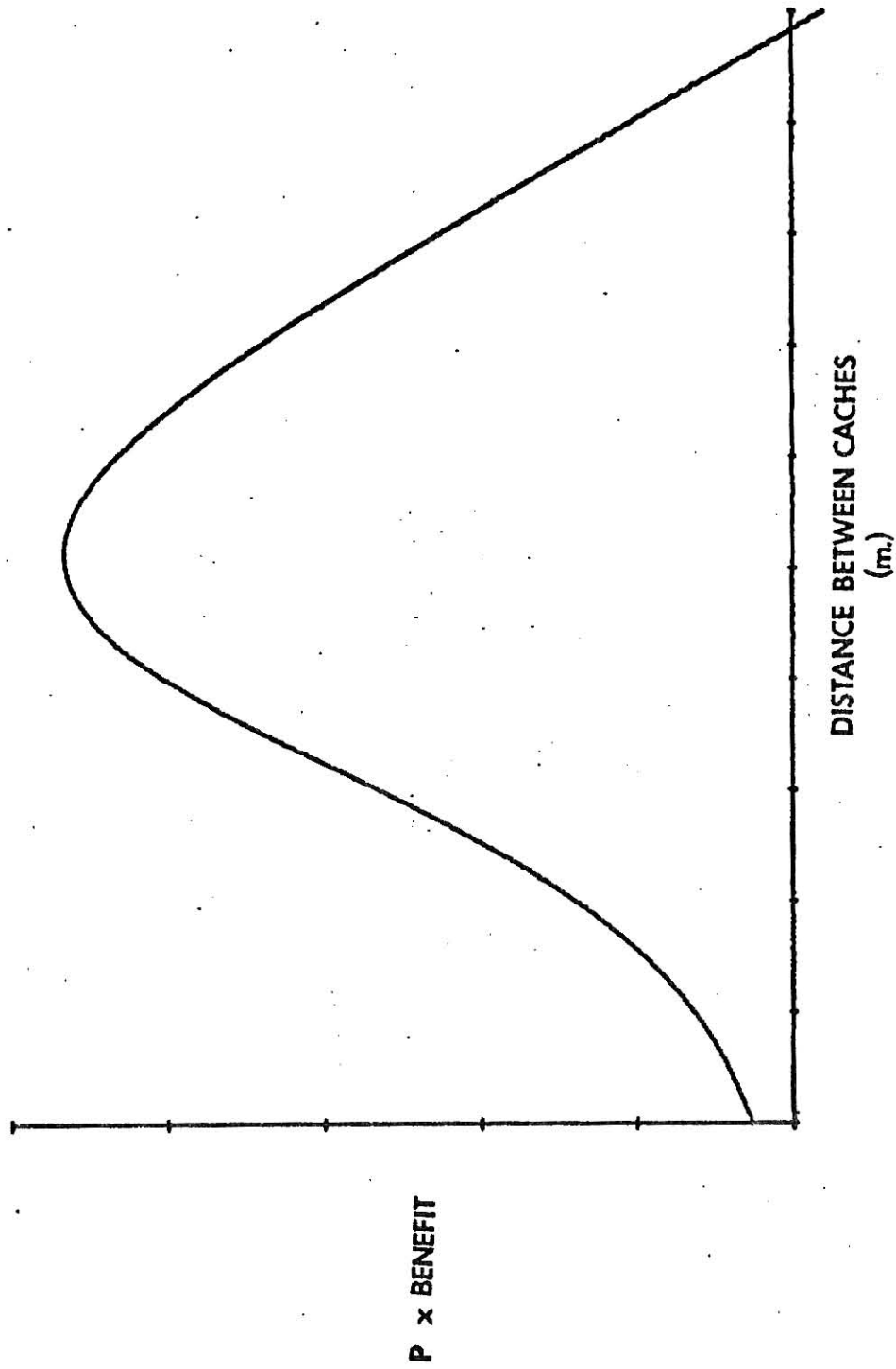
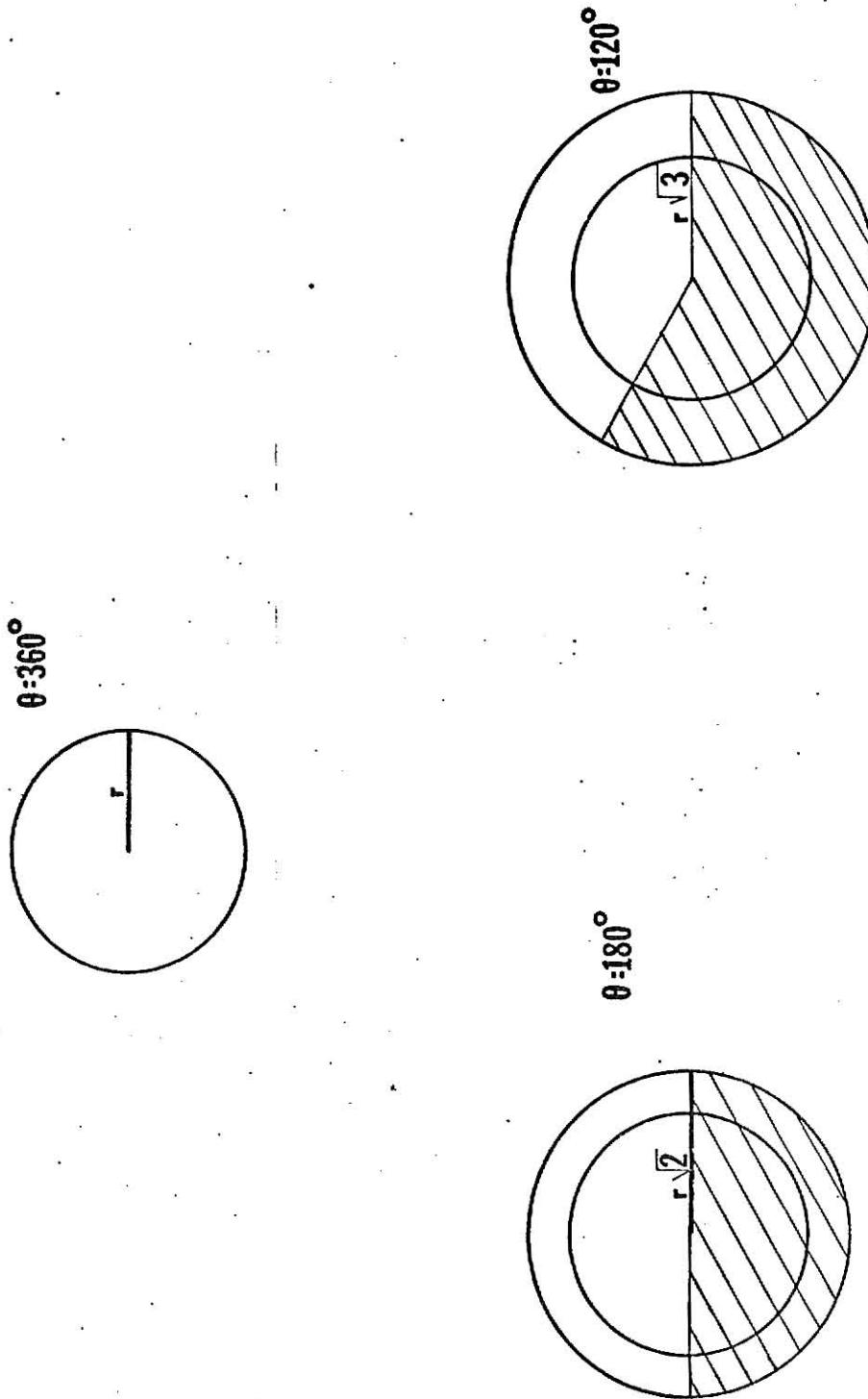


Fig. 2: The product of the Benefit and P equations yield a nearly bell-shaped curve as a function of intercache distance. Optimum intercache distance is where the derivative of the curve = 0.



$$\Delta r = \sqrt{\frac{360}{\theta}}$$

Fig. 3: From the model it would be predicted that a cache should be taken a factor  $\sqrt{\frac{360}{\theta}}$  units farther as the arc of the circle ( $\theta$  = unhatched areas) containing habitat suitable for seed burial is reduced.

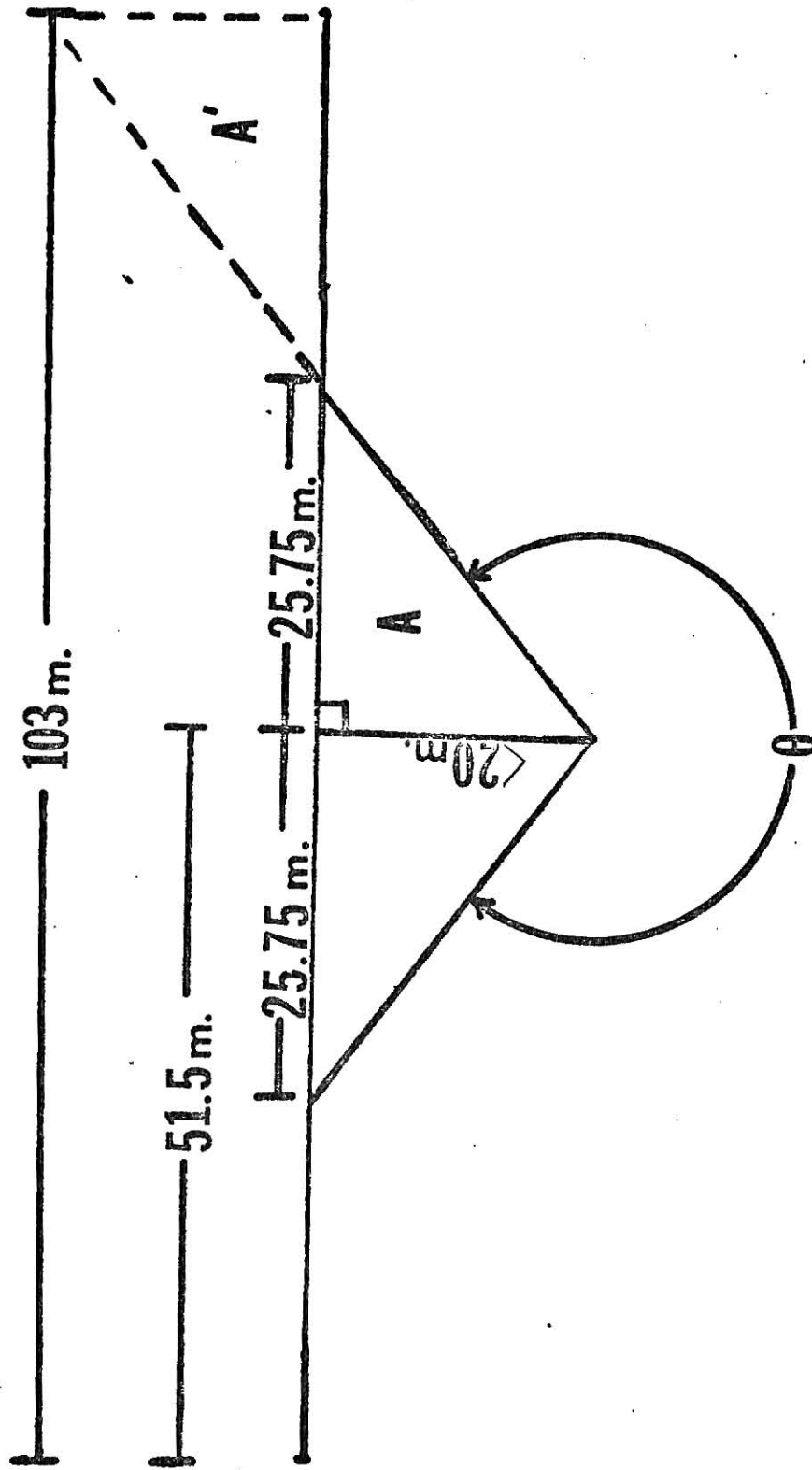


Fig. 4: Calculation of  $\theta$  if barrier to dispersal was located less than 20 m from a parent tree. Area of triangle A = Area of triangle A'. Triangle A' is not available for burial, but it is included in  $\theta$ . This compensates for the loss of the area of triangle A when calculating  $\theta$ .

Fig. 5; Map of burial sites of squirrels in Sunset Cemetery. Symbols: 1 = Squirrel No. 1, ● = Squirrel No. 2, ▲ = Squirrel No. 3, □ = Squirrel No. 4, ★ = Squirrel No. 5, ○ = Squirrel No. 6.

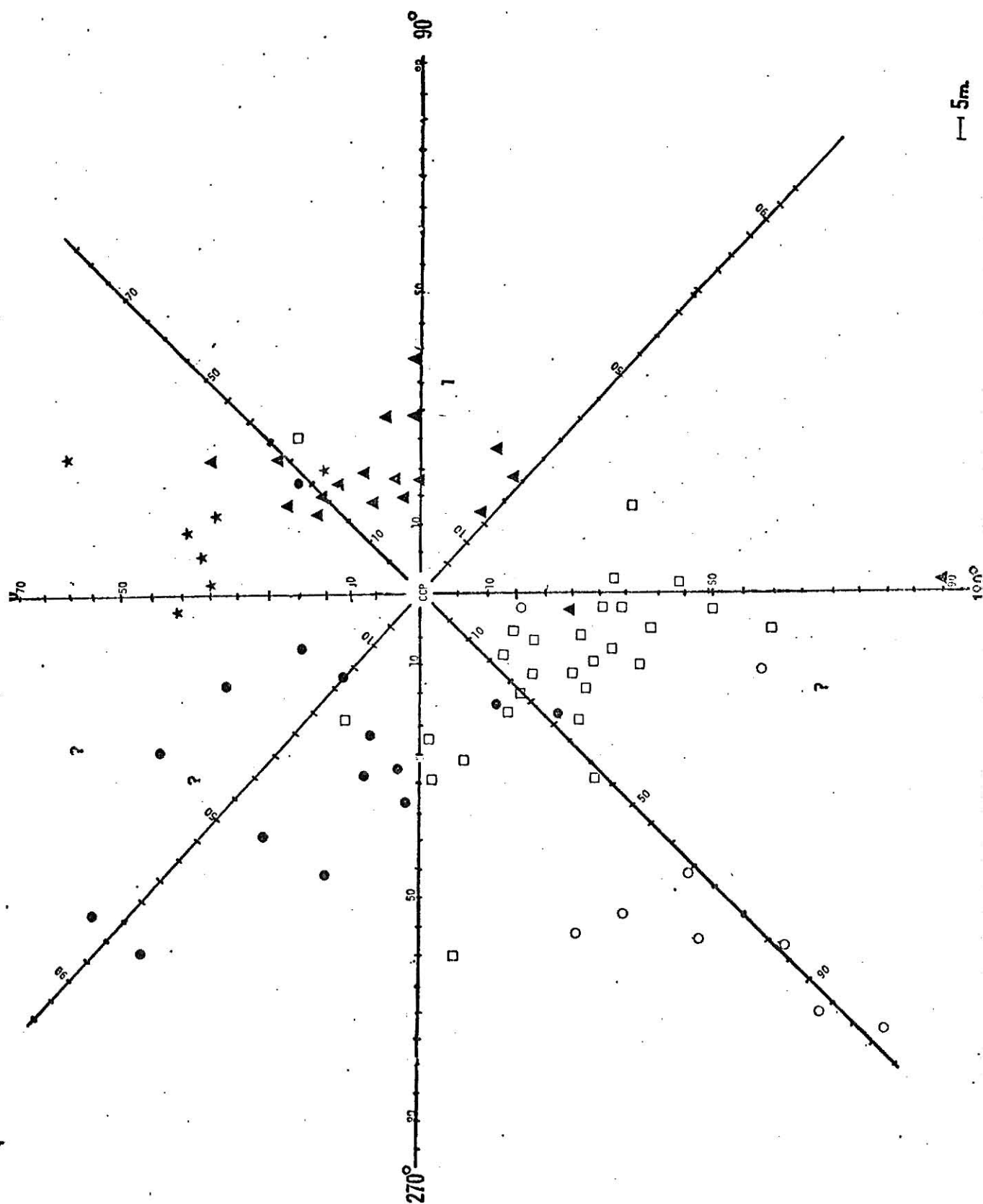
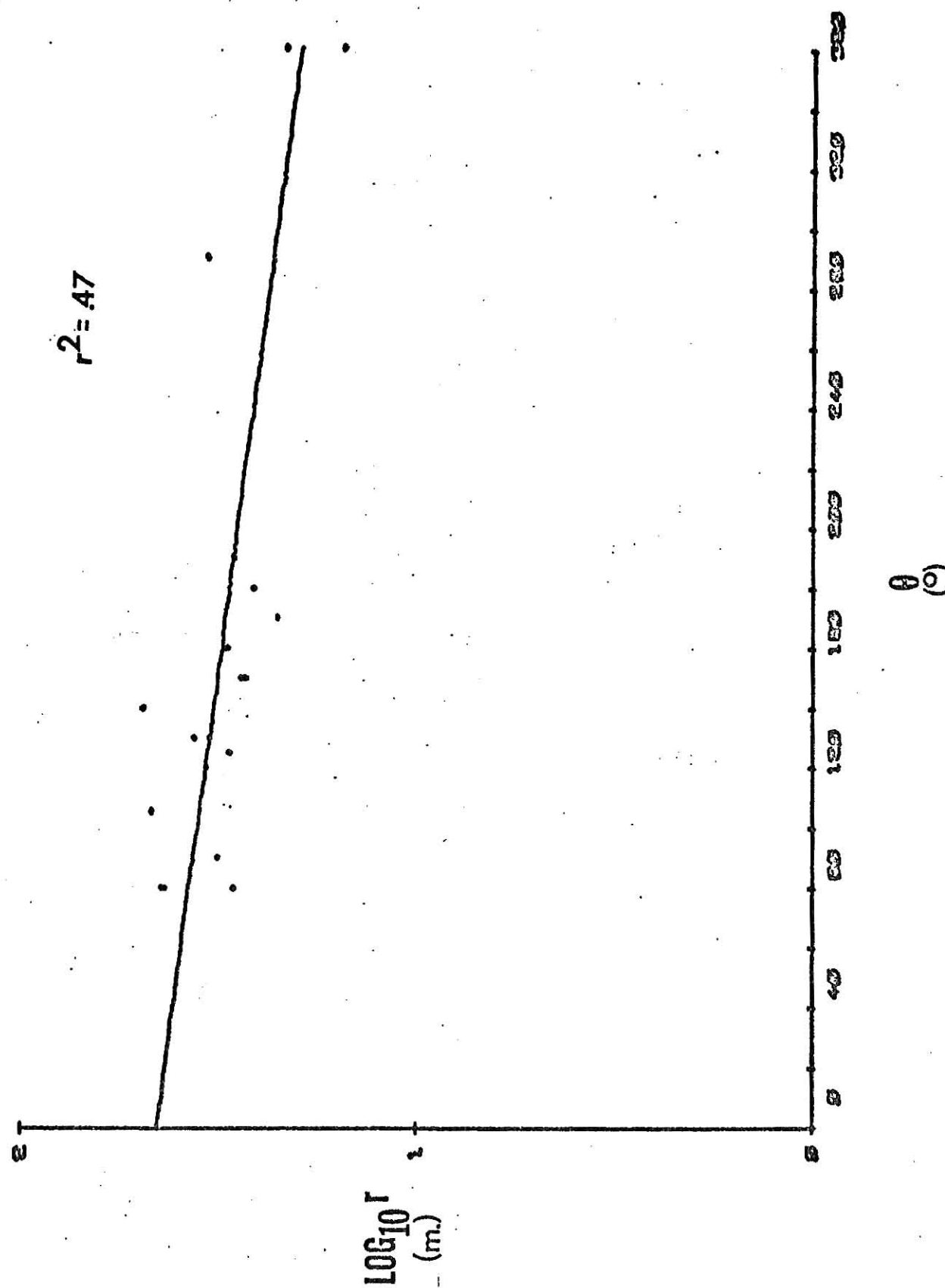


Fig. 6: Regression of  $\log_{10} R = \theta$ . The regression  $r^2 = .47$ .



A MODEL FOR SEED SCATTERHOARDING BY ANIMALS:  
COEVOLUTION OF FOX SQUIRRELS AND BLACK WALNUTS

by

MARTIN ANDRE STAPANIAN

B.A., Ohio State University, 1974

---

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY  
Manhattan, Kansas

1976

## ABSTRACT

The patterns with which granivores store seeds for future use is determined by their ability to defend caches of seeds against interspecific competitors. Scatterhoarding of seeds is employed by a species if it is somehow unable to defend its stored food from other species. This inability may be due to a size differential, or the fact that hoarder and competitors are active during different times of the day. Although more energy must be expended to increase intercache distances, loss to naive competitors decreases over time if caches are widely spaced apart. A mathematical model predicting optimal intercache distances is presented.

One prediction of the model is that as the arc ( $\theta$ ) of habitat suitable for seed burial surrounding a seed source is decreased, the average distance a cache is taken from the source ( $R$ ) should increase by the factor  $\sqrt{\frac{360}{\theta}}$  in order to maintain an optimal intercache distance. Because a scatterhoarder acts as a seed disperser, distance of saplings from a parent tree should be indicative of  $R$ .

Three field tests of the model and that prediction were conducted: (1) Replicate samples of Juglans nigra seeds buried at 3 intercache distances were maintained, and their survival from predation by Sciurus niger in time recorded; (2) Distances J. nigra saplings occurred from 20 isolated parent trees, along with  $\theta$  for each parent, were measured; (3) S. niger individuals were observed scatterhoarding J. nigra and the intercache distances maintained by individual squirrels were measured. Average intercache distances maintained by the observed squirrels very closely approximated one which was found to yield high survival of walnuts from naive predation in the first test. The  $\log_{10}$  of average parent-sapling distance as a function of  $\theta$  had a fairly high correlation ( $r^2 = .47$ ). The results suggest maintenance of optimum intercache distance by S. niger. The coevolution of mast trees and seed dispersal by animal scatterhoarders is discussed.