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EVOLUTIONARY RESPONSES OF PLANTS TO SEED-EATERS:

PINE SQUIRREL PREDATION ON LODGEPOLE PINE

by

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INTRODUCTION

Recent investigations dealing with the predator-prey relationship of seed predators and seeds have led to different opinions in regard to the evolutionary responses of plants to seed predation and the subsequent effects of these responses on the community's structure (Janzen 1969, 1971 and Smith 1970). Janzen, while working with insect predators, concluded that seed predators select primarily for smaller seed size by killing a higher per cent of the seed crop of trees with fewer but larger seeds. Smith, on the other hand, studying squirrels, proposed that predators discriminate between trees on the basis of which tree will give them the highest feeding rate. The basis for this discriminatory behavior could be factors other than seed size, such as the production of chemical deterrents or protective tissue with the seed size remaining constant.

Since there is a close correlation between seed size and the physical environment (Salisbury 1942) and since seed size is one of the least variable of plant characters (Harper 1961), selection for seed size is not likely to be one of the "lines of least resistance" (Stebbins 1967) for seed predator selection to follow. It appears more likely, that if both seed size and effectiveness of seed protection are variable, selective pressure from seed predators will select for greater energy expenditures in seed protection with the seed size remaining constant (Smith 1970). This selective trend would result in an individual plant producing fewer seeds due to the increased production of protective devices.

It seems evident, therefore, that the real problem is concerned with identifying which plant characters most closely resemble predator independent factors, primarily controlled by the physical environment, and which characters are more likely to be predator dependent. The evolutionary responses of plants to seed predators can be determined only by identifying the criteria by which predators discriminate, if they do, between varying prey items. This research is an effort at such a determination.

The pine squirrel (Tamiasciurus hudsonicus) shows discrimination on its feeding behavior among the cones of lodgepole pines (Pinus contorta). This discrimination is based primarily on the number of seeds per cone (Hatt 1929, Smith 1968, 1970), which has been shown to vary by a factor of eight (Smith 1968). Variation between trees has also been shown to exist in the hardness of cones, the size of cones, and the symmetry or shape of cones (Critchfield 1957), all of which have been observed to influence the feeding efficiency of Tamiasciurus (Smith 1970). However, the degree of variation in seed size and its relationship to the effects of seed predators have not been previously studied. Consequently, the critical data for testing the conclusions of Smith and Janzen has not existed prior to this study. If the degree of variation in the cone and seed characters is great enough to allow a squirrel to discriminate among cones, then an effective selective agent exists for determining cone and seed characteristics.

Personal observations of squirrel feeding behavior during the summer of 1971 and by Smith (personal communication) during the summers of 1962-1964 agree that the cones of some pine trees are apparently immune from squirrel predation while others experience varying degrees of predation, even up to 100 per cent. With this knowledge as a foundation, an attempt

was made in this study to quantify the existing variation among trees in the female reproductive characters, including both cones and seeds. Using the differential predation as the dependent variable, an effort was made to isolate and identify the characters most influential in determining a squirrel's preference, and as a result, illustrate which plant characters are most likely to be affected by seed predators.

METHODS

The field work for this research was done during the summers of 1971 and 1972 in the Cascade Mountains just east of Manning Provincial Park in southwestern British Columbia (Figure 1). The forests in this area are quite dry due to the rain shadow created by the Cascade Mountains, and lodgepole pine is the dominant tree species due to its adaptive ability to reseed following forest fires (Critchfield 1957).

Since the pine squirrel is territorial (Smith 1968), it was not difficult to identify the specific trees from which a particular squirrel obtained most of his pine cones. Three territories were identified and in two of the territories every tree was marked with a numbered metal tag. On the third territory, due to its large size and great number of trees, only those trees with a circumference at chest height (CCH) of twelve inches or greater were marked. This amounted to about 40 per cent of the total number of trees on the territory, but provided a much higher per cent of the total cone production of the territory. Two hundred and fifteen trees were marked on Territory I, 256 on Territory II, and 400 on Territory III.

To quantify the variation among the female cones of different trees

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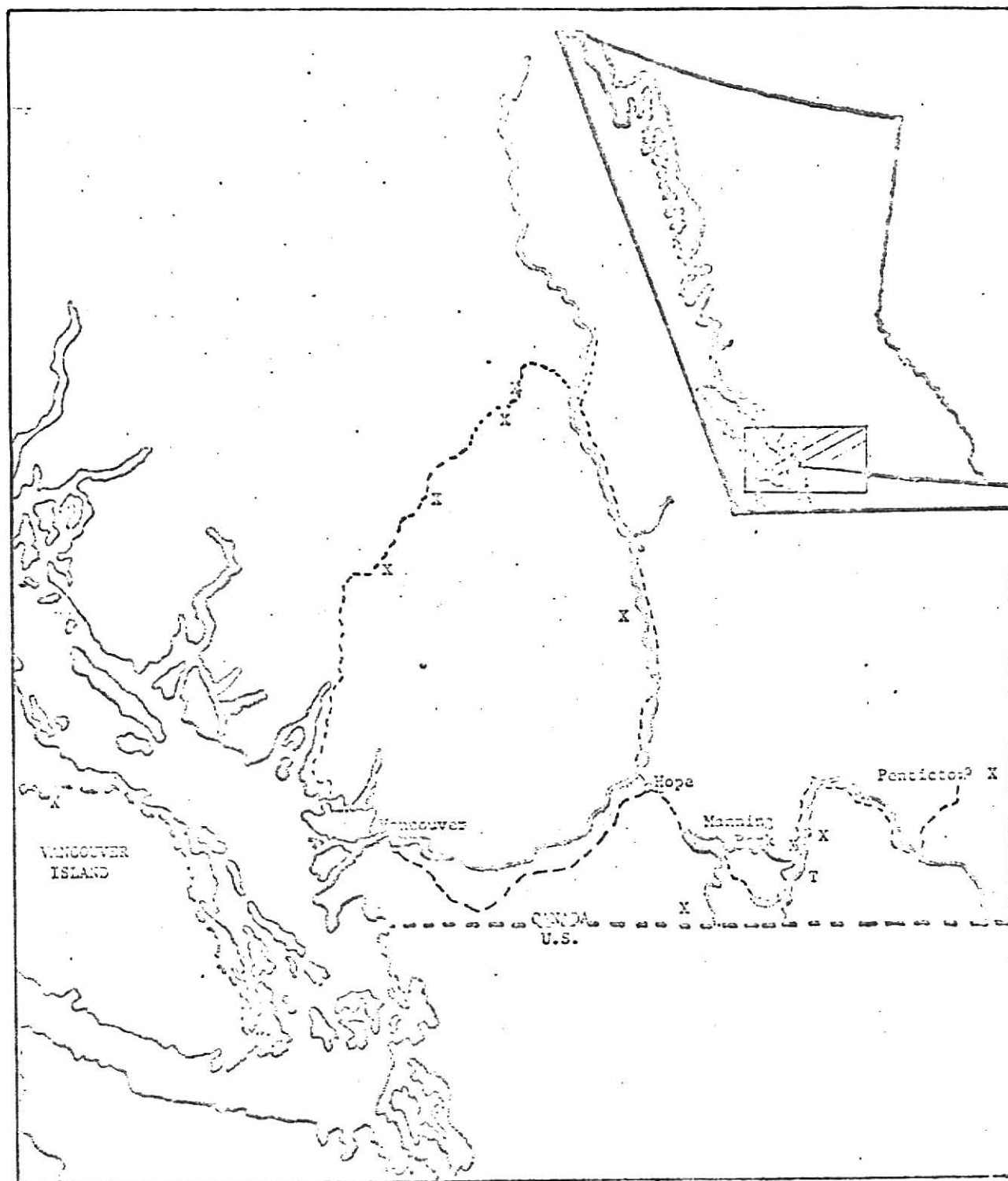


Figure 1. The study area. Locations of geographic samples are marked with X's. The location of the territory studies is marked with a "T".

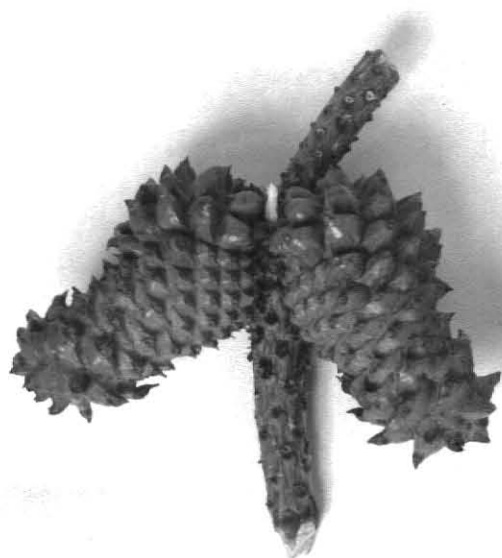
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Figure 2. Illustrates the great amount of variation existing in cones between trees. Each of these cones were taken from trees within 350 meters of one another.

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of a given territory (Figure 2), an effort was made to sample cones from every tagged tree on the three territories. This was done by using tree clippers to cut off the ends of limbs containing old closed cones. Due to the variation in cone morphology various aspects of the cone shape were measured for two cones from each tree sampled. Figure 3 illustrates the morphological measurements taken. The length (Figure 3, A), and the width (Figure 3, B), of the cones were measured in millimeters. The angle of cone attachment to the limb (Figure 3, C), was the angle formed by the cone and limb on the trunk side of the cone attachment. In an effort to quantify the asymmetry of the cone, individual scale widths from opposite sides of the cone were measured (Figure 3, D). Since the cones are generally attached to the limb at an angle, the scales on the more exposed side are usually larger and more prominent than corresponding scales on the opposite side of the cone. Also, in regard to the shape, the distance from the widest point of the cone base to the apex of the cone was measured (Figure 3, E).

The dry weight of the cone and its specific gravity were measured by the same procedure used by Critchfield (1957). Since lodgepole pine cones in the study area are primarily serotinous (Critchfield 1957, Smith 1968, 1970), the sample cones were opened by heating them at approximately 135° C. for 25 minutes, so that the seeds could be removed. The number of seeds and the number of viable seeds per cone were recorded for each of 5 cones per tree. The number of viable seeds was approximated by cutting each seed open and checking for the presence of embryo and female gametophyte. The total weight of all the seeds per cone was recorded, along with the average weight of an individual viable seed, for 2 cones per tree. All seeds were weighed with seed coats but without the wings.

Because lodgepole pine cones remain on the tree for an indefinite

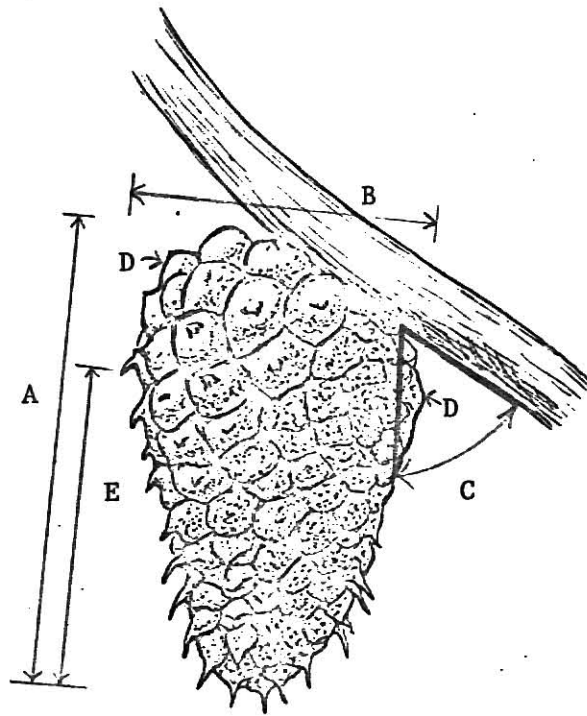


Figure 3. Measurements made of cones. A= Cone Length B= Cone Width C= Angle of Cone Attachment D= Location of the two cone scales whose widths were measured E= Length of Cone from its widest point to its apex. The angle of cone attachment was measured on the trunk side of the cone attachment. The origin of the angle was the point at which the cone and the limb touched. The angle measured subtended an arc at a distance of 2 centimeters from the origin.

number of years (Critchfield 1957), it is possible to estimate the degree of predation experienced by a given tree by dividing the number of old closed cones remaining on a tree by the number of cones produced per year. Sight estimates of old cones remaining on 17 trees that were later felled proved to be 79% accurate (Table 1). Estimates of yearly cone crop sizes were made from the regression shown in Figure 4. This regression is based on counts of the number of cones in the two newest cone crops on 127 trees that were felled. This regression plots the log of the number of cones produced per year as a function of CCH. The actual number of cones plotted in the regression is the average of the two newest cone crops. Since neither of the crops were mature, they had not been subject to squirrel predation. This method of measuring predation intensity, though based on estimations and extrapolations, affords a great advantage in that it takes into account the trees' past history of experienced predation.

The basis on which a squirrel's preference for particular cone phenotypes is founded was analyzed statistically by multiple regression analysis. The statistical model (Table 2) regards the degree of predation experienced by a given tree during its lifetime as the dependent variable, with the cone and seed variables measured serving as the independent variables which dictate a squirrel's feeding preference. When using a statistical analysis of this nature, it is critical to eliminate as much bias as possible in the calculation of the dependent variable. Consequently, to adjust for any trees of the same CCH producing different size crops due to differences in the sizes of cones (thus reducing the accuracy of the regression shown in Figure 4), the estimate of the total number of old closed cones on a tree was multiplied by the mean cone weight of the tree's cones; this value was divided by the number of cones estimated to be in a year's crop for a given

Estimate	Actual	% Dev. of Estimate From Actual	% Correct
187	280	28.5	71.5
0	0	0.0	100.0
137	107	17.7	82.3
350	651	46.2	53.8
105	85	27.6	72.4
30	28	7.2	92.8
0	0	0.0	100.0
450	681	34.2	65.8
150	204	26.5	73.5
43	39	6.8	93.2
238	343	28.6	71.4
48	55	20.5	79.5
58	74	24.0	76.0
600	400	50.0	50.0
88	104	16.7	83.3
288	440	34.9	65.1
363	528	21.6	78.4

Table 1. Estimations of the number of closed cones on 17 individual trees and the actual values determined after the tree had been felled and the cones counted.

Table 2.

 MULTIPLE REGRESSION MODEL

$$Y = \sum \beta_i X_i$$

<u>VARIABLE</u>	<u>CALCULATION</u>
Y = Degree of Predation on a Tree	$\frac{(\text{No. of old closed cones})(\text{Wt. of cone})}{\text{No. of cones in a yearly crop}}$
X ₀ = 1 (for intercept of equation)	
X ₁ = Cone Density	
X ₂ = Angle of Cone Attachment	See Figure III
*X ₃ = Cone Width	See Figure III
X ₄ = Total Seed Weight	Wt. of all the seeds in the cone
X ₅ = Number of Seeds/Cone	
*X ₆ = Number of Viable Seeds/Cone	Seeds with embryo and endosperm
X ₇ = Mean Wt. per Viable Seed	$\frac{\text{Total Weight of Viable Seeds/Cone}}{\text{Number of Viable Seeds/Cone}}$
*X ₈ = Ratio of Cone Length to Cone Width (CONE RATIO)	$\frac{\text{Cone Length}}{\text{Cone Width}}$
*X ₉ = Proportion of Cone Length from the Widest Point to the Apex of the Cone (PLAPEX)	$\frac{\text{Length of cone from widest point to apex}}{\text{Total Length of Cone}}$ See Figure III
X ₁₀ = Ratio of Large Scale Width to Small Scale Width	$\frac{\text{Width of Larger Scale}}{\text{Width of Smaller Scale}}$ See Figure III
X ₁₁ = Per Cent of Total No. of Seeds per Cone that are viable	$\frac{\text{No. of Viable Seeds/Cone}}{\text{No. of Seeds/Cone}}$
*X ₁₂ = Per Cent of Total Cone Weight in Seeds	$\frac{\text{Total Weight of Seeds/Cone}}{(\text{Weight of Empty Cone}) + (\text{Wt. of Seeds})}$

*Significant at P=.05

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Territory I	r ² = .44	n= 415
Territory II	r ² = .12	n= 435
Territory III	r ² = .10	n= 1023

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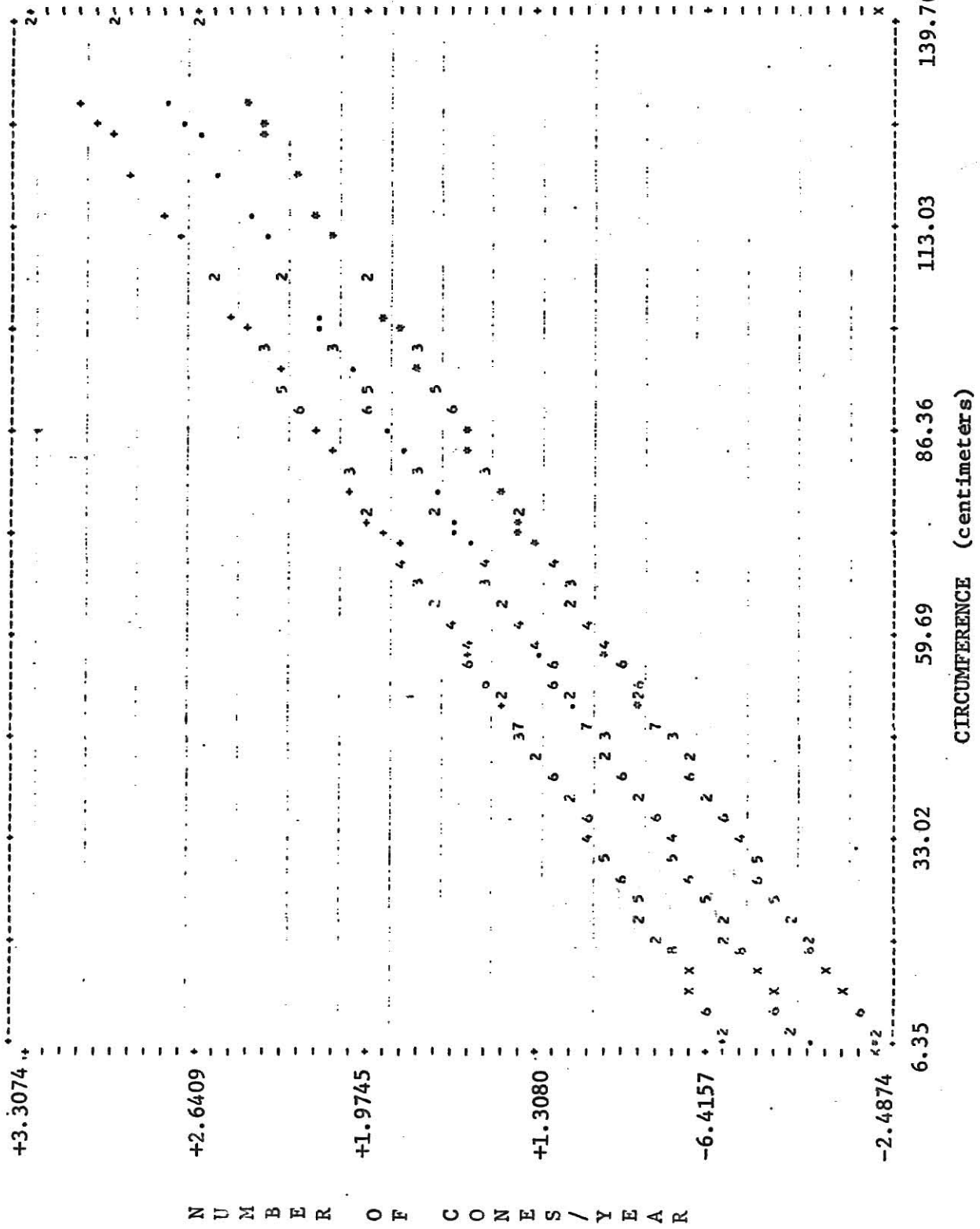


Figure 4. A computer calculated semi-log regression with 95% confidence belts plotting the size of a year's cone crop as a function of a tree's circumference at chest height. The numbers on the graph indicate the number of points at that location. X's = more than 9 points. . = Regression Line + and * = Confidence Belts.

CCH (Table 2, Y Variable). The particular type of multiple regression used was a Stepwise Deletion Procedure which performs the usual multiple regression analysis, and, as an option, provides for building the "best" regression models by successively dropping variables from the regression model that do not contribute sufficient information on the dependent variable. The least significant variables are dropped until all remaining variables are significant at the user specified level of significance (Kemp 1969). This type of analysis was done for each of the three territories.

Seventeen geographic samples of pine cones were made in a more or less east-west transect ranging from 250 miles west of the main study site (Vancouver Island) to approximately 100 miles east of the study area (Penticton) (Figure 1). The same variables were measured for these cones as for the territory cones. Since these samples were made primarily as an effort to explain the cause and maintenance of the variation in lodgepole pine cones of the coastal and interior races, the results of those samples will not be dealt with in detail here, but used only as they apply to this problem.

RESULTS

In only one of the three territories analyzed did the multiple regression model explain enough variation in the dependent variable ($r^2=.44$) to yield statistically meaningful results. The same model, when applied to Territories II and III, explained only 10% and 12% ($r^2=.10$), ($r^2=.12$) of the variation in the dependent variable, and none of the independent variables remained in the model to the $P=.05$ level.

In Territory I the specific cone characters found to be significant ($P=.05$) in explaining the variation in the degrees of predation were (1) width of the cone, (2) the ratio of the cone's length to its width (CONE RATIO), (3) the proportion of the cone's length from its widest point to its apex (PLAPEX),

(4) the number of viable seeds per cone, and (5) the per cent of the total cone weight accounted for in total seed weight.

Although no statistically meaningful results were obtained from Territories II and III, the same trends illustrated by Territory I were also present in the results of the other two territories, in that the last variables deleted from the model were cone width, number of viable seeds per cone, CONE RATIO, and the proportion of the cone's length from its widest point to its apex.

DISCUSSION

The results of the analysis reveal two main points of concern about their validity and value; the first being the r^2 values of the statistical models and the second being the large difference between the r^2 value of Territory I in comparison to the r^2 values of the other two territories. In the first case, a confidence level for r^2 values does not exist, and it is very difficult to determine how much of the variation in the dependent variable must be accounted for by the model before it is biologically significant. Since most biological phenomena are the result of a combination of influencing factors, it is not surprising that the r^2 values are lower than one would like.

It seems more likely that the r^2 values, rather than reflecting the inadequacy of the model, indicate the presence of experimental error. The sight estimates of the total number of cones remaining on a tree and the extrapolations from a regression line of the number of cones produced per year for a given tree size are two sources, in particular, which could account for much of the variation not explained by the model.

A second question raised by the results concerned the very different results obtained by using the same model on the three different territories, in respect to the r^2 values. It appears that there are two main reasons why the r^2 values of Territories II and III are so much lower than that of Territory I. One, the average number of old cones remaining on the trees of the two territories was greater than the average number of cones on the trees of Territory I. This fact enhances the probability of making a critical error in calculating the dependent variable, since errors in sight estimating the number of old closed cones on a tree were found to be greater when there were a high number of cones on the tree. This was determined from the trees that were later felled after sight estimations had been taken (Table 1). Secondly, Bartlett's Test of Homogeneity of Variance of the three territories showed that the variance of 10 out of the 12 independent variables in the model, was greater for the trees of Territory I ($P=.05$). It is also important that all of the variables dealing with cone morphology exhibited greater variances for Territory I. This is significant because, assuming the squirrels were making a conscious discrimination among the cone phenotypes, it would be easier for the squirrels to discriminate and more beneficial to do so, if the variation among prey types is more obvious. Therefore, it is not surprising that the model "fit" this territory so much better than the other two, since the easier it is for a predator to discriminate among prey items, the more predictable the selective pressures.

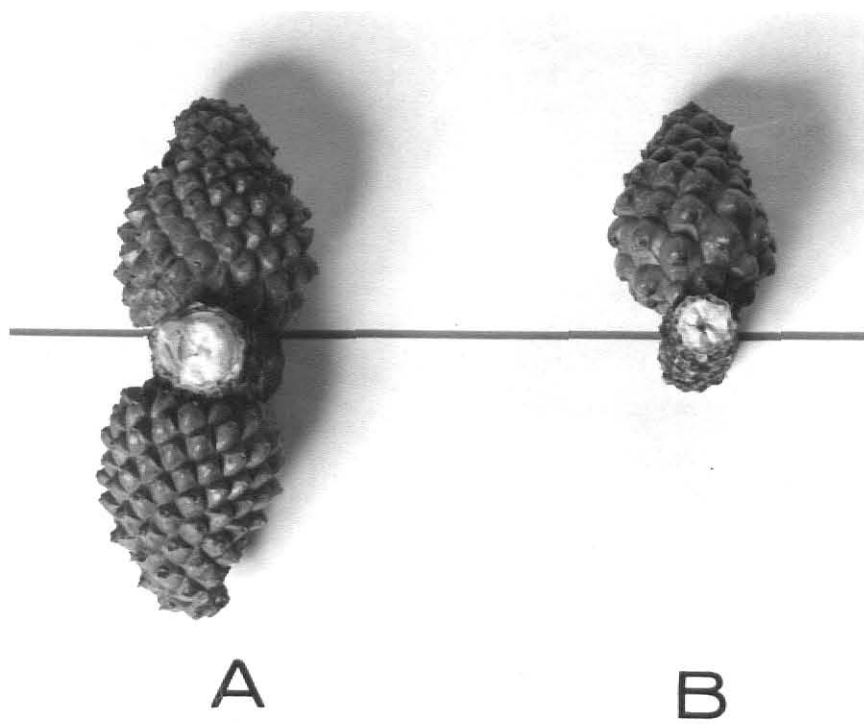
In regard to the specific "selective pressures", what does it mean, biologically, for a variable to be significant at $P=.05$ in a multiple regression model? In respect to this study, the variables found to be significant indicate that, primarily, it is these variables on which squirrels

are basing their discrimination in choosing among cone phenotypes. Specifically, the results indicate that 5 variables are significantly influencing a squirrel's cone preference.

CONE WIDTH. The results indicate that the larger the cone width, the less desirable a cone is. There are two possible reasons for this. One, to cut cones from a limb a squirrel must put its mouth around the base of the cone or the branch in order to get its incisors between the cone and the branch to cut the attachment (Smith 1970). The wider the cone, the more difficult this becomes, to the extent that I have observed a squirrel attempt to detach a cone for over 4 minutes and finally give up altogether. Also, the larger the width, the slower the feeding rate, since the proximal half of the cone, where the greatest width is found, is sterile scales, which the squirrel must remove in order to extract the seeds from the fertile distal scales (Smith 1970).

CONE RATIO and the PROPORTION OF THE LENGTH OF THE CONE FROM THE WIDEST POINT TO THE APEX (PLAPEX). These two variables are discussed together, since both are measurements of morphology. The results indicate that the smaller the ratio of the length to the width of the cone and the larger the PLAPEX, the less the predator pressure. Again, these are variables attempting to quantify shape, and their influence on squirrel predation may be of a mechanical nature, i.e. cone detachment, feeding rate, or they may serve as a visual cue indicating the number of seeds in the cone. As the PLAPEX increases, the widest point of the cone approaches the very base of the cone, making it increasingly difficult for the squirrel to detach it from the limb (Smith 1970), since the cone itself will be sitting "flush" on the limb with its attachment protected. Figure 5 illustrates this morphological advantage. The shape of the cone can also inhibit the

Figure 5. Illustrates how the shape of a cone may inhibit its removal from the limb by squirrels. The widest point of Cone A is practically the same as the width of its base, consequently, the cone's point of attachment is much more protected than that of Cone B, whose base is not nearly as wide as its widest point.



detachment process due to the arrangement of the cones on the limb (Smith 1970). Figure 6 illustrates how some cone arrangements, due to the wide bases of the cones, are characterized by the cones being in contact with one another, thus preventing access to their respective attachments.

On the other hand, a decrease in the ratio of cone length to width appears to influence squirrel predation by indicating a lower proportion of seed weight to cone weight, i.e. protective tissue. Supporting this idea is the fact that an Analysis of Variance of 13 geographic samples reveals that in 6 out of 7 cases where the cone lengths of the trees of two areas were not significantly different ($P=.05$), but the cone ratios were, (indicating a difference in cone widths), it was found that the per cent of the cone weight due to seeds was smaller for the smaller cone ratio, and in 4 of these cases the difference was significant at $P=.05$. These results indicate that selection for a smaller CONE RATIO is a function of selection for larger cone widths.

PER CENT OF TOTAL CONE WEIGHT DUE TO SEEDS (PSEED). The results of the statistical analysis reveal that cones are evidently considered less desirable for squirrels as the amount of protective tissue (cone scales) increases disproportionately to the increase in total seed weight. A predator should avoid an increase in energy expenditure (such as chewing through a larger cone) unless he gets a proportionate increase in energy intake.

NUMBER OF VIABLE SEEDS PER CONE. Selection of cones with higher numbers of seeds has been widely documented in the past (Hart 1929, Smith 1968, 1970). As was expected, it was found to be a significant variable in this model. In terms of feeding efficiency, a squirrel maximizes his rate of ingestion by picking cones with the highest number of viable seeds

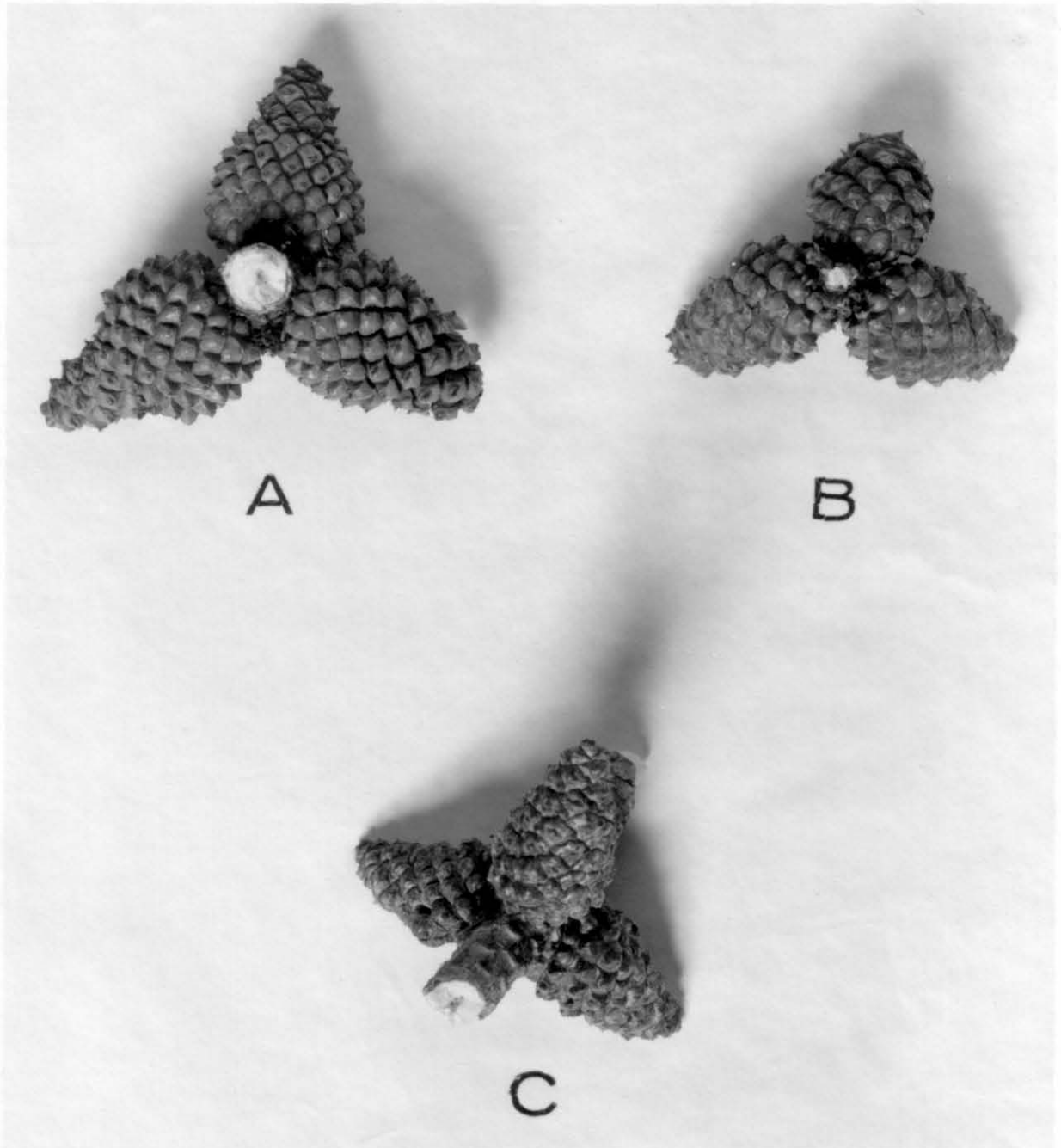


Figure 6. Illustrates how squirrel predation is inhibited by the arrangement of the cones, and the bases of the cones being wide enough to touch one another, thus protecting their point of attachment.

(Smith 1970).

It is important to point out that how a squirrel determines seed number or the proportionate amount of seed weight in the total cone weight is not the critical point in this research. A squirrel may use visual cues of cone morphology, as was previously discussed, or possibly operates on a threshold principle involving the odor of seeds. The main concern of this study has been identifying the effects of this selection in terms of the evolution of plant reproductive characters. The results of this research indicate cone selection by squirrels favors (1) wider cones, (2) a decreasing ratio between the cone length and width, (3) the base of the cone being flush on the limb, (4) cones with a smaller number of viable seeds, (5) a smaller ratio of seed weight to cone weight per cone.

In regard to the controversy previously discussed, the results of this study support Smith's viewpoint in that no evidence was seen for selection of seed size by squirrels and evidence was found indicating that seed predators can select for an increase in plant production of protective tissue with seed size remaining constant, and consequently, fewer seeds being produced. However, it seems that the contrasting opinions of Smith and Janzen concerning plant responses to seed predation may, in a large part, be due to the different predator-prey systems with which each one worked. While Janzen (1969) worked with a bruchid-legume system, in which it generally took two generations of bruchids to destroy a tree's crop, Smith (1970) worked with squirrels which could destroy a tree's cone crop in a day and were critically motivated to maximize their feeding rate. Also, Janzen, working with a host-specific predator, gave no indication that bruchids are selective in their predation of legume seeds. If, indeed, this is the case, Janzen's prediction (1969) of predator satiation, due to larger seed crops with smaller seeds, becomes a more

probable selective trend for plants to follow.

It is possible, however, that the most important difference between the two systems is the different dispersal vectors of the respective seeds, pine seeds being wind dispersed, and the legume seeds studied by Janzen generally animal dispersed. Salisbury (1942), Harper (1965), and Stebbins (1950) have indicated that seed size is a compromise between the requirements of the physical environment for germination and success in dispersal to a "suitable site". Squirrel predation could only affect the dispersal of pine seeds by occurring before the cone opens, but selection for a larger cone or fewer seeds per cone does not influence the successful dispersal of an individual seed. However, if a plant is dependent upon animal vectors for seed dispersal, any selection that would negatively affect the "attractiveness" of a plant product to the dispersal agent, i.e. selection for a tougher seed pod, bitter fruit, etc., would be non-adaptive (Janzen 1971). Consequently, seedling mortality, due to a reduction in seed size, could be more than compensated for, if the diverted energy were used in such a way as to enhance seed dispersal, resulting in a greater percentage of seeds reaching suitable germination sites. Thus, it may be that while seed size is more directly influenced by the physical environment, in some systems it can be indirectly affected by seed predator effects on the seed dispersal mechanism. However, as Harper has suggested (1961, 1965), the physical environment still acts as an independent variable in setting constraints on the evolution of seed size in that successful germination of different size seeds is dependent upon fine heterogeneities in the soil.

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ABSTRACT

The pine squirrel, Tamiasciurus hudsonicus, discriminates in its feeding behavior among the cones of lodgepole pine, which are highly variable in several characteristics including size, shape, hardness, and number of seeds. Multiple regression analysis indicates that a squirrel's preference for a particular cone phenotype is based on (1) width of the cone, (2) the number of viable seeds per cone, (3) the ratio of total seed weight to cone weight, and (4) the shape of the cone in relation to its attachment to the branch. The results are consistent with observations of these squirrel's behavior in their efforts to maximize their feeding rate.

The predator-prey system studied offers an excellent means of determining "selective pressures" applied by seed-eaters and predicting the most probable evolutionary responses of plants to seed predators. Specifically, evidence is shown indicating that lodgepole pine responds to pine squirrel predation primarily by increasing the amount of protective tissue (cone scales) per cone while keeping the seed size relatively constant and reducing the number of seeds per cone.