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PLANT DISPERSION, SEED PREDATION, POLLINATION,
AND THEIR EFFECT ON THE FECUNDITY OF
BAPTISIA SPP. (LEGUMINOSAE)

by

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Dedication

to

Rosemary Kathleen Reed Johnson

who is a source of

inspiration and joy for me.

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INTRODUCTION

Dispersion and density of plants have been of interest for a long time, primarily from the viewpoint of intra and interspecific competition (Clark and Evans 1954, Thompson 1956, Harper 1961a and b). More recently an interest has been expressed in the role of herbivorous insects on plant dispersion and density. Seed predation both before and after dispersal can be substantial (Janzen 1971).

Seed predation may affect gene frequencies and thus have evolutionary effects. Given certain environmental constraints, seed predation by squirrels may lead to character displacement in pines and thus niche shifts (Smith 1970).

Seed predation may also affect population regulation. If the number of adult plants is below the number of possible sites for adult plants because too few seeds survive predation both to hit and germinate at all the "safe" sites (Harper 1961a), then seed predation limits abundance. Predispersal seed predation by obligatorily or facultative host-specific predators can thus theoretically cause a lower density of adult plants than that expected by interspecific competition alone. According to Janzen (1971), a lower density presumably could allow increased plant species diversity in an area if each plant species were affected in this manner. In intertidal animal communities in which space is a limiting factor, Paine (1966) has shown that even a single predator, by reducing the dominant species' population level, can increase species diversity as the populations of the rarer species increase. Predation is

among the theories for factors affecting species diversity according to Pianka's review (1966).

Parent plants are not likely to be equally affected by seed predators due to parental resistance to insect attack, specifically nonpreference, antibiosis, and tolerance (Painter 1951). Nonpreference (the insect prefers not to lay its eggs on, eat, or live on one individual as opposed to another individual) and antibiosis (adverse effect on the growth, survival, and/or fecundity of the young or adult insect) may be due to a plant's chemical defense or mechanical defense. Tolerance on the other hand, is a reaction by the plant which shows its ability to grow and reproduce or to repair itself to a marked extent despite supporting an insect population equivalent to that injuring a susceptible host. Plant breeders expend much effort separating plants which appear resistant in the field into those which truly have characters conferring resistance and those which have pseudo-resistance; that is, by chance, they escaped insect herbivory.

Escape by plants in space in natural ecosystems basically depends on the time and energy budgets of their predators. What is the best foraging strategy of a predator? Much has been written on this problem in other contexts (e.g. review by Schoener 1971), but for this discussion I would like to point out that all other things being equal that an insect seed predator (who is energy and time "wise") will be most likely to attack a near plant within the range of its senses. Relatively isolated plants should have a lower infestation rate than those in a dense stand if the predator differentially responds to varying plant dispersion patterns and if the dispersal agents responds to plant dispersion less than the predator

does (Vandermeer 1975). The advantage a plant may have due to a greater isolation may be diminished as the time a predator has to find it is increased. Pielou (1962) found that relatively isolated Douglas fir trees were as likely to be attacked by a root rot fungus as more crowded trees. She noted that this may be because it was studied a long time after the initial attack. By then the roots of at least 93% of the trees touched and any possible advantage due to original isolation was lost.

In previous models (Janzen 1970, Vandermeer 1975), the plant's strategy has primarily been seen in terms of how fast a plant can produce seed and get them dispersed before they are eaten. The effects of predation on seeds and seedlings once they are dispersed from the parent are seen to be of primary importance and have been modelled. For instance, Janzen (1970) has modelled the effects of two types of postdispersal seed and seedling foraging strategies: the distance-responsive predator and the density-responsive predator as well as different patterns of dispersal. Strong host specificity whether facultative or obligatory is assumed for the model.

However, some plants do not have this problem. They are heavily hit by predispersal predators but predation by host-specific postdispersal seed or seedling predators is relatively minor. Seed and seedling survival is largely determined by physical, competitive and other factors of the site rather than by host-specific seed predators.

In some of these kinds of plants the seeds are hit too early in development for the plant to have much advantage in rushing dispersal. One strategy to deal with this is to produce more flowers and developing embryos than can be supported to maturity. Though many ovules and embryos may be

lost, the number that survive may still exceed the number which can be supported to mature seeds. Abortion of extra embryos would be part of this system.

For an outcrossing insect-pollinated plant, seed predators are not the only insects with which it must interact. Pollination, in addition to escape from seed predation, is important for seed production. Just as an energetically "wise" seed predator will likely choose the nearest desirable individual, we expect a "wise" pollinator to do likewise.

Thus we expect predispersal fitness in an obligately insect-pollinated plant species to be affected by pollinators and host-specific predators which are both influenced in their foraging by the dispersion of the adult flowering plants. Note that this concept may be integrated into other models in systems in which postdispersal predation is important or used directly in systems in which host-specific postdispersal predation is not important.

In this study I seek to model the effect of host-specific predispersal seed predators on the reproductive fitness of individuals in plant populations. Various parameters of the individuals are varied including distance to nearest neighbor, flower production, and plant size. I also seek to model the effects of these parameters on an obligately insect-pollinated species. Predictions are made from these models of a system in which both insect pollinators and host-specific predispersal seed predators are important.

The models were tested with data collected for natural populations of Baptisia australis, blue wild indigo, and B. leucophaca, plains wild indigo, on Kanza Prairie and the adjacent Dewey Ranch in Geary and Riley counties in Kansas.

MODEL DEVELOPMENT

I developed a series of models for how the reproductive aspects of a mature plant's fitness would vary with its isolation from other plants of its species. All models assume that the greatest mortality of ovules occurs by host-specific predators before seed dispersal. While it may be possible to relax this assumption, this was not done.

Isolation may be defined in terms of the relative isolation of a population from other populations, the size or density of the population in which an individual plant is growing, or the relative isolation of a plant within a population. The relative isolation of a plant within a population will be discussed here. Vandermeer (1974) inferred from a study of seed predation in a Guatemalan legume that isolation of an individual within a population rather than occurrence of an individual within a "sparse clump or a hyperdispersed area" contributed to a reduced predation rate.

Janzen (1970) defines two possible strategies of a seed predator which is seeking dispersed seed. The distance-responsive predator responds to the distance from the parent plant to a seed, irrespective of the distance between seeds. I visualize the distance-responsive predator as leaving a plant in search of seed but returning to the base plant periodically. For instance, after travelling a set distance from the plant without finding seed, the predator might return to the plant and then start searching for seed in a different direction. The distance-responsive predator would return to the plant after both successful and unsuccessful searches for seed. The density-responsive predator responds to the density

of seeds, irrespective of the distance of the seed from the parent; thus, the distance between seeds and number of seeds rather than the distance from the parent plant is the important parameter for the density-responsive predator. In the system Janzen modeled, the seed predator fed on seeds both before and after dispersal.

For Baptisia, a mobile predator moves from plant to plant. This mobile predator and/or its immature offspring attack the seeds on the parent plant. The predator strategies as defined by Janzen would not be strictly applicable since the dispersed seeds or juveniles are replaced by co-equal adult plants. In this type of case the distance response if it occurred would probably occur only on unsuccessful foraging trips. That is, the predator would return to its last occupied adult plant only if it did not find a new adult plant within a certain ecological distance. If no "ecologically close" plant is found the predator must leave the plant entirely. At that point chance events as well as biological properties of the insect will operate to determine which, if any, other plant will be found by the adult insect. In another type of distance response, the predator might return to the plant visually rather than physically. In this way it could cover the area around the base plant in concentric bands (the diameter would depend on the species, environmental constraints, etc.). If a new plant is found, it could theoretically become the new base plant. At the limits of its perception of the base plant, the predator would again have to leave the base plant entirely.

The density response might be manifest only in those cases where other plants are perceived before taking off and the plant with the most seeds is selectively attacked irrespective of its distance away relative

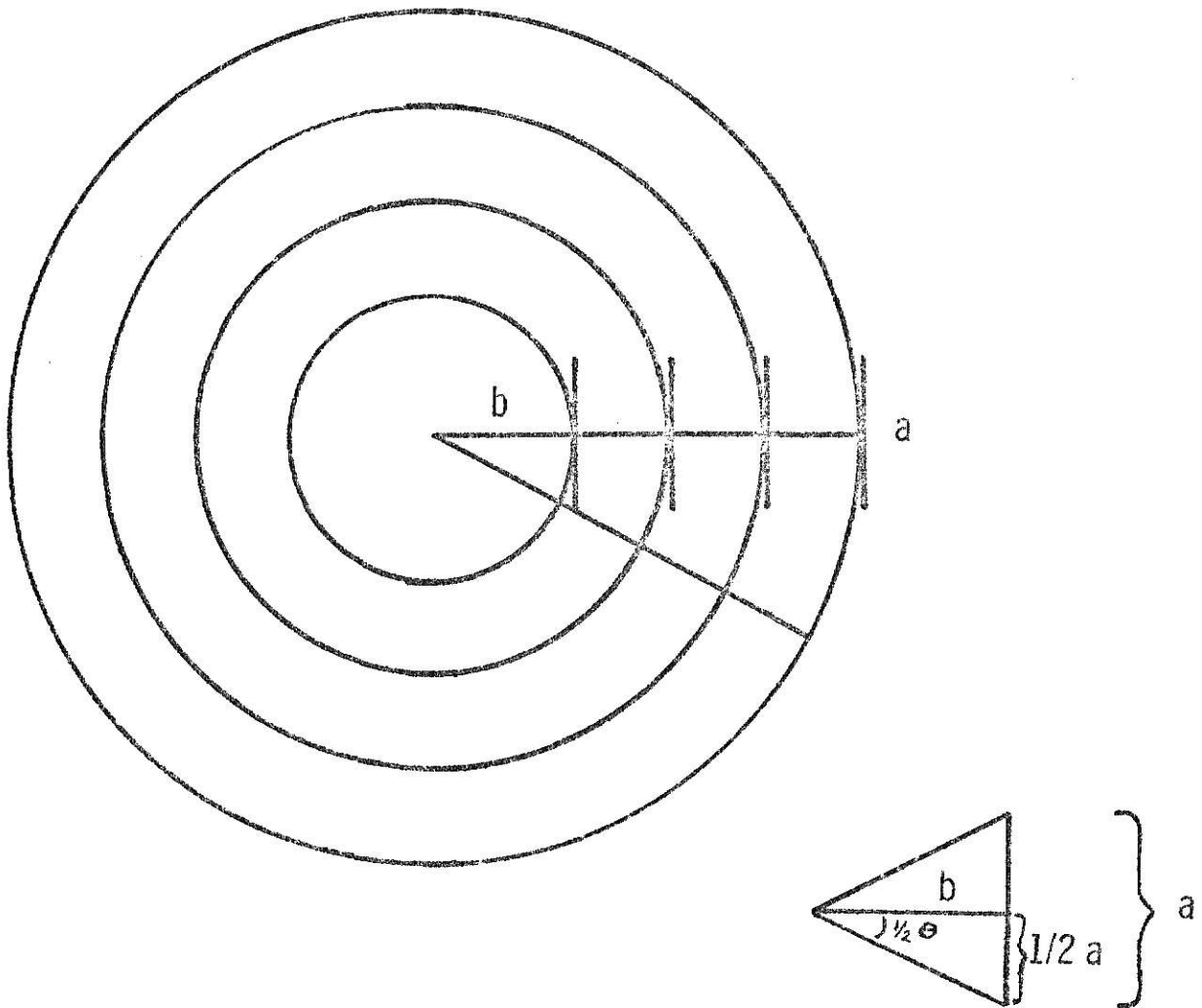
to the other plants within the distance of perception. Another type of density response would occur if the predator preferentially chose individuals which were in clumps. In fact both responses could occur within the same species of predator. For now let us assume that the plants in a population are equal with respect to potential seed production.

How would these responses affect a plant's fitness with increasing isolation? The distance response on unsuccessful foraging trips would theoretically lead to close plants being more likely to be found by predators than far ones. Likewise, the density response has to work within chance events and biological limits which themselves support a decrease in insect attack with increasing isolation. Thus, the density response would also reinforce greater infestation of near plants than far plants.

As the distance to another plant of the same species decreases, the probability of finding the neighbor should theoretically increase. To visualize this, picture a set of concentric circles around a point, which represents an insect on the base plant (see Figure 1). A plant of constant size is drawn on the concentric circles at various distances from the center plant. Note that the angle the neighboring plant intercepts decreases with distance. This relationship is: $\Theta = 2 \tan^{-1}(a/2b)$, where

Θ = the angle the neighboring plant intercepts, a = the width of the neighboring plant, and b = the distance to the neighboring plant. Thus, if the seed predator adult finds its host plant at random the probability of finding a more distant plant should be less than finding a nearer plant of equal size due to chance alone. If the seed predator adults use visual signals from its host plant the magnitude of these, too, are likely to decrease with distance (e.g., Meyer 1975). If the seed predator adults

Figure 1: The angle a plant intercepts on a weevil's horizon. The angle an object intercepts decreases the farther it is away from the point of observation. The center point represents the weevil. The line a represents a plant of size a at various distances b from the weevil. The angle θ is the angle the plant intercepts on the weevil's horizon. The angle θ is equal to $2 \arctan (a/2b)$.

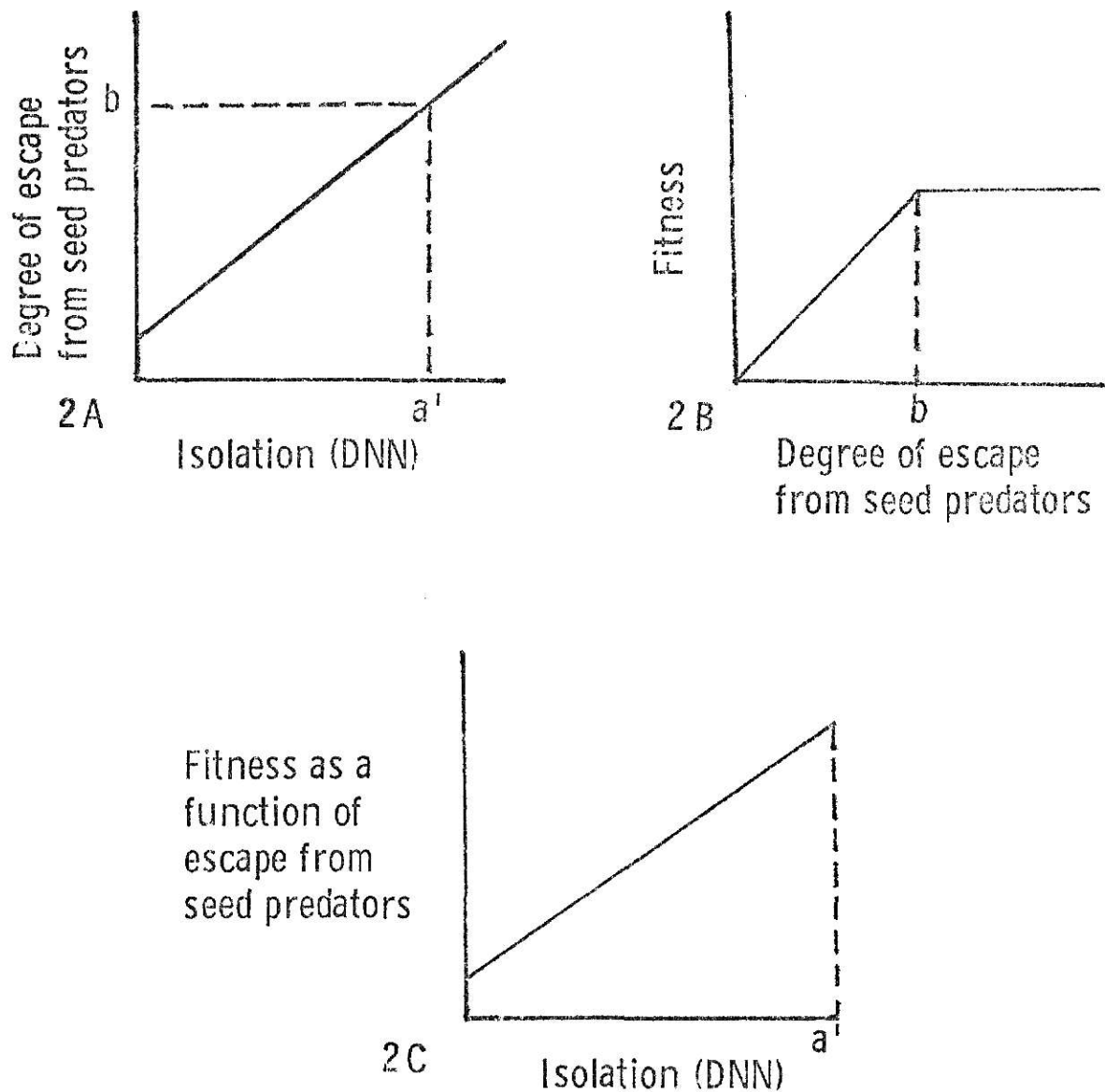


use olfactory signals and if plant chemicals are dispersed like moth sex attractants, these signals would likely remain strong for some distance (inversely proportional to wind speed) and then decrease with further distance (see model by Bossert and Wilson in Wilson, 1963, for the active space of the gypsy moth sex attractant). Biological and chance events may interact in determining the probability that a plant is attacked.

Thus, several lines of reasoning support the hypothesis that the probability that a plant will escape from host-specific herbivory increases with increasing isolation. An energy "wise" predator mentioned in the introduction would yield this result. Chance as well as biological limitations of the sensory apparatus of insects would yield this same prediction. Data from a tropical natural population of legumes (Vandermeer 1974) also support the hypothesis.

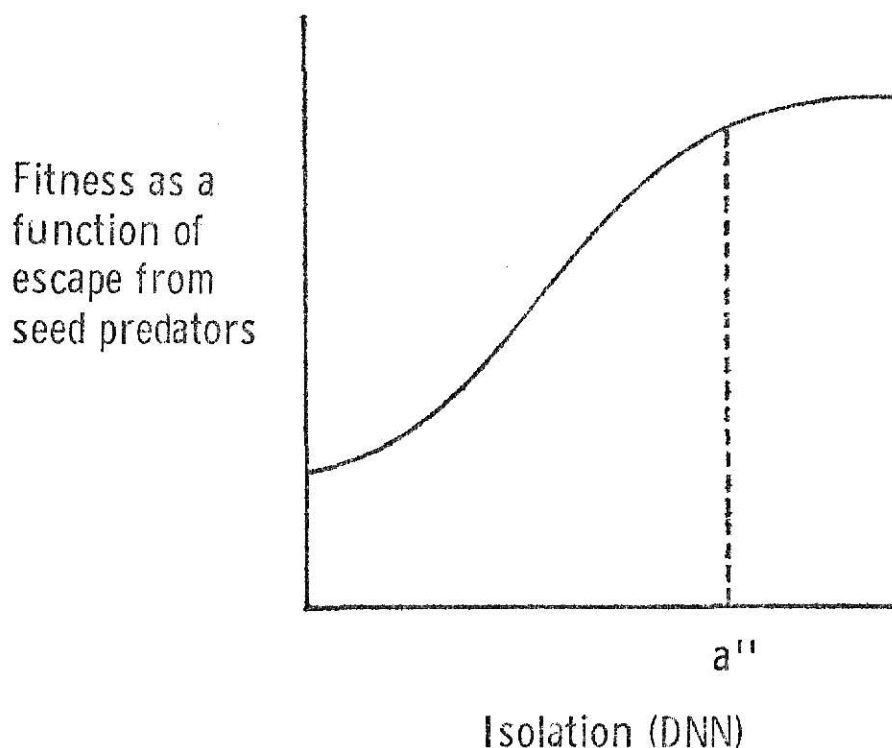
For flowering individuals attacked by host-specific seed predators a decrease in seed predation is expected with increasing isolation. Isolation may be measured as the distance to the nearest neighbor, which may be either its nearest neighbor of the same species, irrespective of reproductive condition, or its nearest flowering neighbor of the same species. Which of the two conditions would depend on the behavior of the host-specific insect. Some seed and fruit predators may be attracted first to the plant and secondarily after landing, to the flowers (Bush 1974). Others may be attracted only to plants with flowers. With the former behavior pattern, the distance to the closest neighbor would be a good measure whereas with the second type of behavior pattern, the distance to the nearest neighbor with flowers would be the better measure of isolation. This relationship is shown in its simplest form in Figure 2A.

Figure 2: Escape from seed predators and isolation. A, the degree of escape from seed predators increases with increasing isolation (DNN). B, fitness of a plant increases as the degree of escape from seed predators increases until the point at which more fertilized ovules escape predation than can be brought to maturity by the plant. C, fitness as a function of escape from seed predators increases as isolation (DNN) increases, for levels of escape below that which allows fertilized ovules to escape which can not be filled due to energy limitations. For a discussion of a' and b see the text.



As isolation increases the degree of escape from the seed predator also increases. Distance to nearest neighbor will for the rest of this section on model development be referred to by the acronym DNN and will be assumed to refer to the nearest neighbor of the same species of the plants (with or without flowers, depending on foraging strategy of the insect under question). Figure 2B shows that fitness should increase as the degree of escape from seed predation increases. Fitness no longer increases after the point at which more fertilized ovules escape predation than can be brought to maturity by the plant. This assumes that the plant has a mechanism to turn off energy to (1) excess fertilized ovules before a major energy expenditure is made and (2) fertilized ovules attacked by seed predators. In Figure 2A the degree of escape at b corresponds to a DNN, a' . Figure 2C shows that for levels of escape below that which allows fertilized ovules to escape which can not be filled (due to energetic limitations), fitness increases with isolation in a similar manner as the degree of escape does with isolation. Fitness is 1.0 at a' . Fitness and degree of escape from seed predators for an ovule are drawn as straight lines with positive slopes for reasons of mathematical simplicity. Due to behavioral characteristics of the predators, based on the sensory mechanisms of host plant recognition, the model might be more accurately drawn as in Figure 3. At "near" DNN's, minor differences in DNN may be relatively unimportant. All neighboring plants at these distances are perceived and easily reached. At distances further away approaching and beyond the limits of sensory perception, stochastic processes become increasingly important, eventually leading to only minor variations in fitness as a function of escape from seed predators at "large" distances. The magnitudes of "near"

Figure 3: Fitness as a function of escape from seed predators increases with certain increases in DNN. However at near DNN's, seed predators may perceive and easily reach most neighboring plants. Then there would be only slight increases or no relationship at all with increases in DNN. At very far DNN's the probability of being found is so low that the rate of increase in fitness with increasing DNN is greatly lowered. For a discussion of a'' see text.



and "large" DNN's would be determined by biological characteristics of the insects and plants. In the models I develop, assume that the importance of "near" DNN's are minor. Fitness varies little with DNN as the asymptotic part of the curve is reached. I shall model DNN's which occur in the region of maximum slope for reasons of mathematical simplicity and interest. The region of maximum slope approaches the straight line function of Figure 2C which will be used in developing the model. There is an upper limit to the relationship between DNN and fitness either because of the decreased slope of the function as the asymptote is reached in Figure 3 or because predation decreases to the point that the plant can not supply energy to fill all the surviving seeds (Figure 2B). DNN thus has biologically determined upper limits determined by a' in Figure 2 and a'' in Figure 3. The upper limit of DNN in this thesis is thus a' or a'' , whichever is lower. At this upper limit fitness as a function of escape from seed predation is defined to be 1.0. The lower limit of DNN is set at 0, although its biological interpretation may be open to question. At the lower limit of DNN, fitness as a function of escape from seed predators is not drawn as zero although it could be zero. Note that if fitness does not vary at "near" DNN's, an estimate of the intercept may be negative if based on the region of maximum slope (Figure 3).

The mode of sensory perception might easily affect the probability that a seed predator adult will sense a neighboring plant at various distances away. In laboratory studies, a herbivore, the alfalfa weevil, visually orients to the presence of alfalfa as long as the alfalfa subtends a certain angle in its field of vision (Meyer 1975). When the alfalfa forms at least that angle the ability of the weevil to orient towards the

alfalfa by visual means remains rather constant but is reduced as the critical angle approaches. At distances beyond, the alfalfa weevil orients toward alfalfa no better than at random. As shown in Figure 4, I would expect that the probability of visually orienting towards a neighboring plant to be relatively stable for distances close to the center plant. As the critical distance is reached I'd expect the probability to decrease and to eventually reach zero.

The ability to detect a plant by olfactory means is dependent on wind direction and distance to the plant. As mentioned earlier if plant kairomones act similarly to female moth sex pheromones (Wilson 1963), seed predators downwind from the plant may move upwind to the plant staying within certain levels of kairomone concentration. The kairomone concentration will remain high enough to stimulate a receptive insect for some distance and then fall off with additional distance. How far the kairomone will remain at a concentration high enough to stimulate receptive seed predators is dependent on wind speed and the resulting air turbulence.

Even though the concentration may remain high for long distances downwind, the farther the kairomone path travels from the plant the smaller the angle it will cut from the plant. The probability then that a seed predator will be downwind decreases with distance from the base plant in a similar manner as shown in Figure 1. Thus the probability of sensing a plant using olfactory means should decline with distance. This relationship is shown in Figure 5. Although the relationship is likely to be non-linear, linearity is assumed for simplicity since although the exact relationship is not known it should be monotonically decreasing. On the average for all plants, the nearest neighbor is as apt to be upwind as

Figure 4: Visual orientation with distance. The probability of visually orienting towards a neighboring plant may be relatively stable for near DNN's. As the critical distance is reached the probability should decrease and eventually reach zero.

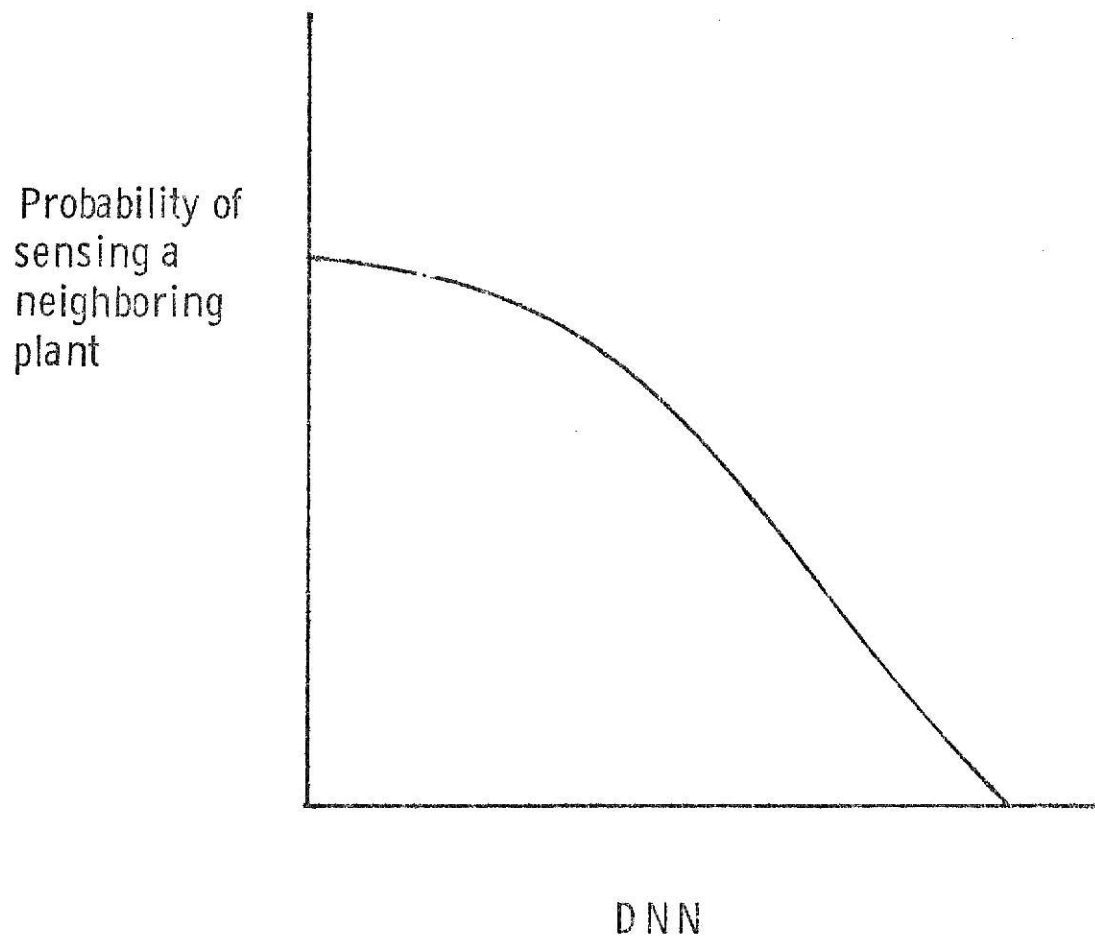
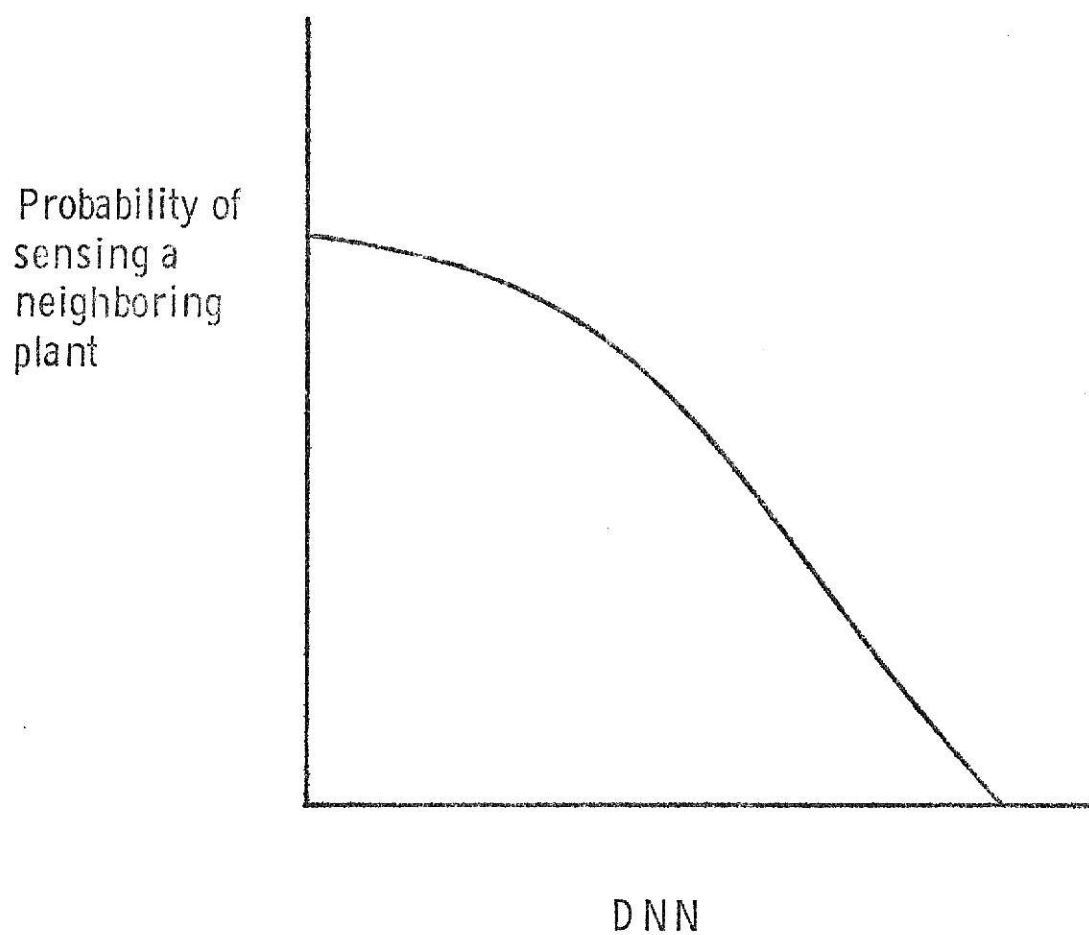


Figure 5: Olfactory orientation with distance. The probability of sensing a neighboring plant through olfactory means may be relatively stable for near DNN's. At more distant DNN's the probability should decrease to zero.

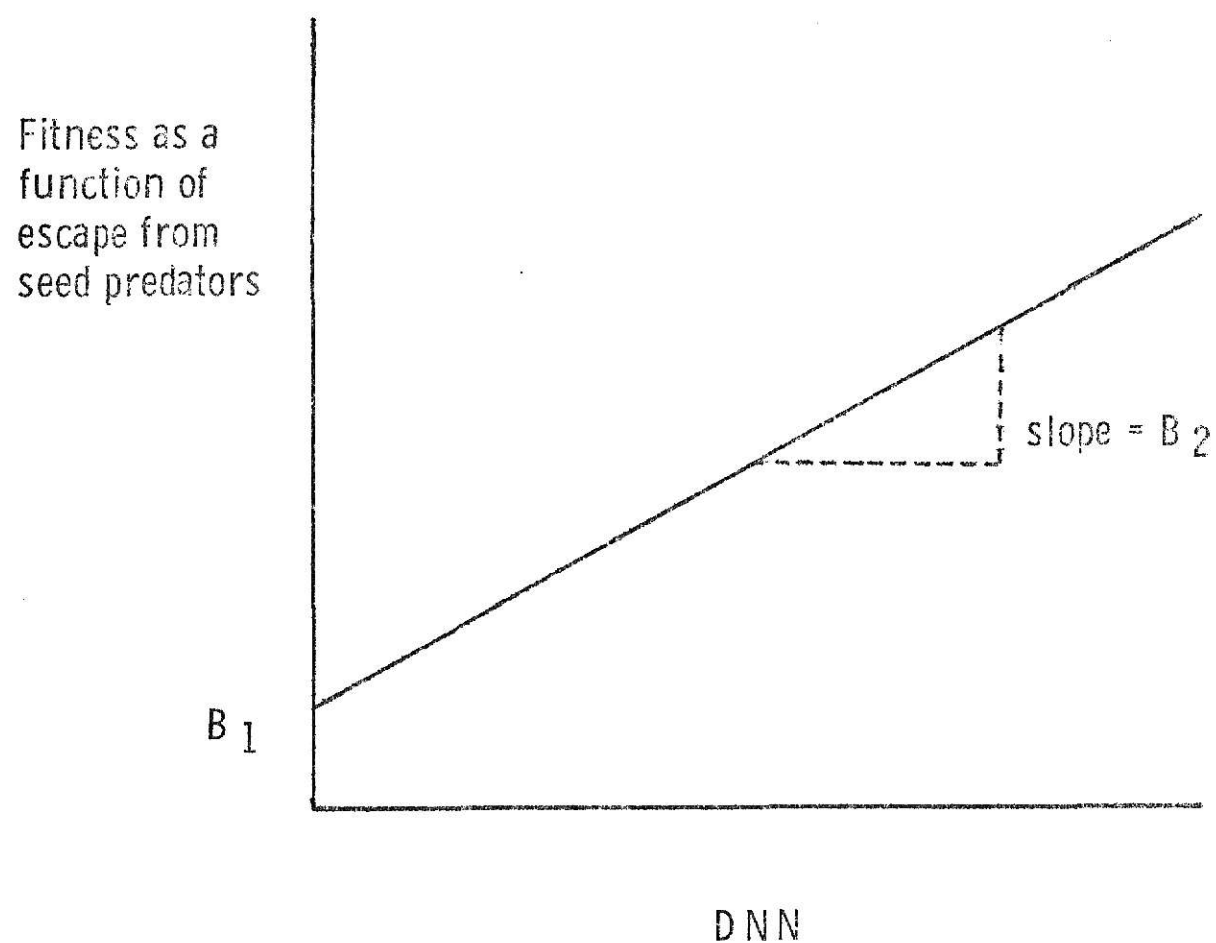


downwind or parallel to the plant. Dependence on the wind to carry kairomones will contribute to the variance of the hypothesized relationship between probability of being sensed and distance to nearest neighbor.

The conclusions to be drawn from the foregoing discussion are that (1) whatever the strategy or mechanism of orienting towards the host plant, the probability of the insect sensing the plant declines with DNN, and (2) within the limitations on DNN and degree of seed predation discussed earlier, fitness as affected by seed predation increases with DNN. Certain factors, like changing (or non-changing) wind direction or foraging strategy are likely only to increase the variance around, but not change the direction of, this general trend.

A graphical model of the relationship between fitness and distance (Model 1A) is shown in Figure 6. The dependent variable is fitness as a function of escape from seed predators. The number of filled, unattacked seeds a plant produces in a season divided by the largest number of filled, unattacked seeds produced by any plant in that season is a direct measure of fitness in an annual plant and an estimate of fitness in a perennial plant. The factors which affect this variable affect the fitness of a plant directly. In a perennial plant, the size or age of a plant may affect the amount of energy it can put into reproductive structures in any particular season without jeopardizing its reproductive future. Assuming that perennial plants are adapted to attempt the maximum number of seeds each year that will not jeopardize future reproduction to the point of reducing total expected life-time reproduction, then the percentage of attempted ovules that survive as seeds is a better estimate of fitness than is total number of seeds. The percentage of ovules that produce seeds that

Figure 6: Model 1A. Fitness as a function of escape from seed predators increases with DNN. The y intercept is B_1 and the slope of the line is B_2 .



survive predation is a particularly good estimate of fitness for the following models of the relationship between escape from seed predation and DNN. However, both measures of fitness are dependent on the degree of escape from seed predators as shown in Figure 2B. Fitness as a function of escape from seed predators may hereafter be referred to as Fitness(Escape) or F(Escape). The lower limit of fitness would be 0 and the upper limit 1.0. The mathematical model, Model 1A, may be derived from Figure 6 as follows. The y intercept is called B_1 and the slope of the line is B_2 . Thus we get:

$$\text{Fitness(Escape)} = B_1 + B_2(\text{DNN}) \quad (\text{Equation 1})$$

The limits are $0 \leq F(\text{Escape}) \leq 1.0$, $0 \leq B_1 \leq 1$, $0 \leq B_2 < \infty$ magnitude biologically determined and influenced by the units of measure of DNN, hereafter DNN units, $0 \leq \text{DNN} \leq \text{the smaller of } a' \text{ and } a''$, which is biologically and ecologically determined, and $0 \leq [B_1 + B_2(\text{DNN})] \leq 1.0$. Assume that these and all B quantities are not negative. Any negative quantities will be delineated as such in the sign before the B.

Neighbors at equal distances away may not be co-equal in attractiveness to the predators, as assumed earlier. Seed predators may be more attracted to plants with many flowers than to a plant with few flowers. On evolutionary grounds this would be expected since the potential food and shelter for their offspring is greater there. On mechanistic grounds, this would be expected since the signal is larger and therefore more apt to be sensed. Meyer (1975) found a size-distance relationship in laboratory studies with the alfalfa weevil. We could thus modify Model 1A as in Figure 7. Having all the lines start at a single point, B_1 , in

Figure 7: Model 1B. The rate of increase in fitness as a function of escape from seed predators with increasing DNN is greater for plants with fewer flowers.

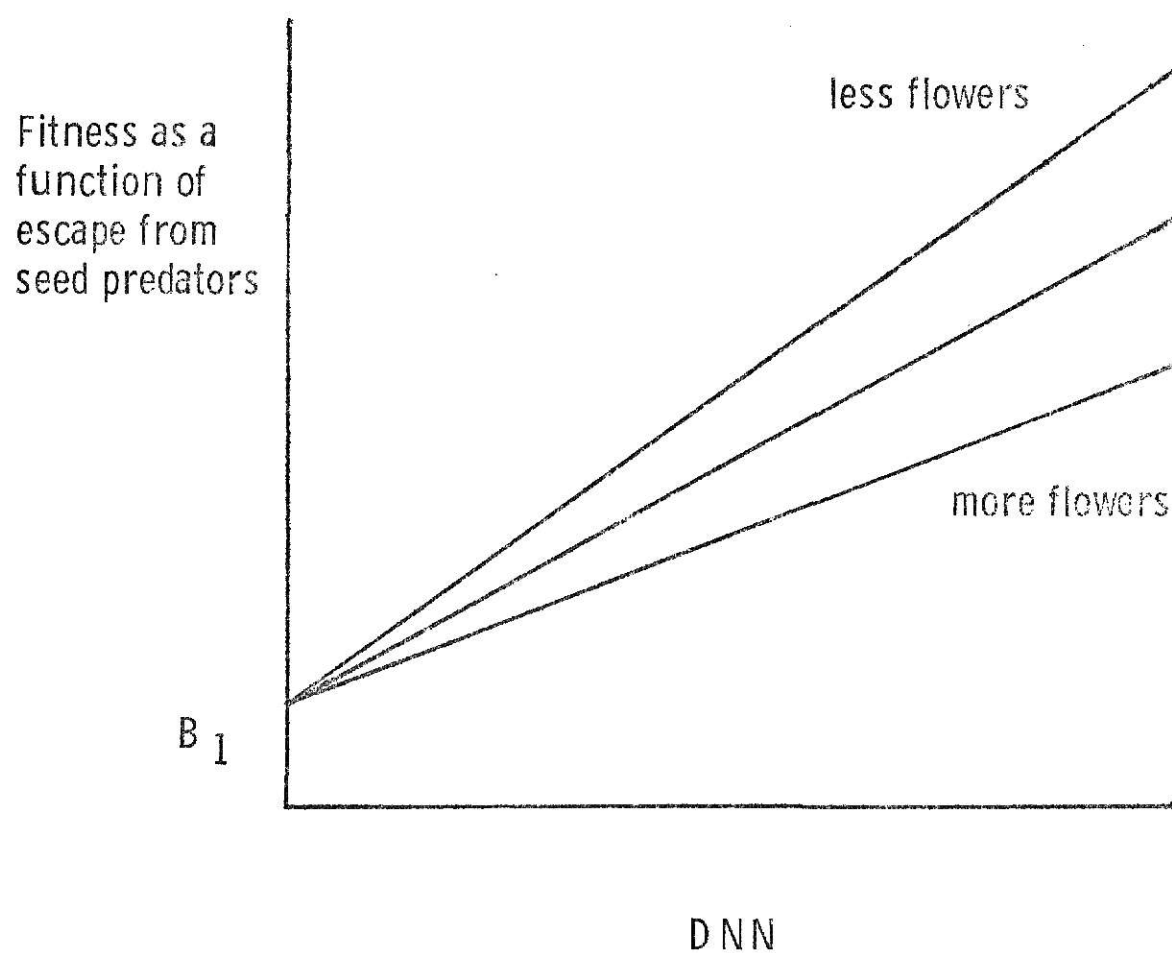


Figure 7 suggests that the number of flowers at close DNN's has less of an effect on Fitness(Escape) than at far DNN's. This reflects the greater ability of the insects to sense plants of whatever signal value at close distances. For simplicity, the relationship of the change in slope (B_2) with the number of flowers is shown as linear in Figure 8. B_{2a} is the y intercept on B_2 . The slope of the line is $-B_{3a}$. The mathematical model of this relationship is

$$B_2 = B_{2a} - B_{3a}(F) \quad (\text{Equation 2})$$

where F = the number of flowers. The limits are $0 \leq B_2, B_{2a}, B_{3a} < \infty$ magnitude biologically determined and influenced by DNN units, $0 < F \leq$ upper flower production capacity of the plant, and $0 < [B_{2a} - B_{3a}(F)] < \infty$ magnitude biologically determined and influenced by DNN units.

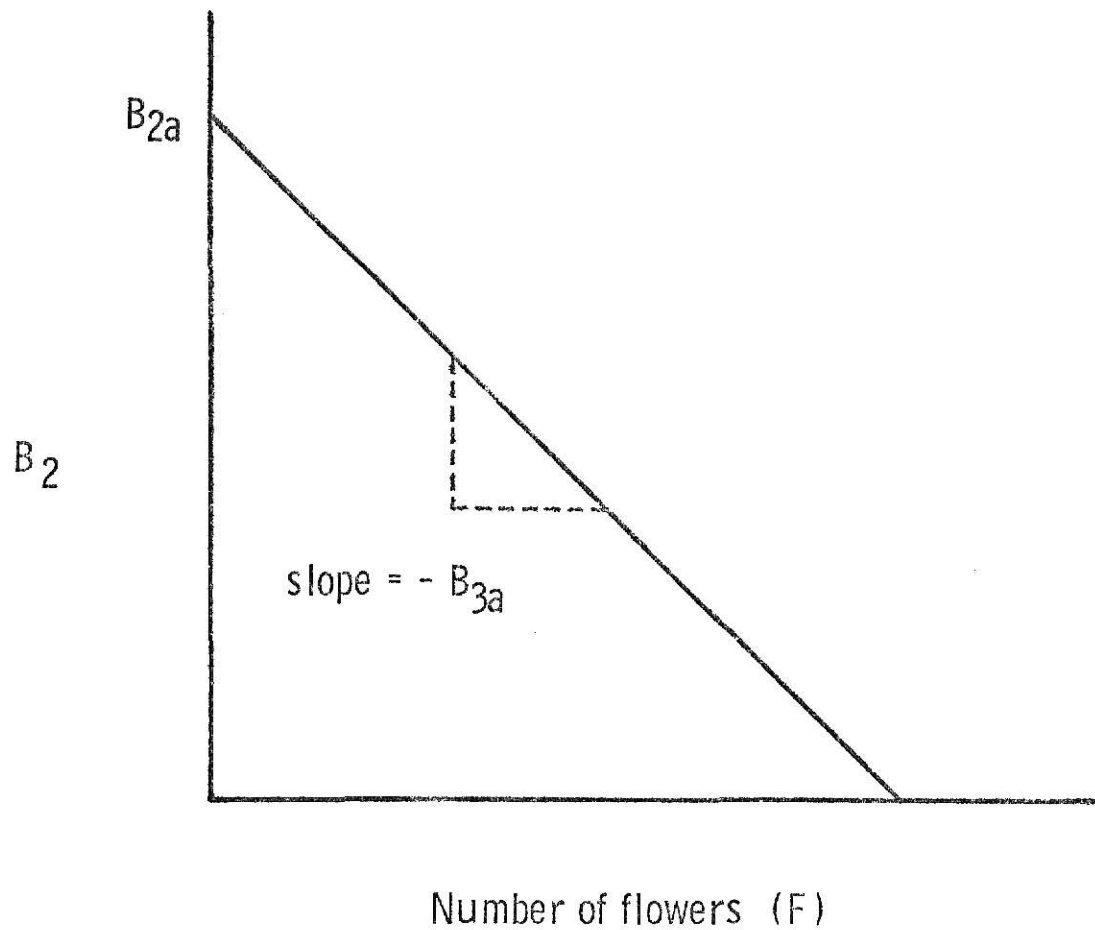
Substituting into Equation 1 we get Model 1B:

$$\text{Fitness(Escape)} = B_1 + B_{2a}(\text{DNN}) - B_{3a}(\text{DNN})(F) \quad (\text{Equation 3})$$

The limits of each element in Equation 3 are those described for Equations 1 and 2. Again, $0 \leq [B_1 + B_{2a}(\text{DNN}) - B_{3a}(\text{DNN})(F)] \leq 1.0$.

I assumed that the increase in attractiveness is directly proportional to the increase in the number of flowers. This yields the linear relationship shown in Figure 8. If attractiveness increased at a slower rate than the rate of increase in number of flowers, then by increasing the number of its flowers, a plant could satiate any additional insects attracted and still have additional flowers (and ovules) left over to mature. If attractiveness increased at a rate faster than the rate of increase in number of flowers, a plant could lose more than it would gain by increasing the number of flowers. In fact, the change in rates of

Figure 3: The slope of the relationship between fitness as a function of escape from seed predators and DNN decreases with an increasing number of flowers on a plant. The y intercept is B_{2a} and the slope is $-B_{3a}$.



attractiveness with number of flowers might depend on the number of flowers itself or on other parameters.

In outcrossing species, seed production is dependent on pollination as well as avoidance of seed predators. To maximize outcrossing a flower must give enough reward to attract the pollinator but also limit it so that the pollinator will move on to other plants (Heinrich and Raven 1972). Animal pollinators usually concentrate their foraging on one plant species according to Grant (1949).

While the evolutionary and ecological interactions between pollinators and flowers are often quite complex, Heinrich and Raven (1972) note that the distance between flowers is one of the factors affecting the energy balance relationships between flowering plants and pollinators. The distance between flowers is ultimately limited by the plant population density but can be altered by the time and duration of flowering (Heinrich and Raven 1972).

Levin et al. (1971) observed that bees and butterflies tend to move in the same general direction on successive flights but note that this does not mean that the foraging trips as a whole are strongly directional. They hypothesize that flight directionality by the insects may be an adaptation to avoid returning to the same plant soon after a previous visit. They suggest that in plant populations with low densities the "pollinators will move from a plant to one of its nearest neighbors without regard to direction of the previous move." Studies by Levin and Kerster (1967) on Phlox which is pollinated by butterflies and by Levin (1968) on Lithospermum which is pollinated primarily by bees show that "both vectors usually work several flowers per plant, and then move to one of the plant's nearest neighbors" (Levin, et al. 1971).

Thus, as in the case with seed predators, several avenues lead to the idea that fitness as a function of pollination is in turn a function of isolation, of which DNN appears a very appropriate measure. The same measures used for Fitness(Escape) may be used in a similar manner for fitness as a function of pollination. This may be seen graphically in Figure 9, where B_4 is the intercept and $-B_5$ is the slope. This relationship may be expressed mathematically as:

$$\text{Fitness as a function of pollination} = B_4 - B_5(\text{DNN}) \quad (\text{Equation 4})$$

Fitness as a function of pollination may hereafter be referred to as Fitness(Pollination) or $F(\text{Pollination})$. The limits are $0 \leq \text{Fitness(Pollination)} \leq 1.0$, $B_4 = 1.0$, $0 < B_5 < \infty$ magnitude determined biologically and by units of DNN, $0 \leq \text{DNN} \leq a'''$, which is biologically and ecologically determined, and $0 \leq [B_4 - B_5(\text{DNN})] \leq 1.0$.

This model might be more realistically drawn as shown in Figure 10. At near DNN's differences in DNN may be relatively unimportant as all the neighbors are perceived and relatively easily reached. At DNN's far away stochastic processes become increasingly important and Fitness(Pollination) becomes asymptotic. Again "near" DNN's will be assumed to be of minor importance and "far" DNN's in the asymptotic part of the curve will be beyond the limits of DNN in the model (a''' in Figure 10). Thus DNN in Equation 4 has as its upper limit a''' in Figure 10. Its magnitude has strong biological and ecological components. The biologically interesting part of the curve is approximated by a straight line with a negative slope as in Figure 9.

To find the fitness as a function of escape from seed predators and of pollination for outcrossing plant species which are attacked by

Figure 9: Fitness as a function of pollination decreases with increasing DNN. The y intercept is B_4 and the slope is $-B_5$.

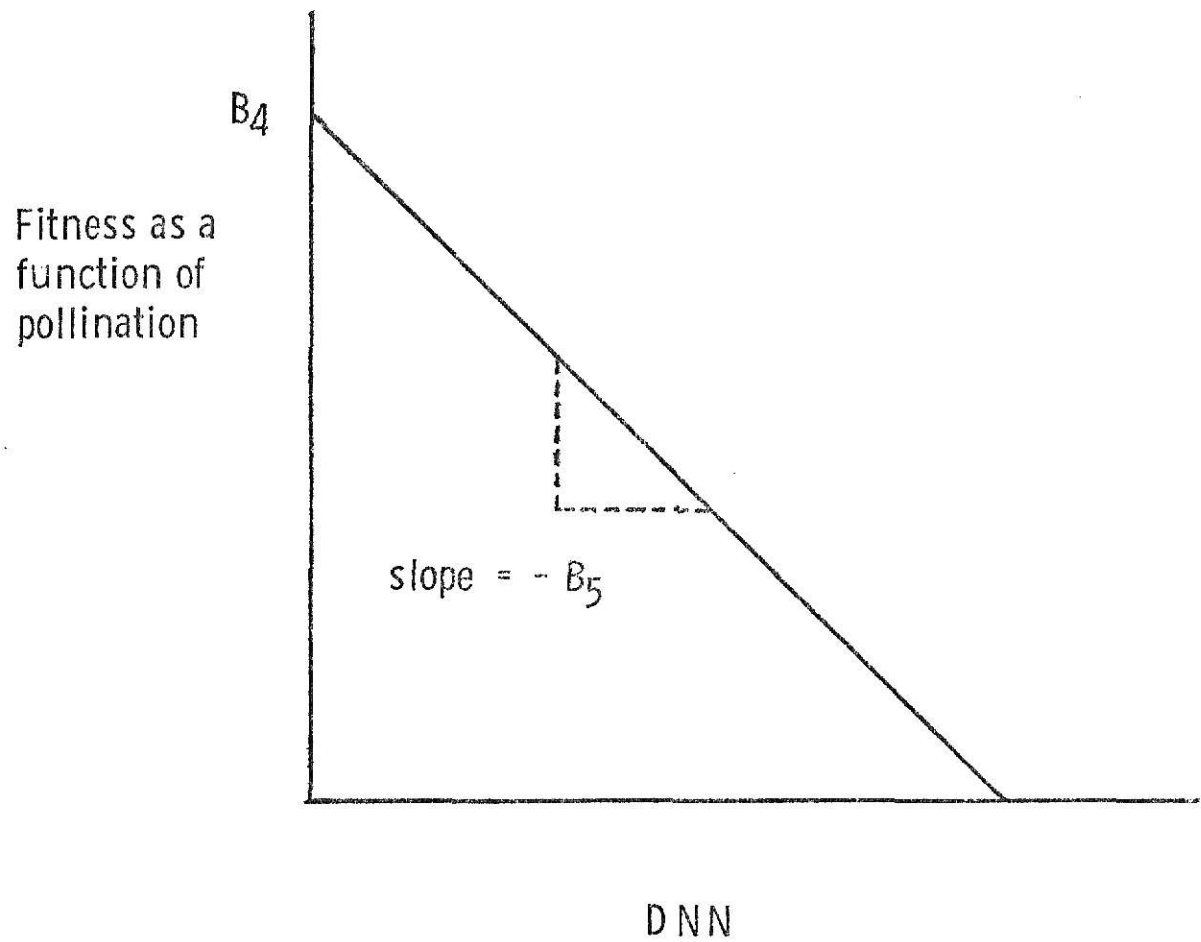
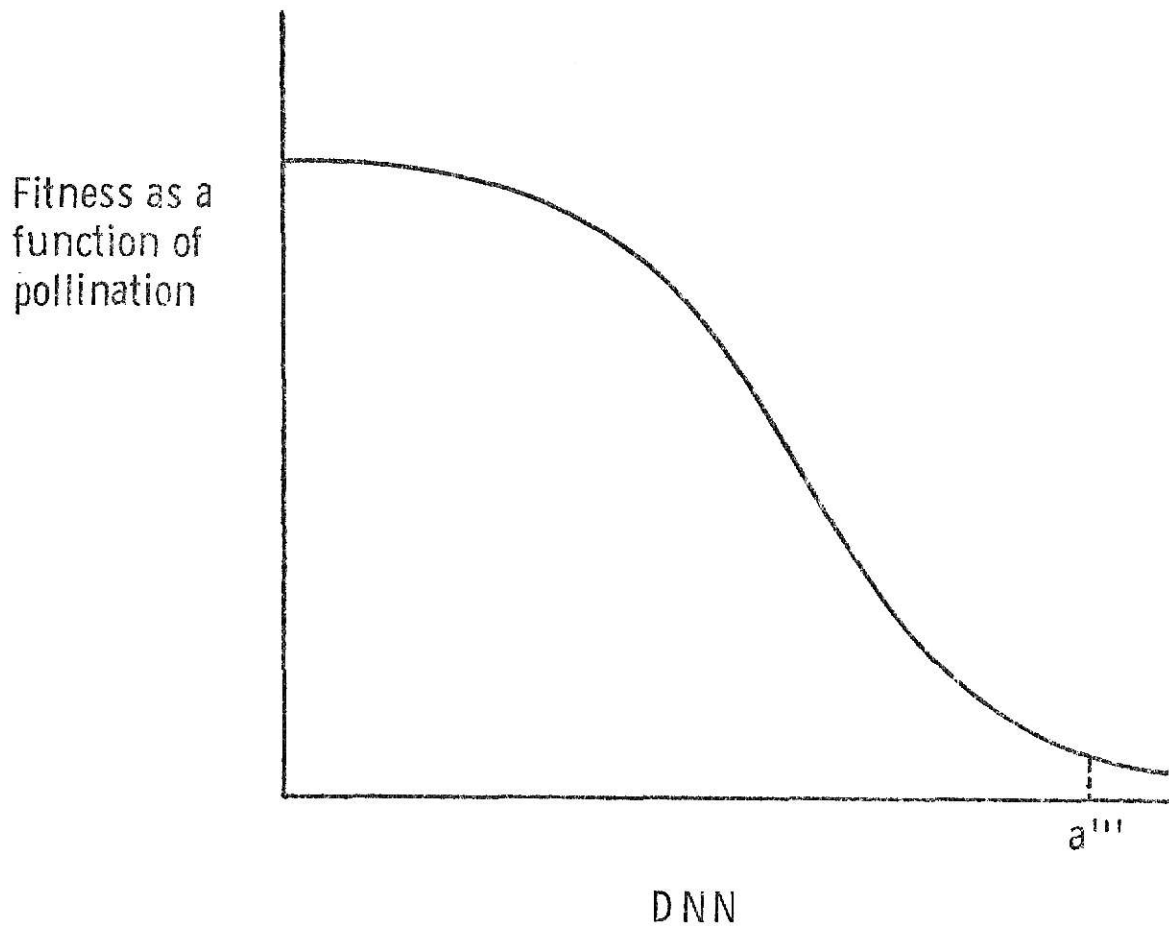


Figure 10: Fitness as a function of pollination decreases with certain increases in DNN. However, at near DNN's, pollinators may perceive and easily reach most neighboring plants. Then there would be only a slight decrease or no relationship at all with increases in DNN. At very far DNN's, the probability of pollination is so low that decreases in it with increasing DNN are minimal. Then the probability of pollination becomes asymptotic.



host-specific seed predators, we may combine Figure 6 and 9 as shown in Figure 11. The product of the two lines, which may be termed Fitness (Success), is shown as a curve which increases to a maximum and then declines. This maximum represents an optimal distance from a nearest neighbor. The mathematical model of this product is the product of Equations 1 and 4:

$$\text{Fitness(Success)} = B_1B_4 + (B_2B_4 - B_1B_5)\text{DNN} - B_2B_5(\text{DNN})^2 \quad (\text{Equation 5})$$

The derivation of Equation 5 (Model 2) is found in Appendix 1. In setting limits on both B values and variables in fitness equations, whatever is on the right of the equation must yield $0 \leq \text{a value} \leq 1.0$. Specific limits are difficult to make because of the interaction between DNN and B values in terms of magnitude as well as ecological and biological components. The most efficient way to assign limits in a more complex model such as in Equation 5 is to assign limits to B values and variables in the simpler equations from which it was derived. As long as proper algebraic procedures are used, $0 \leq \text{Fitness(Success)} \leq 1.0$. The limits of individual B values are those assigned in Equations 1 and 4. In this model $0 \leq \text{DNN} \leq \text{the smallest of } a', a'', \text{ and } a'''$, as seen in Figures 2, 3, and 10. The magnitude of fitness at the least of these DNN's is determined by the relative size of $a', a'', \text{ and } a'''$, which is a function of the biology and ecology of the insects and plants. Equation 5 may be simplified to

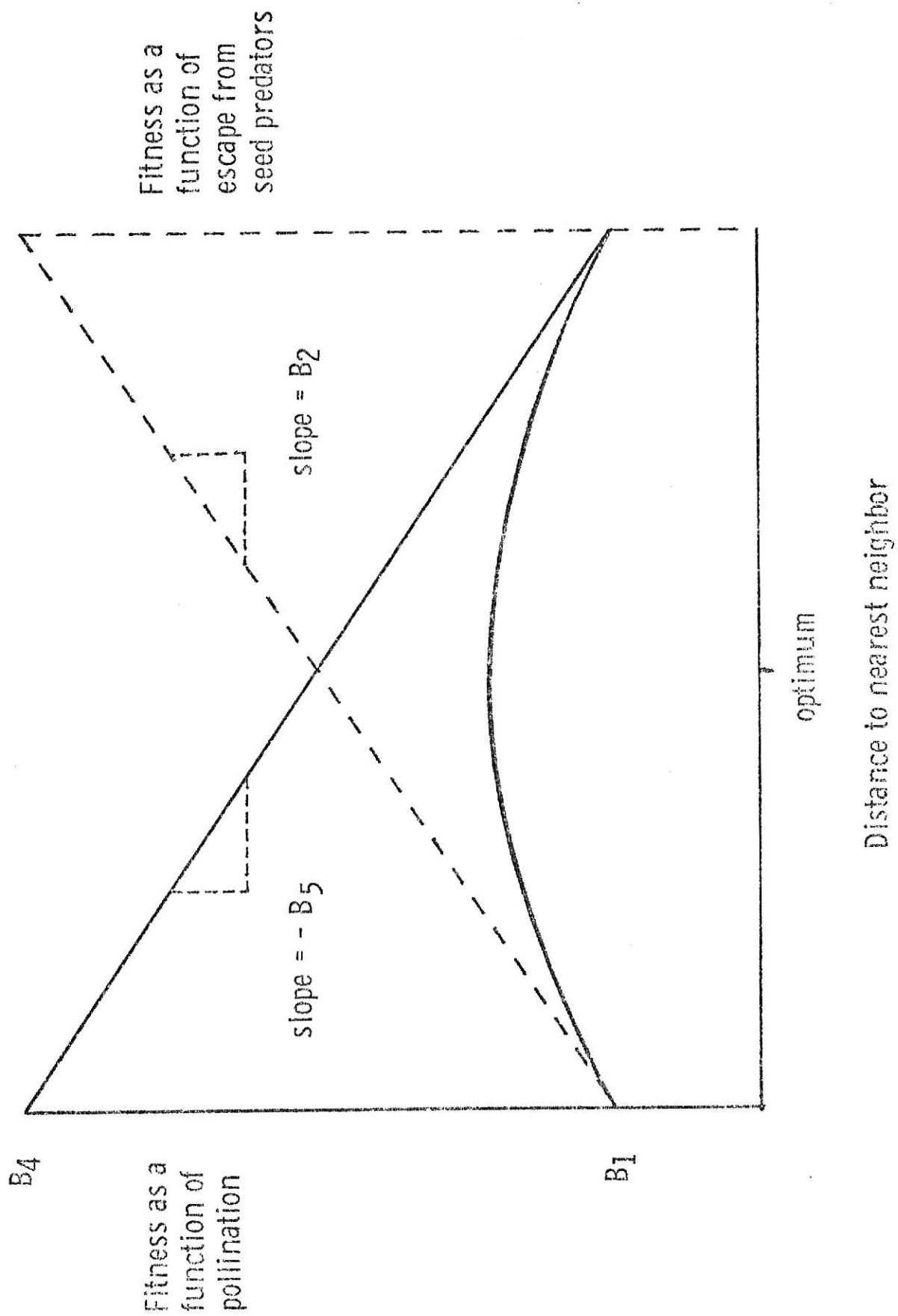
$$\text{Fitness(Success)} = B_7 + B_8(\text{DNN}) - B_9(\text{DNN})^2 \quad (\text{Equation 6})$$

where $B_7 = B_1B_4$, $B_8 = B_2B_4 - B_1B_5$, and $B_9 = B_2B_5$. In this case the limits are as follows: $0 \leq \text{Fitness(Success)} \leq 1.0$, $0 \leq B_7 < 1$, B_8 negative, zero, or positive, its magnitude and sign biologically determined and influenced by DNN units, $0 < B_9 < \infty$ magnitude biologically determined and influenced by

Figure 11: Model 2. Fitness(success) for outcrossing plant species which are attacked by host-specific seed predators may be depicted as the product of the Fitness(Pollination) curve (Fig. 9) and the Fitness(Escape) curve (Fig. 6). For the escape line, the y intercept is B_1 and the slope is B_2 . For the pollination line, the y intercept is B_4 and the slope is $-B_5$.

**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.**



DNN units, $0 \leq \text{DNN} \leq \text{the smallest of } a', a'', \text{ and } a'''$, which are biologically and ecologically determined, and $0 \leq [B_7 + B_8(\text{DNN}) - B_9(\text{DNN})^2] \leq 1.0$.

An assumption of the models in Figure 9 and 11 is that neighbors at equal distances are co-equal in attractiveness. However, pollinators may be more attracted to plants with many flowers than to a plant with few flowers. On evolutionary grounds, a plant with many flowers may be more attractive because a pollinator can get more nectar and/or pollen there. On mechanistic grounds, the plant with many flowers may provide a larger signal to the pollinator. We can thus modify the model in Figure 9 as in Figure 12.

For simplicity the relationship of the change in absolute value of the slope (B_5) with the number of flowers is shown as linear in Figure 13. B_{5a} is the y intercept on B_5 and $-B_{6a}$ is the slope of the line. The mathematical model of this relationship is

$$B_5 = B_{5a} - B_{6a}(F) \quad (\text{Equation 7})$$

The limits are as follows: $0 < B_5, B_{5a}, B_{6a} < \infty$ magnitude biologically determined and influenced by DNN units, and $0 < F \leq \text{upper flower production capacity of the plant}$. The values of the B's and F must be such that $0 < [B_{5a} - B_{6a}(F)] < \infty$ magnitude biologically determined and influenced by DNN units.

Substituting into Equation 4 we get

$$\text{Fitness(Pollination)} = B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN}) \quad (\text{Equation 8})$$

The limits are as follows: $0 \leq \text{Fitness(Pollination)} \leq 1.0$, $B_4 = 1.0$, $0 < B_{5a}, B_{6a} < \infty$ magnitude biologically determined and influenced by DNN, $0 < F \leq \text{upper flower production capacity of the plant}$, $0 \leq \text{DNN} \leq a'''$, which

Figure 12: Fitness as a function of pollination and the effect of the number of flowers. Fitness decreases with DNN more rapidly the fewer the flowers a plant has.

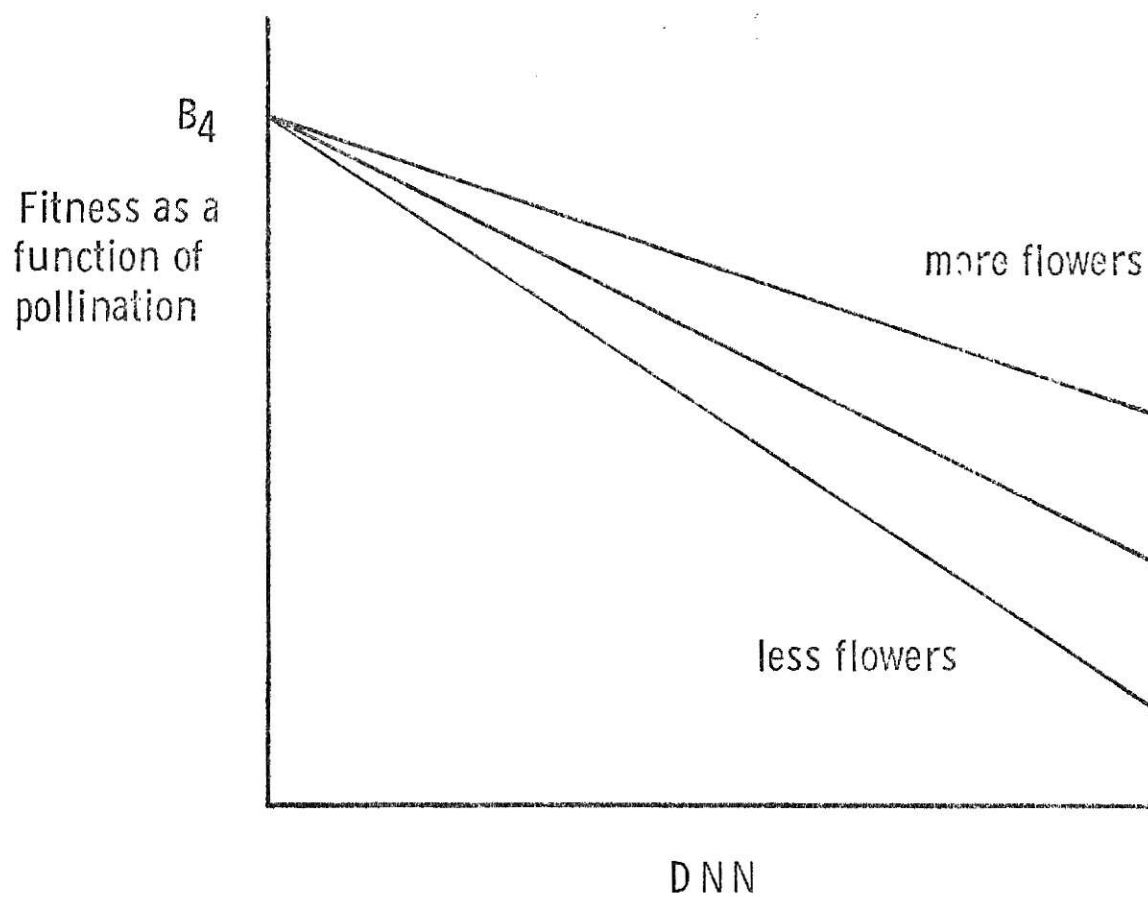
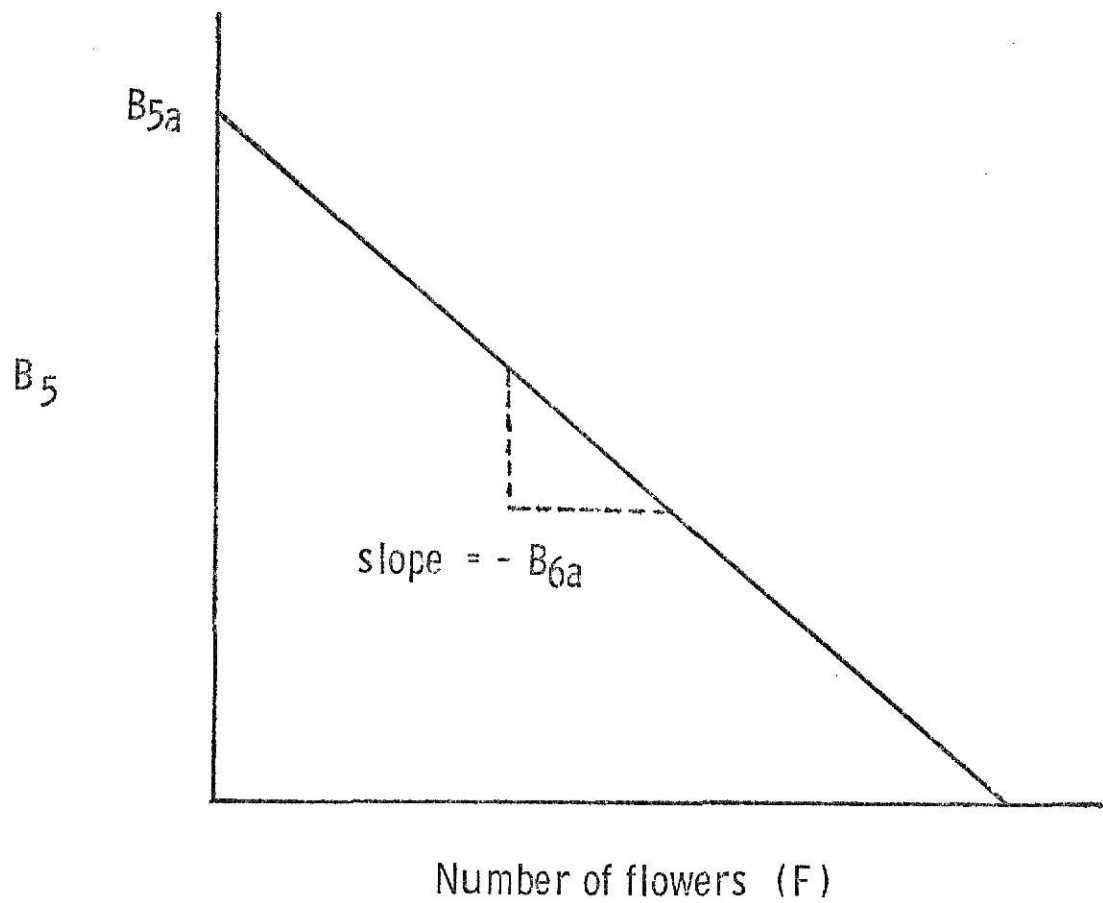


Figure 13: The absolute value of the slope of the relationship between fitness as a function of pollination and DNN decreases with an increasing number of flowers on a plant. The y intercept is B_{5a} and the slope is $-B_{6a}$.



is biologically and ecologically determined, and $0 \leq [B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})] \leq 1.0$.

We can alter Figure 11 to include this relationship between pollination and the number of flowers as shown in Figure 14. Fitness(Success) is represented by the product of these 2 sets of curves. This may be expressed in mathematical form as follows:

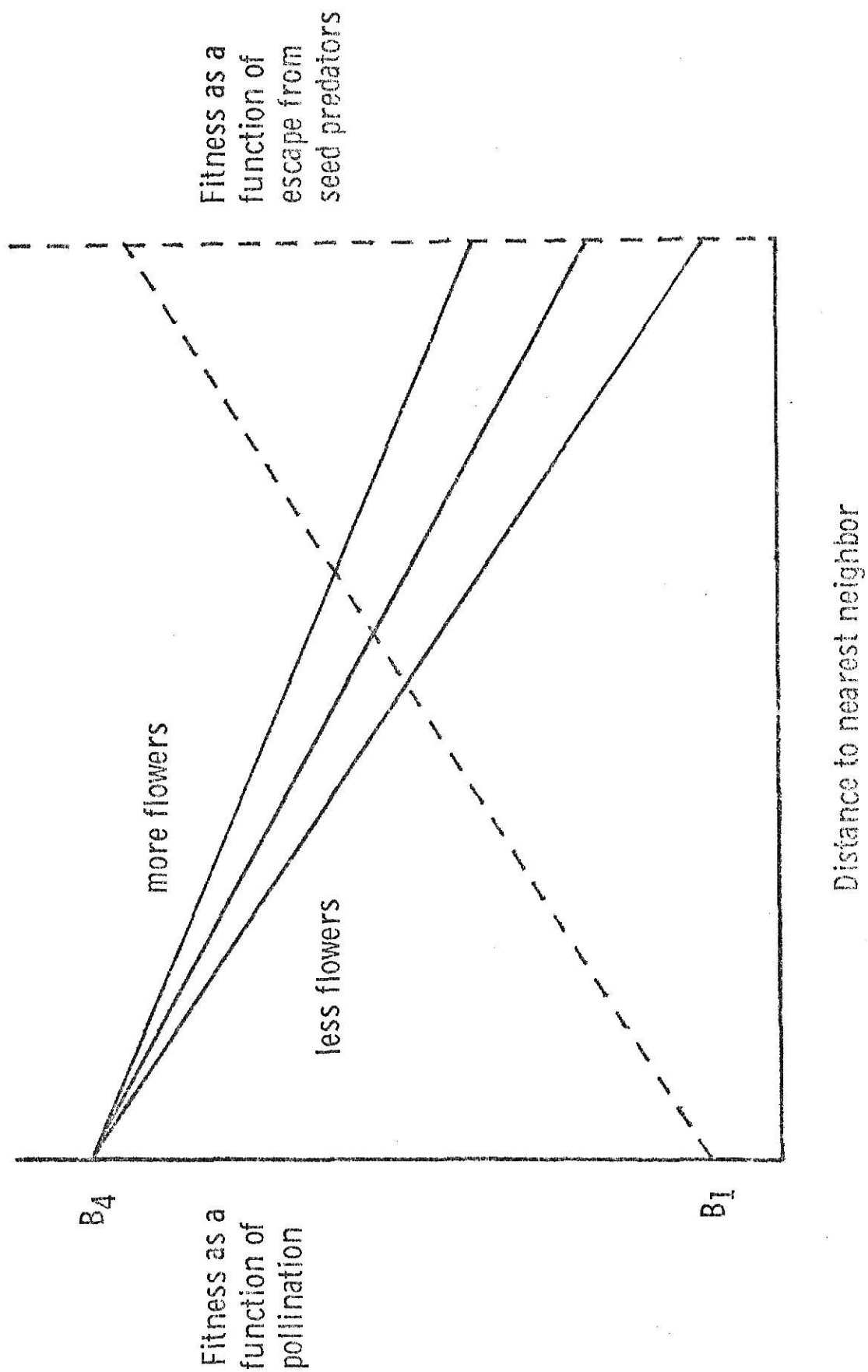
$$\begin{aligned} \text{Fitness(Success)} = & B_1 B_4 + (B_2 B_4 - B_1 B_{5a}) \text{DNN} \\ & + B_1 B_{6a} (F)(\text{DNN}) - B_2 B_{5a} (\text{DNN})^2 + B_2 B_{6a} (F)(\text{DNN})^2 \end{aligned} \quad (\text{Equation 9})$$

The derivation of Equation 9 (Model 3A) is in Appendix II. The limits of each B value are those previously described for Equations 1, 4, 7, and 8, with $0 \leq \text{DNN} \leq$ the smallest of a' , a'' , and a''' , which are biologically and ecologically determined. The limits of either side of the equation are from 0 to 1.0. Equation 9 may be simplified to:

$$\begin{aligned} \text{Fitness(Success)} = & B_7 + B_{10}(\text{DNN}) + B_{11}(F)(\text{DNN}) \\ & - B_{12}(\text{DNN})^2 + B_{13}(F)(\text{DNN})^2 \end{aligned} \quad (\text{Equation 10})$$

where $B_7 = B_1 B_4$, $B_{10} = B_2 B_4 - B_1 B_{5a}$, $B_{11} = B_1 B_{6a}$, $B_{12} = B_2 B_{5a}$, and $B_{13} = B_2 B_{6a}$. The limits are as follows: $0 \leq \text{Fitness(Success)} \leq 1.0$, $0 \leq B_7 \leq 1.0$, B_{10} : negative, zero, or positive, its magnitude and sign biologically determined as well as being influenced by DNN units, $0 \leq B_{11} \leq$ magnitude biologically determined and influenced by DNN units, $0 \leq B_{12} \leq$ magnitude biologically determined and influenced by DNN units, $0 \leq B_{13} \leq$ magnitude biologically determined and influenced by DNN units, $0 \leq F \leq$ upper flower production capacity of the plant, $0 \leq \text{DNN} \leq$ the smallest of a' , a'' , and a''' , which are biologically and ecologically determined, and $0 \leq [B_7 + B_{10}(\text{DNN}) + B_{11}(F)(\text{DNN}) - B_{12}(\text{DNN})^2 + B_{13}(F)(\text{DNN})^2] \leq 1.0$. The optimal distance to its nearest neighbor depends on the number of flowers a plant has and vice versa. This optimal distance increases as the number of

Figure 14: Model 3A. Fitness as a function of pollination is modified by the number of flowers as well as DNN and fitness as a function of escape from seed predators is modified by DNN as shown. The mathematical model of the product of the curves is found in Equations 9 and 10.



flowers increases. Fitness(Success) also increases with the number of flowers.

The model as shown in Figure 14 assumes that the number of flowers does not affect Fitness(Escape). If seed predators are more attracted to plants with many flowers as shown in Figure 7 we may modify Figure 14 to that shown in Figure 15. The product of these 2 sets of curves may be expressed in mathematical form as follows:

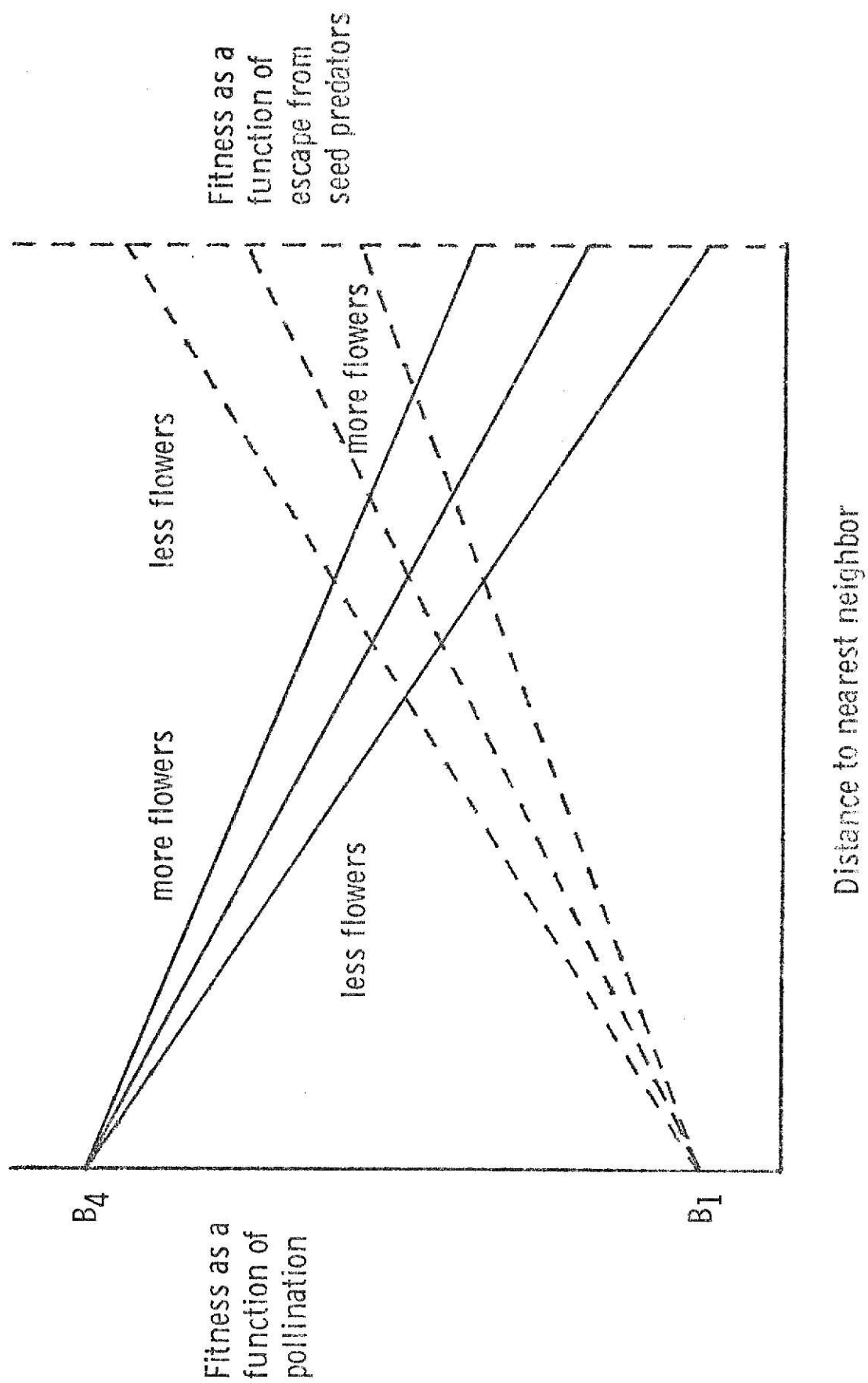
$$\begin{aligned} \text{Fitness(Success)} &= B_1B_4 + (B_{2a}B_4 - B_1B_{5a})(DNN) \\ &+ (B_1B_{6a} - B_{3a}B_4)(F)(DNN) - B_{2a}B_{5a}(DNN)^2 \\ &+ (B_{2a}B_{6a} + B_{3a}B_{5a})(F)(DNN)^2 - B_{3a}B_{6a}(F)^2(DNN)^2 \end{aligned} \quad (\text{Equation 11})$$

The derivation of Equation 11 (Model 3) is in Appendix III. The limits of each B value and F are those previously described for Equations 1, 2, 3, 4, 7, and 8, with $0 \leq DNN \leq \text{the smallest of } a', a'', \text{ and } a'''$, which are biologically and ecologically determined. The limits of either side of the equation are from 0 to 1.0. Equation 11 may be simplified to:

$$\begin{aligned} \text{Fitness(Success)} &= B_7 + B_{14}(DNN) + B_{15}(F)(DNN) \\ &- B_{16}(DNN)^2 + B_{17}(F)(DNN)^2 - B_{18}(F)^2(DNN)^2 \end{aligned} \quad (\text{Equation 12})$$

where $B_7 = B_1B_4$, $B_{14} = B_{2a}B_4 - B_1B_{5a}$, $B_{15} = B_1B_{6a} - B_{3a}B_4$, $B_{16} = B_{2a}B_{5a}$, $B_{17} = B_{2a}B_{6a} + B_{3a}B_{5a}$, $B_{18} = B_{3a}B_{6a}$. The limits are $0 \leq \text{Fitness(Success)} \leq 1.0$, $0 \leq B_7 < 1.0$, B_{14} , B_{15} : negative, zero, or positive, the magnitude and sign biologically determined and influenced by DNN, $0 < B_{16}$, B_{17} , $B_{18} < \infty$ magnitude biologically determined and influenced by DNN units, $0 < F \leq \text{upper flower production capacity of the plant}$, and $0 \leq DNN \leq \text{the smallest of } a', a'', \text{ and } a'''$, which are biologically and ecologically determined. The

Figure 15: Model 3. Fitness as a function of pollination and fitness as a function of escape from seed predators are modified by the number of flowers as well as DNN is shown.



limits of either side of the equation are from 0 to 1.0. The optimum distance to the nearest neighbor increases continuously with increasing flower number.

Attractiveness to seed predators may also be affected by the size of the plant. On evolutionary grounds we might expect larger plants to be more attractive. A plant with good growth would provide better protection for the seed predator itself. It would also be more likely to produce shelter and food for its offspring. On mechanistic grounds, especially for those insects which initially orient to the whole plant, a larger plant would provide a larger signal and therefore be more apt to be sensed. If we assume the number of flowers to be equal, the effect of plant size on Fitness(Escape) with DNN is seen in Figure 16. Figure 17 shows graphically how the slope of the line might change with plant size. This may be stated mathematically as:

$$B_2 = B_{2b} - B_{3b}(\text{Size}) \quad (\text{Equation 13})$$

The limits are $0 < B_2, B_{2b}, B_{3b} < \infty$ magnitude biologically determined and influenced by DNN units, $0 < \text{Size} \leq \text{upper size limit of the plant}$, and $0 < [B_{2b} - B_{3b}(\text{Size})] < \infty$ magnitude biologically determined and influenced by DNN units.

Equation 13 may be substituted into Equation 1 to yield the following model for plants in which flower number is held constant.

$$\text{Fitness(Escape)} = B_1 + B_{2b}(\text{DNN}) - B_{3b}(\text{Size})(\text{DNN}) \quad (\text{Equation 14})$$

The limits of each element in Equation 14 are those described for Equation 1 and 13, such that $0 \leq [B_1 + B_{2b}(\text{DNN}) - B_{3b}(\text{Size})(\text{DNN})] \leq 1.0$.

If both the number of flowers and plant size have an impact on host selection we may combine Equations 2 and 13 to get:

Figure 16: Fitness as a function of escape from seed predators increases with DNN more for small plants than for large plants. The y intercept is B_1 and the slope is B_2 .

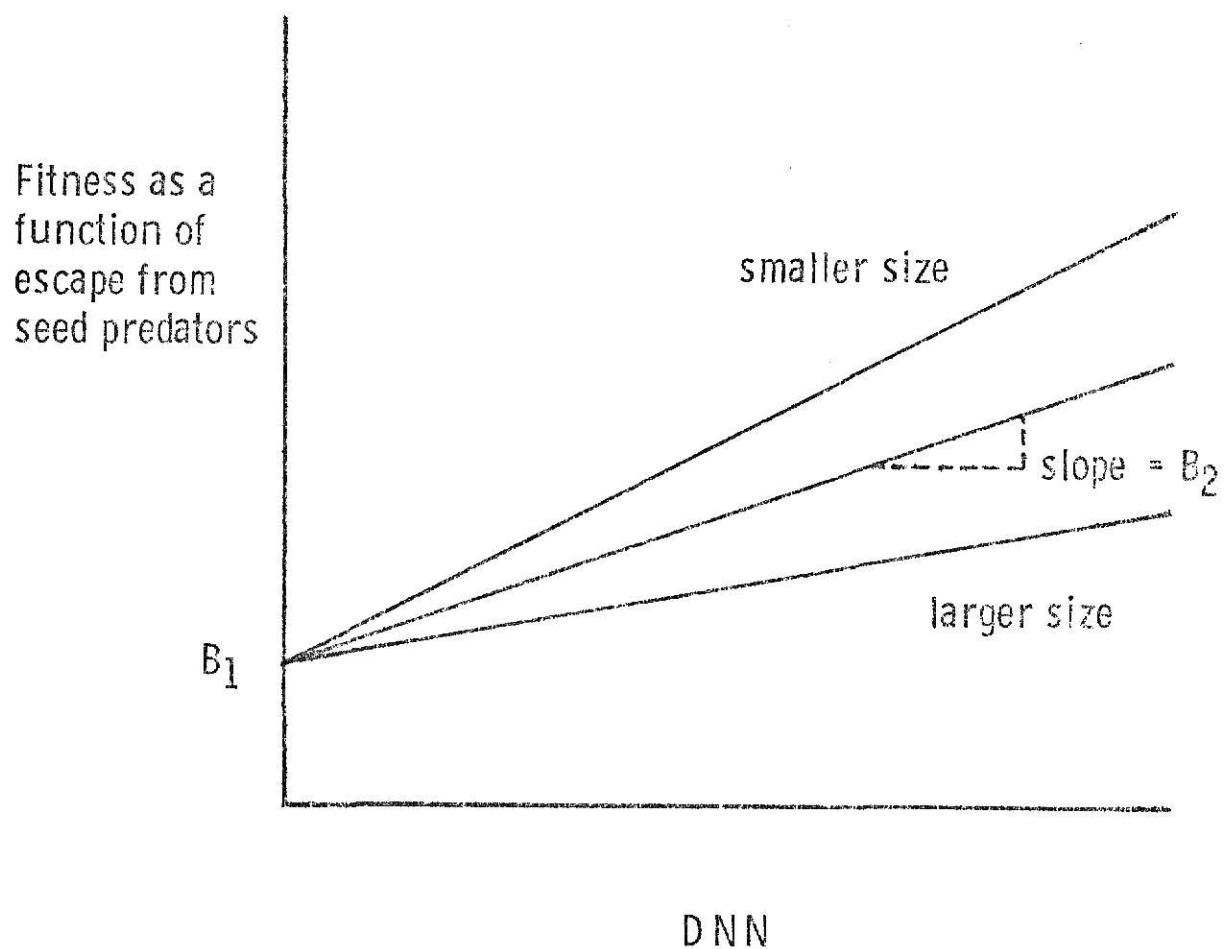
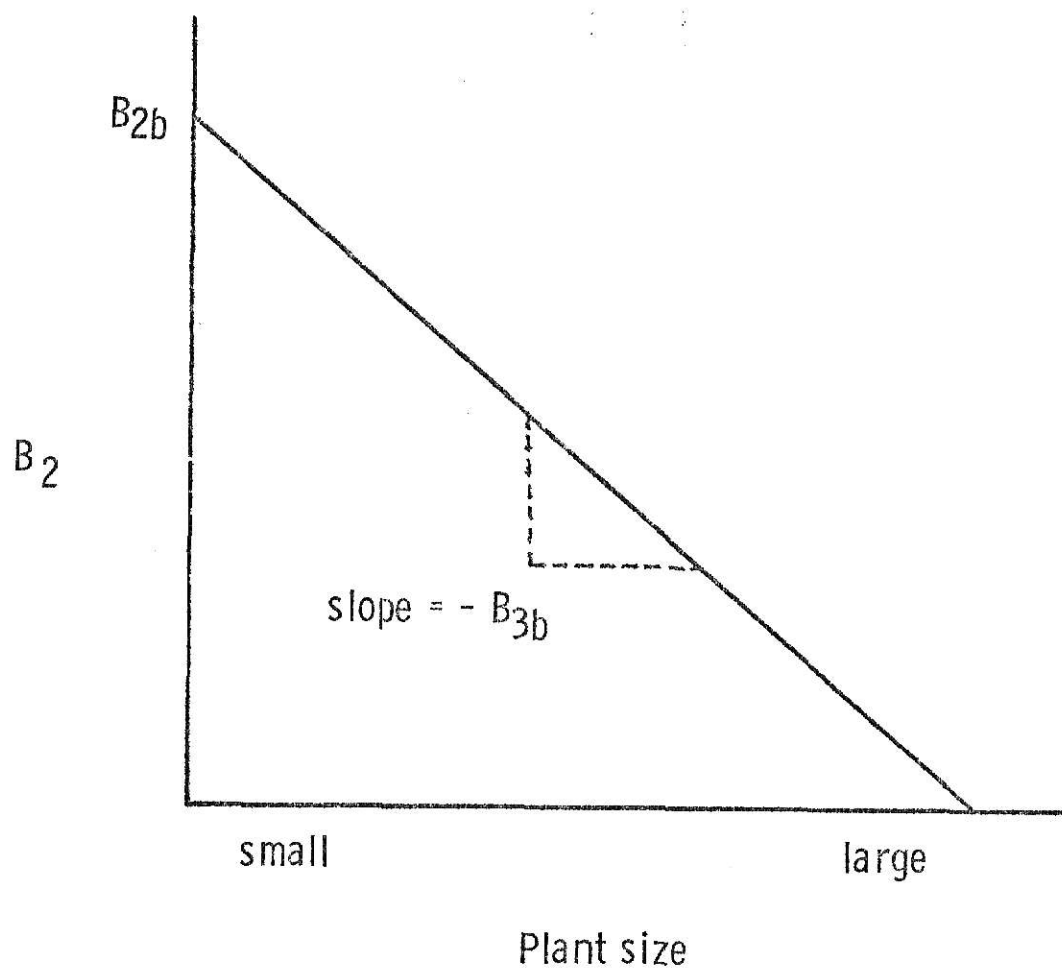


Figure 17: The slope of the relationship between fitness as a function from seed predators and DNN decreases the larger the plant is. The y intercept is B_{2b} and the slope is $-B_{3b}$.



$$B_2 = B_{19} - B_{20}(F) - B_{21}(\text{Size}) \quad (\text{Equation 15})$$

The derivation of Equation 15 is in Appendix IV. The limits are $0 < B_2, B_{19}, B_{20}, B_{21} < \infty$ magnitude biologically determined and influenced by DNN units, $0 < F \leq$ upper flower production capacity of the plant, $0 < \text{Size} \leq$ upper size limit of the plant, and $0 < [B_{19} - B_{20}(F) - B_{21}(\text{Size})] < \infty$ magnitude biologically determined and influenced by DNN units.

Since pollinators may initially orient towards the plant itself we might expect larger plants to attract more pollinators than smaller plants at any specified DNN. Figure 18 which is a modification of Figure 9, shows this relationship. Figure 19 shows graphically how the slope of the line might change with plant size. This relationship may be stated mathematically as:

$$B_5 = B_{5b} - B_{6b}(\text{Size}) \quad (\text{Equation 16})$$

The limits are $0 < B_5, B_{5b}, B_{6b} < \infty$ magnitude biologically determined and influenced by DNN, $0 < \text{Size} \leq$ upper size limit of the plant, and $0 < [B_{5b} - B_{6b}(\text{Size})] < \infty$ magnitude determined biologically and influenced by units of DNN.

If both the number of flowers and plant size affect Fitness(Pollination), we may combine Equations 7 and 16 to get:

$$B_5 = B_{22} - B_{23}(F) - B_{24}(\text{Size}) \quad (\text{Equation 17})$$

The derivation of Equation 17 is in Appendix V. The limits are $0 < B_5, B_{22}, B_{23}, B_{24} < \infty$ magnitude biologically determined and influenced by DNN, $0 < F \leq$ upper flower production capacity of the plant, $0 < \text{Size} \leq$ upper size limit of the plant, and $0 < [B_{22} - B_{23}(F) - B_{24}(\text{Size})] < \infty$ magnitude determined biologically and by units of DNN.

Figure 18: Fitness as a function of pollination decreases with DNN more for small plants than for large plants. The y intercept is B_4 and the slope is $-B_5$.

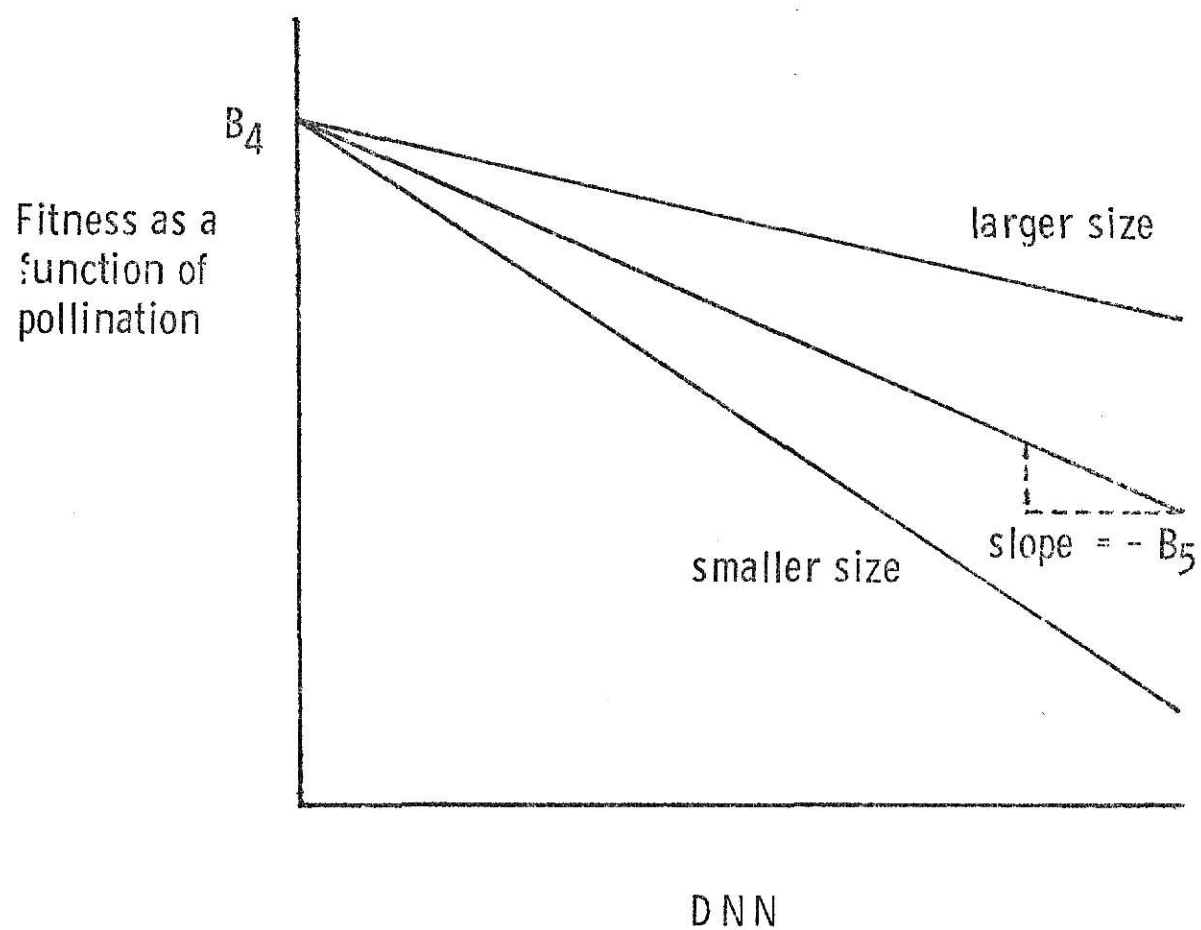
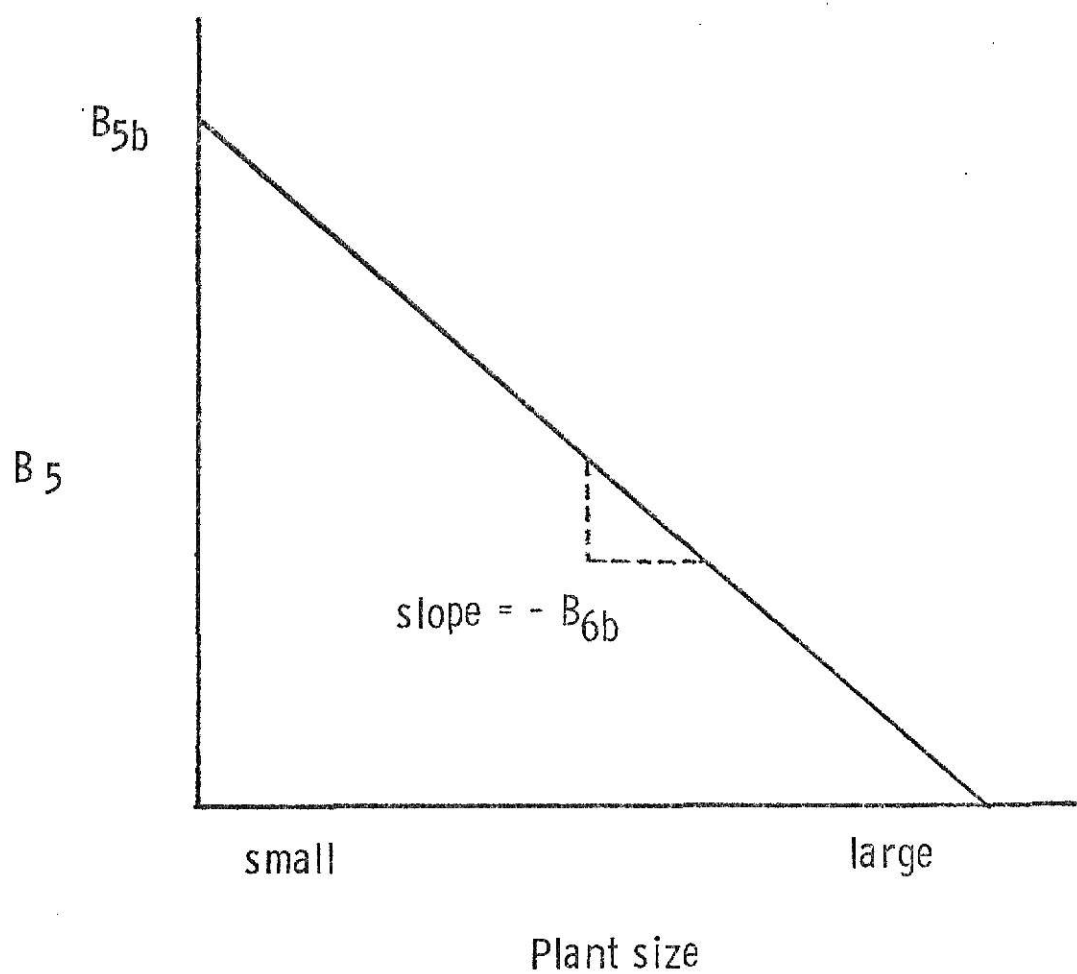


Figure 19: The absolute value of the slope of the relationship between fitness as a function of pollination and DNN decreases with increasing plant size. The y intercept is B_{5b} and the slope is $-B_{6b}$.



Let us look at the case in which foraging by both pollinators and seed predators is affected by DNN and further modified by the number of flowers and the number of stalks as has already been hypothesized. To do this we need merely substitute Equation 15 into Equation 1 and Equation 17 into Equation 4. The same result may be obtained by substituting Equation 15 and 17 into Equation 5. The product of the modified Equations 1 and 4, or similarly simply the modified Equation 5, is

$$\begin{aligned}
 \text{Fitness(Success)} = & B_1 B_4 + (B_4 B_{19} - B_1 B_{22}) \text{DNN} \\
 & + (B_1 B_{23} - B_4 B_{20}) (F) (\text{DNN}) + (B_1 B_{24} - B_4 B_{21}) (\text{Size}) (\text{DNN}) \\
 & - B_{19} B_{22} (\text{DNN})^2 + (B_{19} B_{23} + B_{20} B_{22}) (F) (\text{DNN})^2 \\
 & - B_{20} B_{23} (F)^2 (\text{DNN})^2 + (B_{21} B_{22} + B_{19} B_{24}) (\text{Size}) (\text{DNN})^2 \\
 & - (B_{21} B_{23} + B_{20} B_{24}) (F) (\text{Size}) (\text{DNN})^2 \\
 & - B_{21} B_{24} (\text{Size})^2 (\text{DNN})^2
 \end{aligned} \tag{Equation 18}$$

The limits of each B value, F, and Size are those previously described for or derived from Equations 1, 2, 4, 5, 7, 13, 15, 16, and 17, with $0 \leq \text{DNN} \leq$ the smallest of a' , a'' , and a''' , which are biologically and ecologically determined. The limits of either side of the equation are from 0 to 1.0. The derivation of Equation 18 (Model 4) using the former method is found in Appendix VI.

This equation may be simplified to:

$$\begin{aligned}
 \text{Fitness(Success)} = & B_{25} + B_{26} (\text{DNN}) + B_{27} (F) (\text{DNN}) \\
 & + B_{28} (\text{Size}) (\text{DNN}) - B_{29} (\text{DNN})^2 + B_{30} (F) (\text{DNN})^2 \\
 & - B_{31} (F)^2 (\text{DNN})^2 + B_{32} (\text{Size}) (\text{DNN})^2 \\
 & - B_{33} (F) (\text{Size}) (\text{DNN})^2 - B_{34} (\text{Size})^2 (\text{DNN})^2
 \end{aligned} \tag{Equation 19}$$

where $B_{25} = B_1 B_4$, $B_{26} = B_4 B_{19} - B_1 B_{22}$, $B_{27} = B_1 B_{23} - B_4 B_{20}$

$$B_{28} = B_1 B_{24} - B_4 B_{21}, B_{29} = B_{19} B_{22}, B_{30} = B_{19} B_{23} + B_{20} B_{22}$$

$$B_{31} = B_{20} B_{23}, B_{32} = B_{21} B_{22} + B_{19} B_{24}, B_{33} = B_{21} B_{23} + B_{20} B_{24}$$

$$\text{and } B_{34} = B_{21} B_{24}.$$

The limits are $0 \leq B_{25} < 1.0$, B_{26} , B_{27} , and B_{28} : negative, zero, or positive, magnitude and sign biologically determined and influenced by DNN units, $0 < B_{29}, B_{30}, B_{31}, B_{32}, B_{33}, B_{34} < \infty$ magnitude biologically determined and influenced by DNN units, $0 < F \leq$ upper flower production capacity of the plant, and $0 \leq \text{DNN} \leq$ the smallest of a' , a'' , and a''' , which are biologically and ecologically determined. The limits of either side of the equation are from 0 to 1.0.

In this model an optimum DNN exists for any specified number of flowers and size of plants. Conversely for any specified DNN an optimum number of flowers and size of plant exists.

The major prediction from these models is that an optimum DNN exists for plants which have effective host-specific seed predators and host-specific (although they may be facultatively so) pollinators. This optimum distance may be modified by the size of the plant and its flower production. Also for any distance an optimum number of flowers exists. This optimum number of flowers may be relative to the size of the plant. The existence of an optimum distance, predicted by the models, may have effects on community structure but these will not be discussed here.

METHODS AND PERTINENT NATURAL HISTORY

Konza Prairie, containing 371 hectares (916 acres) of Tallgrass Prairie in Geary County, has as its northern border Riley County and as its southern border Interstate 70. The last grazing by cattle on Konza Prairie occurred in 1971. The areas on the Dewey Ranch used in this study were immediately adjacent to the northern border of Konza Prairie and were grazed by cattle previous to and during this study.

This study was limited to Konza Prairie and adjacent areas on the Dewey Ranch for three reasons. First the soil types had already been mapped for both areas. Second, due to the occurrence of the populations of Baptisia in the same general area, factors (other than those deliberately varied) affecting the Baptisia populations should be most similar. Third, having all sites within the same general area made access to the sites more convenient.

Plots were chosen on two soil types, Benfield silty clay loam, and Florence cherty silt loam or cherty silty clay loam. They occur fairly frequently on Konza Prairie and adjacent areas on the Dewey Ranch and commonly support populations of Baptisia. Florence soils occur on upland sites while Benfield soils usually have 5 to 20% slopes.

All the grazed sites in this study had been burned the previous year in 1972, but none of the ungrazed sites were burned in 1972 (Dr. Hulbert, personal communication, 1973). Some sites were burned during spring 1973, and others were not. Wherever the terms, burned and unburned, are used in this paper, they will refer to the spring 1973 burning treatment.

Some sites contained virtually all B. australis, while others contained B. leucophaea alone, or combinations of the two species. Table 1 lists each plot and shows its grazing condition, burning regime, soil type, and number of individuals of each Baptisia species. Figure 20 shows the location of each plot on either Konza Prairie or the Dewey Ranch.

While an attempt was made to find populations of B. australis and B. leucophaea for each set of conditions, I was not able to find populations of each species for each of the conditions on these two areas in the right stage of development. Reasons for this are: (1) the areas burned were dependent on the requirements of another long-term study on the effect of various burning regimes on the prairie plant community, and of accidental burning, (2) the areas grazed and not grazed were arbitrarily set by property boundaries, and (3) a strong tendency for B. australis populations to occur at the West end of Konza Prairie, for B. leucophaea populations to occur at the East end of Konza Prairie, and for both types of populations as well as mixed populations to occur in the central area was noted.

Populations to be sampled were chosen on the basis of burning and grazing regime, soil type, species present, and stage of development of individuals in the population. Since measures of seed production were desired, populations with individuals whose pods had already started to open or with several individuals which had broken off at ground level and started to "tumble", were not desired. Eventually, senescent plants break off at ground level and are blown away by the wind. This appears to be a method of seed dispersal in Baptisia.

For each population meeting the requirements above, two 400 m² plots were chosen at random. Plots were used instead of point or line sampling

Table 1: Description of plots by burning and grazing regime, soil type, and number of plants of B. leucophaea and B. australis.

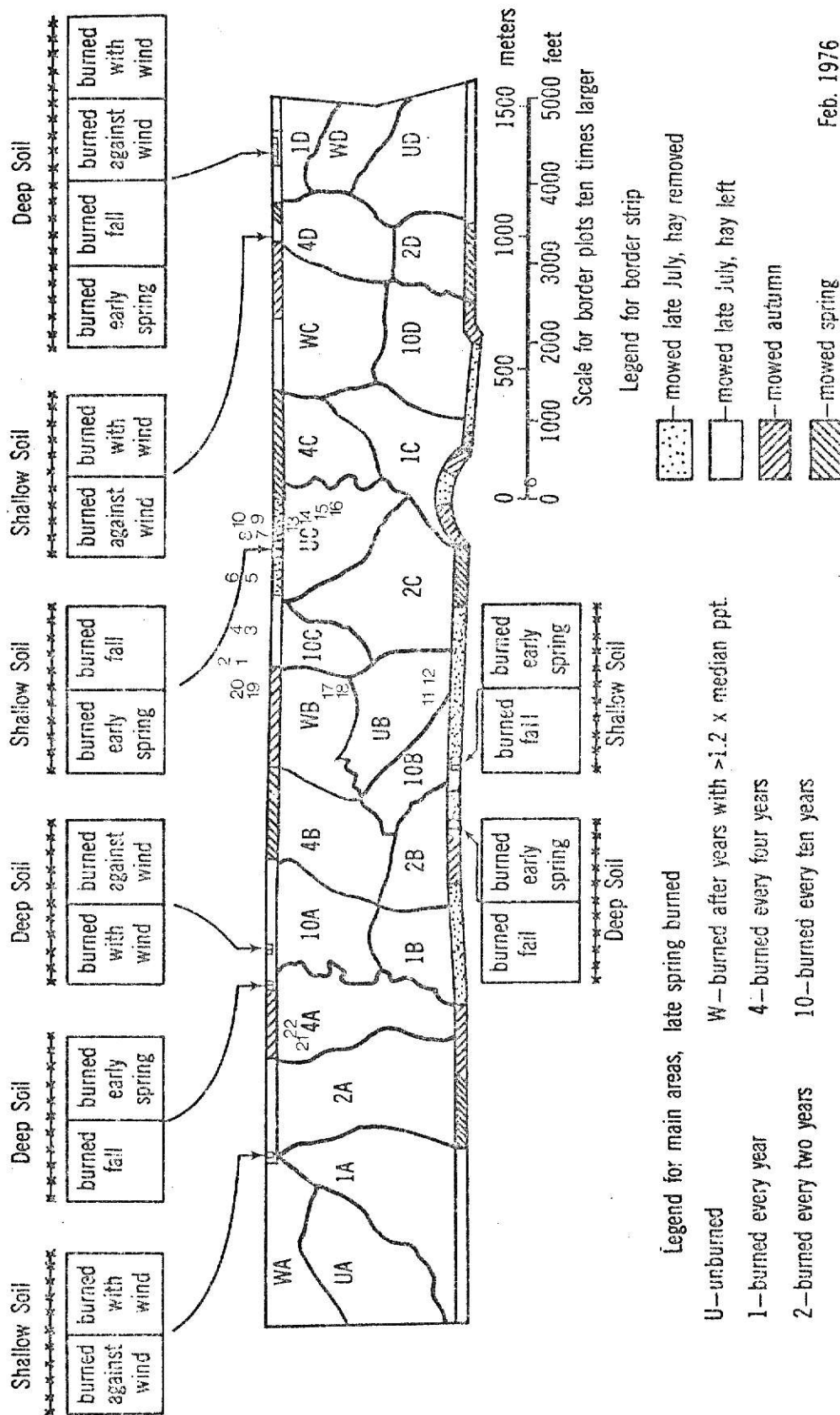
	Soil Type	Plot Number	Number of individuals	
			<u>B. leucophaea</u>	<u>B. australis</u>
B U R N E D				
GRAZED				
	Benfield	9	38	0
		10	83	2
		3	1	17
		4	0	18
	Florence	7	31	0
		8	26**	0
		5	8	9
		6	5	4
UNGRAZED				
	Benfield	13	67	6
		14	58	1
	Florence	15	13	7
		16	22	1
U N B U R N E D				
GRAZED				
	Benfield	19	0	90
		20	0	69*
	Florence	1	0	10
		2	3	35
UNGRAZED				
	Benfield	21	0	16
		22	0	30
	Florence	17	4	36*
		18	0	29
		11	36	12
		12	22	6

*A plant field-identified as B. australis was seen in the laboratory to have certain inflorescence characters of B. leucophaea.

**This includes four nonflowering plants later found in the plot after the inflorescences had been collected. Distance measures were not taken for these plants.

Figure 20. Location of plots on Konza Prairie. The location of each plot is indicated by its number on the map.

Konza Prairie Research Natural Area Management Plan



for several reasons. Plots provided a relatively easy and quick way to choose individuals to be measured, since only the plot itself need be randomly placed; each individual need not be randomly chosen. Plots also gave an independent measure of density. Two plots, rather than one, were chosen so that possible differences affected by varying densities in similar areas might be detected.

Two methods were used to choose plot sites. The first was to throw a survey flag high into the air with eyes shut and after turning around several times so as to lose sense of direction. The point of the flag became either (1) a given corner of a square plot 20 m x 20 m, or (2) the center of a circular plot with radius 11.28 m (area equals that of the square plots). Another, more satisfactory method for selecting plots was developed and used for most of the plots. After a suitable population was located, I walked through the center of the population counting my steps. Actual selection of the centers of the two plots within a single population was based on the numbers of paces from the edge of the population. The numbers of steps paced to the centers were taken from a random numbers table. Restrictions on the random numbers were that (1) the radius of each circle could not go beyond the area originally paced, and (2) the two plots could not overlap. By this method the plot was randomly placed within the area of the population.

The first four plots, 11, 12, 17, and 18, were all square plots, staked out using an engineering transit. This was very tedious and time-consuming. Using meter tapes, flags were placed along the four sides to determine if specific plants were inside the plot. Rarely, it was questionable as to whether a plant was inside the plot or not. Then, the

decision to include or exclude it was based on which side of the plot the plant was on. On two predetermined sides the plant was included and on the other two sides the plant was excluded. Each Baptisia individual within the plots was marked with a numbered survey flag.

All the other plots were circular plots of 400 m^2 area. Since no trees were present on the plots, a circular plot could be used more efficiently and easily. In addition, for equal-sized plots, a circular plot reduced the edge effect by reducing the amount of edge.

To mark the individuals within the circular plot with numbered survey flags, usually one person held a rope tied to a ring pin at the center of the plot. When held taut, the rope was marked at 11.28 m from the ring pin. By holding the rope taut and walking in a circle around the ring pin, the person walked the circumference of the plot. Usually another person then followed the rope around, and with the rope holder, staked all Baptisia individuals with numbered flags.

During the period May 21-29, 1973, plants in Plots 11 and 12 were flagged and data taken on species, number of stalks/plant, coverage of plant, whether it was flowering that year, number of inflorescences, and stage of development and damage to the flowers on each inflorescence. In Plot 12 the number of inflorescences counted on each plant in May matches exactly the number picked in July for pod analysis. In Plot 11 the number of inflorescences also matches at both times with two exceptions. I found an additional inflorescence on one plant in July and another plant which earlier had one inflorescence was missing in July; two new small green stems were growing where the larger plant had earlier been. Thus, only two plants out of an original 60 flowering showed any change in number of

inflorescences from counts done early in the season to counts taken when the pods were harvested.

In the field the following measurements were made on every Baptisia plant in each plot: number of inflorescences, number of vegetative stalks, the plant number and species, the number of and distance to the nearest Baptisia plant, the number of and distance to the nearest Baptisia plant of the same species, and the number of and distance to the nearest Baptisia plant of the same species with an inflorescence. The plants broken from their roots were not included in any of the data analyses. All distance measurements were taken from the center of one plant to the center of the other. In the case of multi-stemmed plants the center of the group was estimated by eye. The individuals in each circular plot were marked with survey flags, the above counts and measurements taken, and the inflorescences individually tagged with at least the number of the plant it was found on. At harvest, each inflorescence was then placed into a plastic freezer bag and sealed. All the inflorescences from a single plot were harvested within a two day period, placed in from one to three large brown paper bags, and put in a freezer (to inhibit possible growth of fungi and bacteria within the pods) until the inflorescences could be individually analyzed for several parameters. Inflorescences from all plots were harvested between July 13-28, 1973. Individuals in plots 11, 12, 17, and 18 had the distance measures taken and stems counted, if necessary, earlier between June 30 and July 2, 1973. Like the other plots, their inflorescences were harvested between July 13-28, 1973, and placed in a freezer.

The measurements made in the field for the 22 populations are summarized in Tables 2A through 2D.

TABLE 2A: Field measurements for burned and grazed plots. The standard deviation is found in parentheses to the right of the mean values for each character measured. DNN is the distance in meters to the nearest neighbor of either species. DSSI is the distance in meters to the nearest neighbor of the same species which has an inflorescence.

Soil Type: Florence		5		7		8	
Plot number:							
Plant species:		<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea</u>		
Character:							
No. of plants		8	9	31	26		
No. plants flowering							
No. stalks per flowering plant		3	4	25	13		
No. stalks per non-flowering plant		7.33 (5.86)	1.25 (0.50)	5.48 (2.63)	7.23 (2.83)		
No. inflorescences per flowering plant		7.60 (4.51)	1.80 (1.30)	3.50 (2.43)	11.15 (9.85)		
Flowering plants: DNN		3.67 (2.08)	1.25 (0.50)	2.32 (1.46)	2.46 (1.66)		
		1.22 (0.71)	1.14 (0.89)	1.49 (1.19)	1.84 (1.22)		
DSSI							
Nonflowering plants: DNN		2.62 (1.71)	1.46 (1.15)	1.88 (1.39)	2.38 (1.68)		
		2.50 (1.82)	2.05 (2.45)	1.01 (1.08)	1.62 (1.00)		
DSSI		6.09 (5.39)	2.82 (1.82)	2.63 (2.38)	3.18 (1.64)		

TABLE 2A: Continued

Soil Type: Benfield

Plot Number:	3	4	9	10
Plant species:	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea*</u>
Character:				
No. of plants	17	18	38	83
No. plants flowering				
No. stalks per flowering plant	11	13	21	30
No. stalks per non-flowering plant	2.27 (1.95)	2.85 (1.63)	5.95 (5.00)	7.63 (5.24)
No. inflorescences per flowering plant	1.83 (0.75)	1.20 (0.45)	9.47 (11.61)	10.68 (9.56)
Flowering plants:	2.82 (2.96)	3.23 (2.31)	2.57 (1.78)	1.50 (0.90)
DNN	1.60 (1.56)	1.97 (1.01)	1.84 (0.93)	1.00 (0.71)
DSSI	2.24 (2.12)	2.11 (0.95)	2.65 (1.44)	1.64 (1.44)
Nonflowering plants:				
DNN	2.43 (2.46)	2.45 (2.05)	1.41 (0.81)	1.13 (0.63)
DSSI	3.58 (2.04)	2.69 (2.24)	1.81 (0.80)	1.96 (1.14)

*One plant was noted in the field to have two inflorescences but only one inflorescence was found during laboratory examination. This plant is included in this analysis.

TABLE 2B: Field measurements for burned and ungrazed plots. The standard deviation is found in parentheses to the right of the mean values for each character measured. DNN is the distance in meters to the nearest neighbor of either species. DSSI is the distance in meters to the nearest neighbor of the same species which has an inflorescence.

Soil Type: Florence			
Plot number:	15	16	
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>
Character:			
No. of plants	13	7	22
No. plants flowering			
No. stalks per flowering plant	3	3	4
No. stalks per non-flowering plant	6.00 (2.65)	2.67 (1.15)	2.75 (1.26)
No. inflorescences per flowering plant	5.80 (4.61)	1.50 (0.58)	3.44 (1.65)
Flowering plants: DNN	1.67 (0.58)	1.67 (0.58)	1.50 (0.58)
	1.14 (0.48)	2.42 (1.10)	1.58 (0.98)
DSSI	3.41 (4.41)	3.86 (0.41)	7.58 (2.27)
Nonflowering plants: DNN	1.69 (0.51)	2.42 (2.15)	1.28 (0.85)
DSSI	5.10 (2.30)	7.66 (6.64)	4.09 (2.08)

TABLE 2B: Continued

Soil Type: Benfield

Plot Number:

13

14

Plant Species:

Baptisia
leucophaeaBaptisia
australisBaptisia
leucophaea

Character:

No. of plants

67

6

58

No. plants flowering

14

4

8

No. stalks per

flowering plant

4.93 (3.05)

1.75 (1.50)

No. stalks per non-

flowering plant

8.08 (5.92)

1.00 (0.00)

8.90 (7.95)

No. inflorescences per

flowering plant

1.71 (0.91)

2.00 (2.00)

1.13 (0.35)

Flowering plants:

DNN

1.46 (0.30)

0.60 (0.15)

1.49 (0.75)

DSSI

2.87 (1.71)

2.32 (3.50)

4.56 (0.54)

Nonflowering plants:

DNN

1.11 (0.65)

1.23 (0.02)

0.94 (0.64)

DSSI

2.55 (1.07)

1.24 (0.01)

3.11 (1.29)

TABLE 2C: Field measurements for unburned and grazed plots. The standard deviation is found in parentheses to the right of the mean values for each character measured. DNN is the distance in meters to the nearest neighbor of either species. DSSI is the distance in meters to the nearest neighbor of the same species which has an inflorescence.

Soil Type:	Florence			Benfield	
	1	2		19	20
Plot number:					
Plant species:	<u>Baptisia australis</u>	<u>Baptisia australis</u>		<u>Baptisia australis</u>	<u>Baptisia australis</u>
Character:					
No. of plants	10	35		90	69
No. plants flowering					
No. stalks per flowering plant	1.29 (0.49)	1.32 (0.67)		1.49 (0.76)	1.60 (0.99)
No. stalks per non-flowering plant	1.00 (0.00)	1.44 (0.63)		1.29 (0.61)	1.21 (0.54)
No. inflorescences per flowering plant	1.29 (0.49)	1.63 (1.30)		1.70 (1.24)	1.58 (0.84)
Flowering plants:					
DNN	1.78 (1.43)	1.53 (0.94)		1.20 (0.70)	1.06 (0.80)
DSSI	1.78 (1.43)	2.25 (1.77)		1.28 (0.79)	1.23 (0.97)
Nonflowering plants:					
DNN	5.54 (2.07)	1.05 (0.92)		1.12 (0.73)	1.04 (0.94)
DSSI	5.67 (2.12)	1.50 (1.08)		1.12 (0.73)	1.27 (0.92)

TABLE 2D: Field measurements for unburned and ungrazed plots. The standard deviation is found in parentheses to the right of the mean values for each character measured. DNN is the distance in meters to the nearest neighbor of either species. DSSI is the distance in meters to the nearest neighbor of the same species which has an inflorescence.

Soil Type: Florence			
Plot Number:	11	12	
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>
Character:			
No. of plants	36	12	22
No. plants flowering			6
No. stalks per flowering plant	26	12*	6
No. stalks per non-flowering plant	5.81 (3.50)	1.42 (0.79)	6.44 (6.05)
No. inflorescences per flowering plant	6.00 (5.56)	--	5.67 (4.08)
Flowering plants:			
DNN	2.42 (1.58)	1.25 (0.62)	3.00 (2.58)
DSSI	1.33 (0.44)	1.35 (0.96)	1.81 (1.15)
Nonflowering plants:			
DNN	1.75 (0.70)	2.09 (1.40)	2.36 (1.33)
DSSI	1.37 (0.63)	--	1.89 (1.03)
	1.86 (0.69)	--	1.89 (1.03)

*On one plant the stalk which was present earlier in the season was not there when the inflorescences were harvested on July 17. Only two new tiny green stems were present.

TABLE 2D: Continued

Soil Type:	Florence		Florence	Benfield
Plot Number:	17		18	21
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>
Character:				
No. of plants	4	35	29	16
No. plants flowering				
No. stalks per flowering plant	3	25	19	12
No. stalks per non- flowering plant	5.33 (2.52)	1.40 (1.15)	1.53 (0.70)	1.25 (0.45)
No. inflorescences per flowering plant	1 (0.00)	1.40 (0.84)	1.10 (0.32)	1.25 (0.50)
Flowering plants:	1.33 (0.58)	1.32 (1.14)	1.63 (0.68)	1.75 (1.14)
DNN	2.01 (0.76)	1.53 (0.81)	1.65 (0.95)	2.04 (1.52)
DSSI	3.76 (0.28)	1.76 (1.02)	1.95 (1.13)	2.53 (2.18)
Nonflowering plants:				
DNN	1.84 (0.00)	1.35 (0.65)	1.30 (1.08)	3.02 (2.41)
DSSI	1.84 (0.00)	2.30 (1.19)	1.39 (1.04)	3.02 (2.41)

Although no studies were done to specifically demonstrate intra-specific competition for nutritive resources, e.g. light, water, minerals, two different sets of results do suggest that if it occurs, it is not great. First, if competition were occurring I would expect it to occur most severely among individuals which were close together. I would also expect it to reduce the amount of resources for sexual reproduction, thereby reducing the probability of flowering. Of nine plots containing only one species, eight showed no significant difference in the distances between nearest neighbors for plants with inflorescences versus plants without inflorescences. In the one significant plot, nonflowering plants had a larger average DNN than did the flowering plants. When all plots were analyzed together, no significant difference ($F = .432$, d.f. 1, 119) between DNN's of flowering and nonflowering plants was indicated. Second, uniform dispersion can result from intense competition for a limiting resource. It is clear from Table 3 that the Baptisia plants within the plots have random dispersion patterns or occasionally clumped dispersion patterns. Only plot 19 with the highest density of plants, .225 individuals per m^2 , has an uniform distribution.

From these two lines of evidence we may infer that intraspecific competition is rare if it occurs at all. However, interspecific competition between Baptisia individuals and other members of the prairie plant community may be inferred from other studies. For instance, Plantago media and P. lanceolata increased both their plant density and seed production per unit area when plots in permanent grassland communities were sprayed with an herbicide which is specifically effective against grasses (Harper 1961b).

TABLE 3. Dispersion of the plants in Plots 1-22.

Plot No.	Actual Density (plants/m ²)	X*	c**	Dispersion: Conclusion
1	.0250	.212	-.483	Random
2	.0975	.155	-2.537	Clumped
3	.0525	.210	-.734	Random
4	.0450	.199	-.872	Random
5	.0425	.141	-1.967	Clumped
6	.0225	.359	1.140	Random
7	.0775	.151	-2.372	Clumped
8	.0550	.168	-1.619	Random
9	.0950	.257	.173	Random
10	.2125	.263	.466	Random
11	.1200	.217	-.919	Random
12	.0700	.258	.167	Random
13	.1825	.242	-.253	Random
14	.1475	.149	-3.344	Clumped
15	.0500	.173	-1.437	Random
16	.0575	.097	-3.451	Clumped
17	.1000	.229	-.514	Random
18	.0725	.169	-1.837	Random
19	.2250	.315	2.239	Uniform
20	.1725	.191	-1.991	Clumped
21	.0400	.209	-.660	Random
22	.0750	.217	-.714	Random

*X = .25 may be interpreted as a random dispersion with $x > .25$ being uniform dispersion and $x < .25$ being clumped dispersion (Clark and Evans 1954).

**The c statistic lets us know if X is significantly different from .25. For $p < .05$, the critical value for c is 1.9668 (Clark and Evans 1954).

As a basis for estimating fitness for the 1973 season I counted the number of filled, uneaten seeds produced. A measure of efficiency of seed production for the 1973 season was also made by dividing the number of filled, uneaten seeds produced by the total number of flowers produced. The efficiency measure assumes that the number of ovules per flower is the same for all flowers on all plants on all plots. To check this assumption and to provide a possible mechanism for estimating the number of ovules a particular plant produces, I counted the number of pedicels (stalks supporting each ovule or seed) present, or if pedicels were not present due to injury, the number of vascular traces which supplied each ovule or seed. When due to injury of the pod, very small parts of the pod had neither pedicels nor traces clearly visible, the number of ovules was extrapolated from the spacing of the pedicels or traces that did remain. Only for pods for which the number of ovules was fairly easy to estimate, was an estimate made. Where only one side of the pod was easily estimated, only that side was estimated. To get the number of ovules per pod I doubled that number. Where both sides of the pod were estimable, I estimated both. The total number of ovules in that case was merely the sum of the two sides. In some cases I counted the total number of ovules in the pod directly. This occurred mostly with unattacked, undeveloped pods.

For each inflorescence on each plant, each pod or flower scar present was evaluated for (1) number of ovules, (2) number of filled, uneaten seeds, and (3) damage. The damage ratings were 0 = no pod present, 1 = damaged, no filled, unhit seeds produced, 2 = damaged, 1 filled, unhit seed(s) produced, and 3 = no insect damage. Rating 3 included pods ranging from those which had developed very little through pods which had fully

developed and had produced 1 or more filled seeds. Some inflorescences had their tips rubbed or broken off. This does not change at all our measure of number of seeds produced per plant, but lessens the accuracy of the efficiency measure by overestimating efficiency. Plants with such inflorescences were included with the rest of the plants. It is felt that the number of remaining scars or pods give the best estimate available at this point for the number of buds, flowers, and/or pods produced and made available for action by insect pollinators and ovule and/or seed eaters. A summary of these data is included in Tables 4A-D and 5A-D. Data on Plot 22 were not taken because several of the plants had pods which had already opened, thereby making estimates of fitness and efficiency difficult to make.

Several of the models developed were tested using Baptisia leucophaea and B. australis and their insect seed predators and insect pollinators. The host plants and the insects in this system are described below.

This system was originally picked to test models of isolation and the effect of seed predation on seed production. It was observed that Baptisia occurs relatively widely spaced on the prairie and that its seeds were heavily hit by host-specific seed predators. It was hypothesized that these two observations were related and that plants which were farther away from other plants would be more successful in avoiding seed predators and therefore in producing seed than plants which were closer to their nearest neighbor.

The models assume host specificity (at least facultative) of the seed predators and pollinators to the plants. They also assume that the seed predators and pollinators can move from plant to plant at some finite

TABLE 4A: Laboratory measures of reproductive parameters for burned and grazed plots. Where appropriate, the standard deviation is found in parentheses to the right of the mean value for the character measured.

Soil Type: Florence		5		7	8
Plot number:					
Plant species:		<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea</u>
Character:					
No. flowers per inflorescence		14.00 (4.49)	23.60 (7.60)	17.74 (8.36)	19.94 (11.46)
No. flowers per flowering plant		51.33 (25.32)	29.50 (7.72)	41.16 (34.69)	49.08 (46.12)
No. flowers per plot		154	118	1029	638
No. seeds per plant		3.38 (6.30)	7.56 (14.35)	3.13 (10.99)	2.85 (9.63)
No. seeds per inflorescence		2.45 (5.50)	13.60 (17.59)	1.67 (7.62)	2.31 (6.37)
No. seeds per plant with seeds		13.50 (2.12)	17.00 (18.31)	19.40 (22.60)	18.50 (19.67)
No. seeds per flower scar in plot		.175	.58	.094	.116
No. seeds per plot		27	68	97	74

TABLE 4A: Continued

Soil Type: Benfield

Plot number:

10

9

4

3

Plant species:

Baptisia
australisBaptisia
australisBaptisia
leucophaeaBaptisia
leucophaea*

Character:

No. flowers per
inflorescence

18.39 (5.77)

No. flowers per
flowering plant

26.97 (17.47)

No. flowers per plot

809

No. seeds per plant

.16 (0.82)

No. seeds per
inflorescence

.30 (1.11)

No. seeds per plant
with seeds

3.25 (2.22)

No. seeds per flower
scar in plot

.02

No. seeds per plot

13

*One plant was noted in the field to have two inflorescences but only one inflorescence was found during laboratory examination. This plant is included in this analysis.

TABLE 4B: Laboratory measures of reproductive parameters for burned and ungrazed plots. Where appropriate, the standard deviation is found in parentheses to the right of the mean value for the character measured.

Soil Type: Florence			
Plot number:	15	16	
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>
Character:			
No. flowers per inflorescence	14.60 (7.77)	20.40 (14.08)	18.50 (9.63)
No. flowers per flowering plant	24.33 (3.06)	34.00 (13.23)	27.75 (13.96)
No. flowers per plot	73	102	111
No. seeds per plant	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
No. seeds per inflorescence	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
No. seeds per plant with seeds	--	--	--
No. seeds per flower scar in plot	.00	.00	.00
No. seeds per plot	0	0	0

TABLE 4B: Continued

Soil Type: Benfield

Plot number:	13	14
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>
Character:		
No. flowers per inflorescence	21.04 (11.48)	19.44 (6.69)
No. flowers per flowering plant	36.07 (28.60)	21.88 (12.81)
No. flowers per plot	505	175
No. seeds per plant	0.00 (0.00)	0.00 (0.00)
No. seeds per inflorescence	0.00 (0.00)	0.00 (0.00)
No. seeds per plant with seeds	--	--
No. seeds per flower scar in plot	.00	.00
No. seeds per plot	0	0

TABLE 4C: Laboratory measures of reproductive parameters for unburned and grazed plots. Where appropriate, the standard deviation is found in parentheses to the right of the mean value for the character measured.

Soil Type:	Florence		Benfield	
	1	2	19	20
Plot number:				
Plant species:	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>
Character:				
No. flowers per inflorescence	27.67 (10.70)	25.61 (13.51)	27.97 (13.98)	29.51 (15.22)
No. flowers per flowering plant	35.57 (20.61)	41.79 (35.53)	47.47 (31.21)	46.62 (37.70)
No. flowers per plot	249	794	3608	2331
No. seeds per plant	10.90 (22.29)	11.46 (27.90)	10.54 (24.53)	11.65 (28.57)
No. seeds per inflorescence	12.11 (20.67)	12.94 (17.05)	7.36 (18.83)	10.18 (25.05)
No. seeds per plant with seeds	36.33 (29.16)	40.10 (40.79)	24.97 (32.83)	30.92 (40.01)
No. seeds per flower scar in plot	.44	.51	.26	.36
No. seeds per plot	109	401	949	804

TABLE 4D: Laboratory measures of reproductive parameters for unburned and ungrazed plots. Where appropriate, the standard deviation is found in parentheses to the right of the mean value for the character measured.

Soil Type: Florence		11		12	
Plot number:		11		12	
Plant species:		<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>
Character:					
No. flowers per inflorescence		21.22 (11.62)	23.36 (10.38)	20.92 (10.78)	25.00 (16.46)
No. flowers per flowering plant		51.42 (35.14)	29.73 (16.47)	62.75 (55.92)	54.17 (42.91)
No. flowers per plot		1337	327	1004	325
No. seeds per plant		.47 (2.51)	.42 (1.16)	.50 (1.95)	.50 (1.22)
No. seeds per inflorescence		.27 (1.57)	.36 (1.08)	.23 (1.19)	.23 (.83)
No. seeds per plant with seeds		8.50 (9.19)	2.50 (2.12)	5.50 (4.95)	3.00 (0.00)
No. seeds per flower scar in plot		.01	.02	.01	.01
No. seeds per plot		17	5	11	3

TABLE 4D: Continued

Soil Type:	Florence		Florence	Benfield
Plot number:	17		18	21
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>
Character:				
No. flowers per inflorescence	15.75 (12.76)	25.09 (12.27)	26.58 (16.47)	21.95 (16.64)
No. flowers per flowering plant	21.00 (14.11)	33.12 (33.74)	43.37 (28.21)	38.42 (38.07)
No. flowers per plot	63	828	824	461
No. seeds per plant	0.00 (0.00)	3.09 (14.19)	1.62 (7.09)	44.38 (101.49)
No. seeds per inflorescence	0.00 (0.00)	3.27 (14.61)	1.57 (6.98)	33.81 (90.01)
No. seeds per plant with seeds	--	54.00 (36.77)	11.75 (17.63)	101.43 (137.85)
No. seeds per flower scar in plot	.00	.13	.06	1.54
No. seeds per plot	0	108	47	710

TABLE 5A: Laboratory measures of insect attack and reproductive parameters for burned and grazed plots.
The standard deviation is found in parentheses to the right of the mean values for the character measured.

Soil Type: Florence					
Plot Number:	5	5	7	8	
Plant species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea</u>	
Character:					
No. seeds per partly attacked pods	2.00 (0.00)	5.38 (8.52)	4.60 (4.99)	2.0 (0.0)	
No. seeds per unattached pods	2.50 (5.28)	6.25 (12.50)	1.95 (4.39)	2.0 (4.20)	
No. seeds per unattached pod with seeds	12.50 (0.71)	25.00 (0.00)	9.25 (4.98)	10.00 (2.58)	
No. seeds per flowering plant	9.00 (7.94)	17.00 (18.31)	3.88 (12.16)	5.69 (13.26)	
In each plot:					
No. partly attacked pods	1.0	5	5	2	
No. unattached pods with seeds	2	1	8	7	
No. unattached pods without seeds	8	3	30	28	
No. attacked pods left	74	24	524	311	
Total no. pods	84	28	562	346	

TABLE 5A: Continued

Soil Type: Benfield

Plot Number:

Plant Species:

Character:

	3	4	9	10
	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea</u>
No. seeds per partly attacked pods	5.17 (4.71)	6.34 (5.89)	--	2.60 (1.95)
No. seeds per unattacked pods	7.05 (10.12)	17.27 (10.84)	1.28 (4.43)	0.0
No. seeds per unattacked pod with seeds	16.27 (9.25)	18.90 (9.90)	16.00 (0.0)	--
No. seeds per flowering plant	62.91 (87.23)	48.69 (69.28)	1.52 (4.81)	0.43 (1.33)
In each plot:				
No. partly attacked pods	52	70	0	5
No. unattacked pods with seeds	26	10	2	0
No. unattacked pods without seeds	34	1	23	18
No. attacked pods left	220	235	393	399
Total no. pods	280	246	418	417

TABLE 5B: Laboratory measures of insect attack and reproductive parameters for burned and ungrazed plots. The standard deviation is found in parentheses to the right of the mean values for the character measured.

Soil Type: Florence	15	16
Plot Number:		
Plant Species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>
Character:		
No. seeds per partly attacked pods	--	--
No. seeds per unattacked pods	--	0.00
No. seeds per unattacked pod with seeds	--	--
No. seeds per flowering plants	0.00	0.00
In each plot:		
No. partly attacked pods	0.00	0.00
No. unattacked pods with seeds	0.00	0.00
No. unattacked pods without seeds	0.00	2
No. attacked pods left	43	29
Total no. pods	43	31

TABLE 5B: Continued

Soil Type: Benfield	13		14
Plot Number:			
Plant Species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia leucophaea</u>
Character:			
No. seeds per partly attacked pods	--	--	--
No. seeds per unattacked pods	0.00	--	0.00
No. seeds per unattacked pod with seeds	--	--	--
No. seeds per flowering plants	0.00	0.00	0.00
In each plot:			
No. partly attacked pods	0.00	0.00	0.00
No. unattacked pods with seeds	0.00	0.00	0.00
No. unattacked pods without seeds	5	0.00	7
No. attacked pods left	231	3.00	64
Total no. pods	236	3.00	71

TABLE 5C: Laboratory measures of insect attack and reproductive parameters for unburned and grazed plots. The standard deviation is found in parentheses to the right of the mean values for the character measured.

Soil Type:	Florence			Benfield		
	1	2		19	20	
Plot Number:						
Plant Species:	<u>Baptisia</u> <u>australis</u>	<u>Baptisia</u> <u>australis</u>		<u>Baptisia</u> <u>australis</u>	<u>Baptisia</u> <u>australis</u>	
Character:						
No. seeds per partly attacked pods	4.95 (3.57)	6.10 (5.19)		5.28 (5.36)	6.28 (6.34)	
No. seeds per unattacked pods	0.00	2.30 (7.27)		3.89 (10.59)	8.50 (12.81)	
No. seeds per unattacked pods with seeds	--	23.00 (0.00)		17.50 (20.51)	19.83 (12.53)	
No. seeds per flowering plants	15.57 (25.70)	21.11 (35.43)		12.49 (26.26)	16.08 (32.57)	
In each plot:						
No. partly attacked pods	22	62		173	109	
No. unattacked pods with seeds	0	1		2	6	
No. unattacked pods without seeds	8	9		7	8	
No. attacked pods left	111	256		1373	674	
Total no. pods	119	266		1382	688	

TABLE 5D: Laboratory measures of insect attack and reproductive parameters for unburned and ungrazed plots. The standard deviation is found in parentheses to the right of the mean values for the character measured.

Soil Type: Florence		
Plot Number:	11	12
Plant Species:	<u>Baptisia leucophaea</u>	<u>Baptisia leucophaea</u>
Character:	<u>Baptisia australis</u>	<u>Baptisia australis</u>
No. seeds per partly attacked pods	4.25 (2.22)	1.25 (0.50)
No. seeds per unattached pods	0.00	--
No. seeds per unattached pods with seeds	--	--
No. seeds per flowering plants	0.65 (2.95)	0.42 (1.16)
In each plot:		
No. partly attacked pods	4	4
No. unattached pods with seeds	0	0
No. unattached pods without seeds	52	0
No. attacked pods left	580	74
Total no. pods	612	74
		1
		2
		0.00
		0.00
		35
		35
		1.50 (0.71)
		0.86 (3.61)
		5.00 (4.24)
		0.69 (2.27)
		.50 (1.22)

TABLE 5D: Continued

Soil Type:	Florence		Florence	Benfield
Plot Number:	17	18	21	
Plant Species:	<u>Baptisia leucophaea</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>	<u>Baptisia australis</u>
Character:				
No. seeds per partly attacked pods	--	8.20 (5.67)	2.89 (1.54)	12.84 (8.01)
No. seeds per unattacked pods	0.00 (0.00)	13.00 (2.00)	21.00	18.52 (15.03)
No. seeds per unattacked pod with seeds	--	13.00 (2.00)	21.00	25.93 (10.80)
No. seeds per flowering plants	0.00 (0.00)	4.32 (16.73)	2.47 (8.72)	59.17 (114.42)
In each plot:				
No. partly attacked pods	0	5	9	25
No. unattacked pods with seeds	0 (0)	3	1	15
No. unattacked pods without seeds	2 (5)	0	0	6
No. attacked pods left	24 (31)	140	97	96
Total no. pods	26 (36)	143	98	117

rate. Both these assumptions appear to be generally true.

The host plants:

The two closely related plant species, Baptisia leucophaea Nutt. and B. australis var. minor (Lehm.) Fern. occurred on the study sites. According to Hulbert (1963), from Gates' observations for 24 years, B. leucophaea flowers earlier in the spring than B. australis. My observations support these earlier observations of Gates.

B. leucophaea has yellow flowers on inflorescences which are generally horizontal and relatively close to the ground. B. australis has bluish-purple flowers on inflorescences which are held vertically and relatively high in the air. Morphologically the zygomorphic flowers are very similar and appear to be adapted to insect pollination. In the absence of insects to pollinate them, Baptisia grown by B. L. Turner in the greenhouse did not set seed (Turner, personal communication). Bagging experiments suggest that Baptisia is predominately self-sterile (Turner, personal communication, 1976). For this study, I conclude that we can at least functionally call Baptisia insect-pollinated outcrossers.

Unless otherwise noted the generic use of Baptisia refers to either or both species of Baptisia found on the study site: B. australis and B. leucophaea. Since both these plants support the same seed predators it was decided to include both in this study.

The Insects: Pollinators

Bumblebees were observed visiting both B. leucophaea and B. australis flowers. I attempted to determine if bumblebees were carrying Baptisia pollen and were thus likely pollinators. I found that B. leucophaea

and B. australis pollen are not easily distinguished using light microscopy so I used the scanning electron microscope in an attempt to distinguish them. On May 26, 1975 in the early evening I caught a bumblebee on a B. leucophaea blossom near the shed on Konza Prairie. A grasshopper, caught at the same time, was placed in the same container. It is unlikely it was a source of pollen. This bumblebee has been identified by Dr. Charles D. Michener of Kansas University as Bombus americanorum (Fabr.). The nearby flowers in bloom were mainly B. australis and B. leucophaea. A few composites and an Asclepias were also in bloom. They were collected and pressed.

Pollen from the composite collected May 26, 1975, as well as from B. leucophaea and B. australis were prepared according to the procedure of Erdtman (1960) as modified by Faegri and Iverson (1964). Differences between the two Baptisia species were not striking under the S.E.M. The pollen grains of both Baptisia species were triculate and reticulate except along the culpi. The polar view of a B. leucophaea pollen grain (Figure 21) clearly shows that it is triculate. A lateral view centering on an aperture is shown in Figure 22. A close up view of the reticulate pores is shown in Figure 23. Figure 24 shows a highly magnified view of an aperture. Note the non-reticulate edge bordering the culpus.

The lateral view of the B. australis pollen grain shown in Figure 25 suggests its triculate nature. A lateral view centering on an aperture is shown in Figure 26. A highly magnified close up view of its reticulate surface is shown in Figure 27. An aperture of a B. australis pollen grain is shown in Figure 28. In general, the pollen of B. leucophaea seems more prolate and the os more elongate than in B. australis. B. australis pollen seems more spherical.

Figure 21. SEM micrograph of a pollen grain of B. leucophaea, polar view, 3900 X.

Figure 22. SEM micrograph of a pollen grain of B. leucophaea, lateral view of aperture, 4700 X.

Figure 23. SEM micrograph of a pollen grain of B. leucophaea, lateral view of reticulate pores, 9400 X.

Figure 24. SEM micrograph of a pollen grain of B. leucophaea, lateral view of aperture, 10000 X.

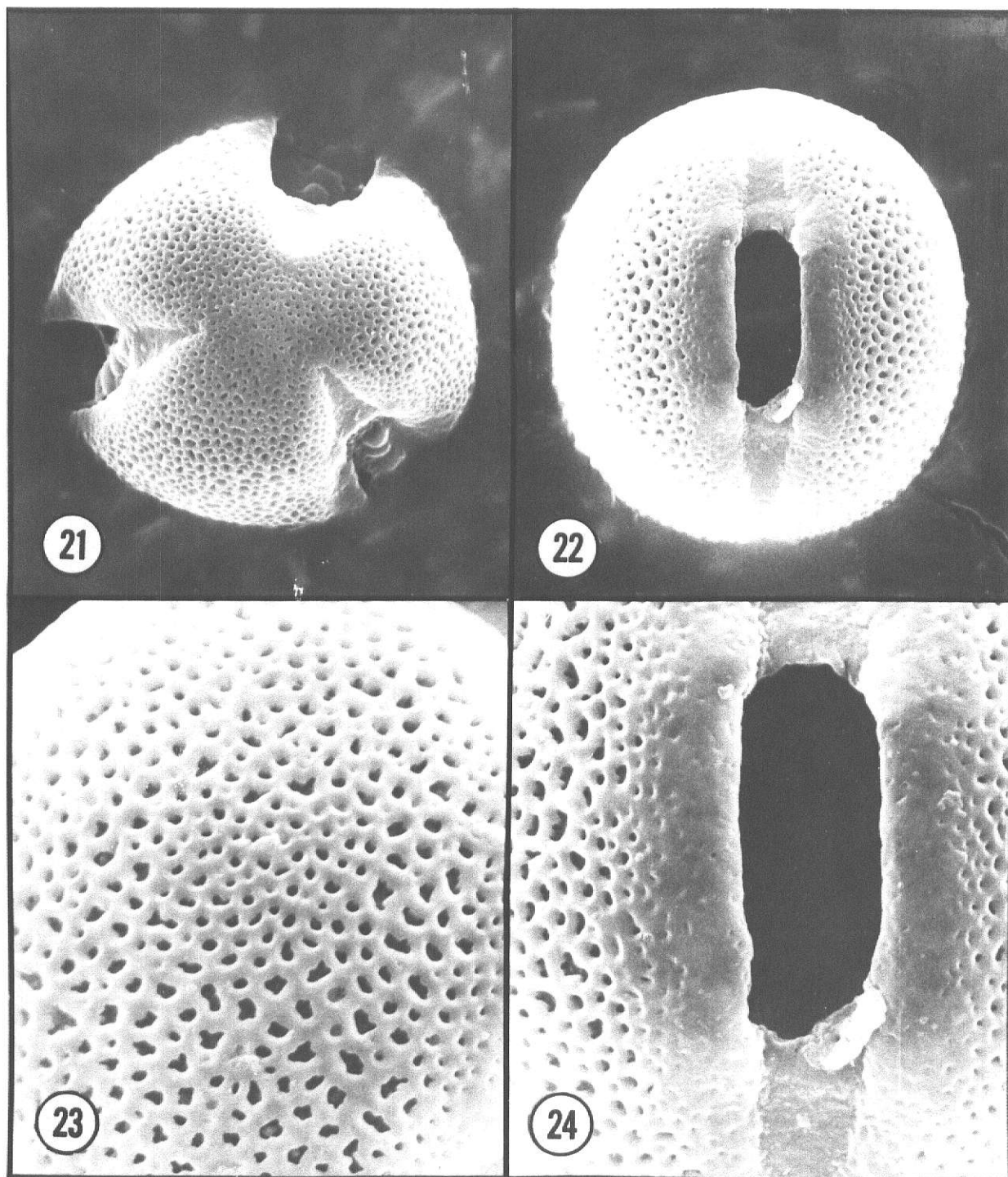
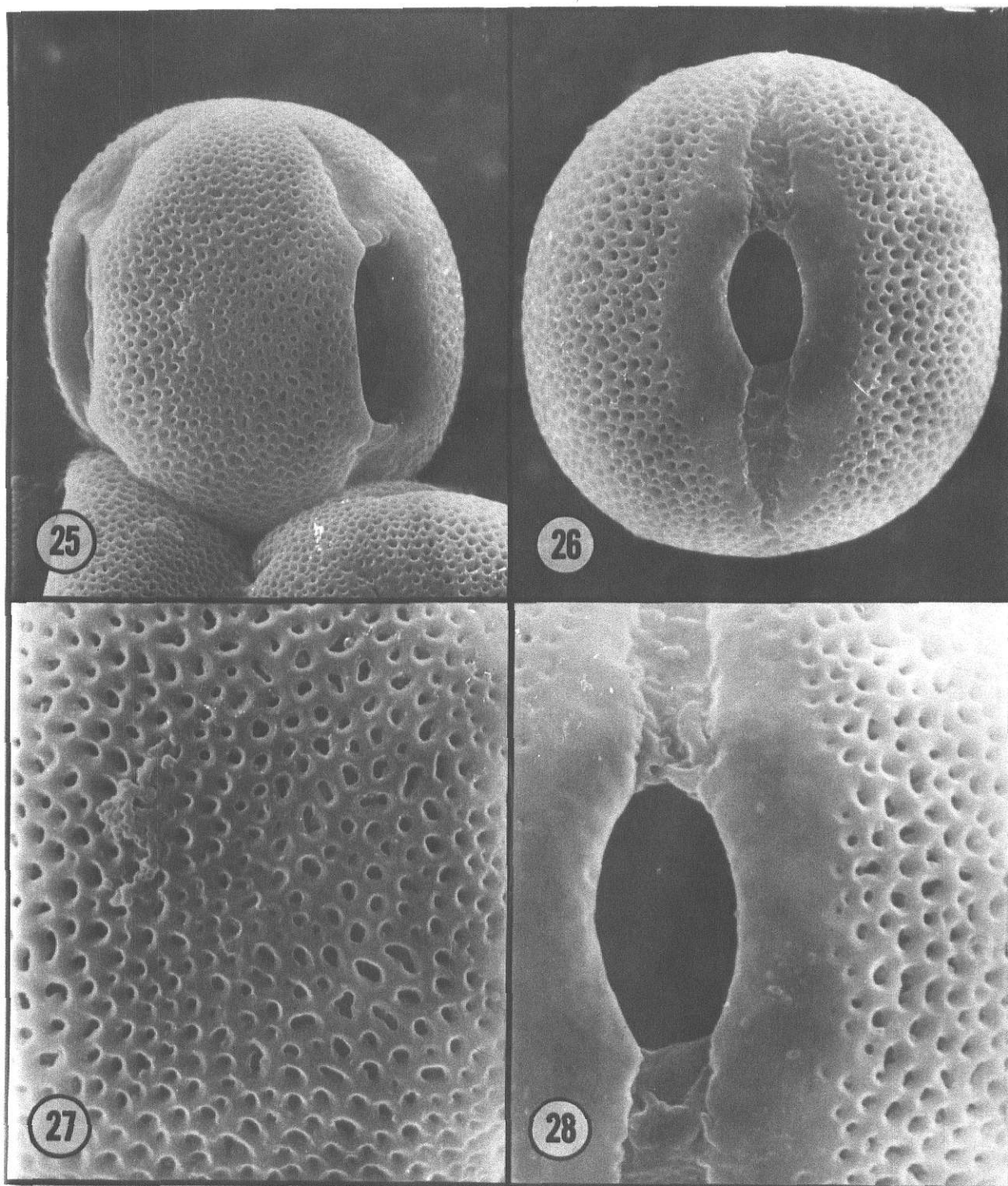


Figure 25. SEM micrograph of a pollen grain of B. australis, lateral view, 3900 X.

Figure 26. SEM micrograph of a pollen grain of B. australis, lateral view of aperture, 4700 X.

Figure 27. SEM micrograph of a pollen grain of B. australis, lateral view of reticulate pores, 9300 X.

Figure 28. SEM micrograph of a pollen grain of B. australis, lateral view of aperture, 9400 X.



The same technique was used for pollen taken from the B. americanorum (Fabr.) bumblebee (labeled BBBL) captured on a B. leucophaea blossom on May 26, 1975. Pollen from bumblebees (two B. nevadensis auricomus (Rabt.) and one B. fraternus (Smith) captured on or near B. australis on June 1 and June 2, 1973, (labeled BBBA1 and BBBA2) was also put through this procedure. Only Baptisia pollen was seen on the stub prepared from the BBBA1 specimens. On the stub prepared from the BBBA2 specimen, two composite pollen grains and 1 unidentified pollen grain were seen but the rest of the pollen was Baptisia pollen. Pollen observed from the stub labeled BBBL was all Baptisia pollen with the exceptions of a single Lactuca pollen grain contaminant and two other composite pollen grains (Figure 29). A view of a cross section of the pollen wall of a broken Baptisia pollen grain is shown in Figure 30.

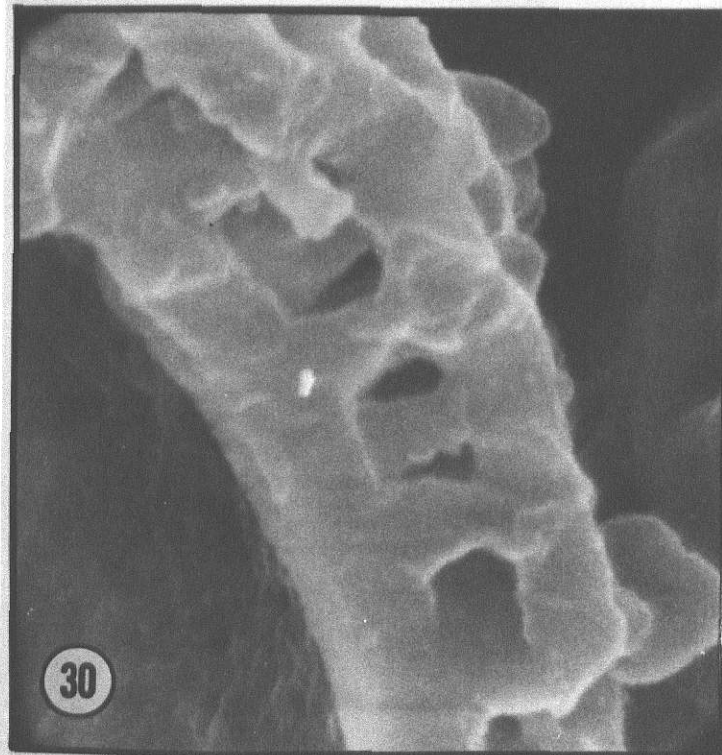
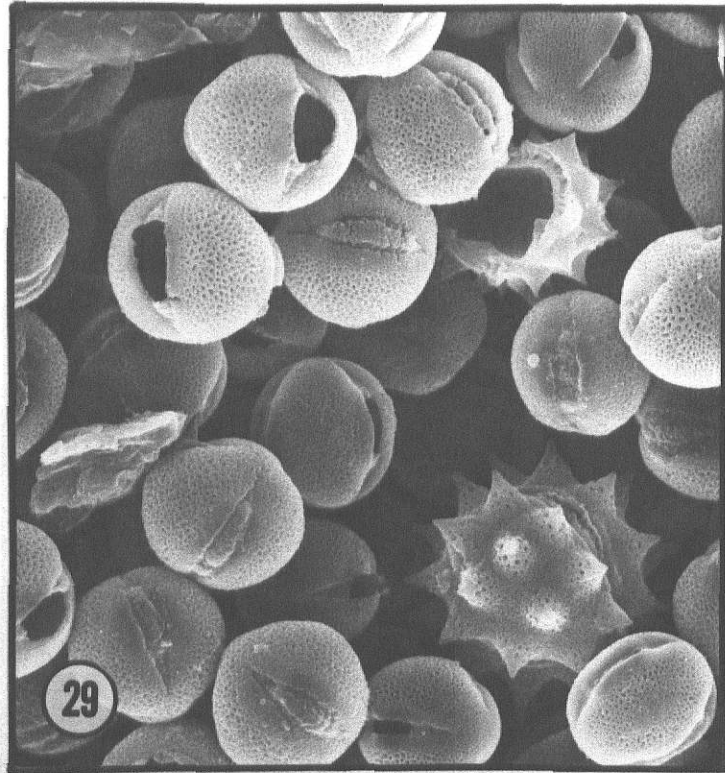
I concluded that these bumblebees carried primarily Baptisia pollen and are likely the primary pollinators of Baptisia.

The Insects: Seed Predators and Their Predators

There are two major host-specific insect predators on the developing seed of B. leucophaea and B. australis. One is the Coleopteran seed predator, Tychius sordidus, which is a weevil in the family Curculionidae. Adults collected from B. australis and B. leucophaea were identified by Dr. Charles W. O'Brien at Florida A & M University as Tychius sordidus LeConte. Clark (1971) lists Baptisia leucantha, B. bracteata, B. cuncata, B. villosa, Acerates and Croton as hosts which have been recorded for T. sordidus. Clark (personal communication, 1974) has reared it from B. leucophaea. Bertwell (1972) reported finding large numbers of adults on both B. leucophaea and B. minor (referred to herein as B. australis) in

Figure 29. SEM micrograph of pollen taken from a Bombus americanorum bumblebee captured on a Baptisia leucophaea blossom, 1200 X.

Figure 30. SEM micrograph of a cross section of the pollen wall of a broken Baptisia pollen grain, taken from a Bombus americanorum bumblebee captured on a Baptisia leucophaea blossom, 31300 X.



Kansas. According to Clark (1971) all species of Tychius infest legume pods, so far as is known.

The adults of T. sordidus appear in the spring about the time B. leucophaea has well-developed buds and are found in the field until the pods are well developed on at least some of the B. australis individuals. An adult weevil was observed in the field ovipositing into a B. australis bud. Adult weevils have been observed both in the field and in the laboratory within the wings of the flower chewing on the petals and presumably ovipositing. Other activity on Baptisia includes mating and chewing on the stems and sepals yielding minimal damage. Adult T. sordidus have wings. One adult was observed by an assistant to fly from a Baptisia plant in the field. Adults were observed on Baptisia plants in plots and then marked. Their location on plants in the plots was then periodically checked. Movement between plants was often rapid enough that it is unlikely that it occurred by walking. While flight was not generally observed in the day time and feigning "death" was a common behavior with disturbance, flight from Baptisia plant to Baptisia plant seems likely. The female weevil oviposits her yellow-orange eggs into the ovary of the plant. The young larvae hatch and eat the developing ovules and seed. Weevil larvae collected from Baptisia were determined by D. M. Anderson to be Tychius sordidus LeConte. According to Mitchell and Pierce (1911) the larvae emerge from the seed pods to pupate in the soil. In the laboratory I observed a mature weevil larvae eat a hole through a green Baptisia pod and emerge from the pod through the hole. The larva dessicated in the soil beneath the pod probably due to the low ambient relative humidity.

The other major host-specific insect, Grapholitha tristegama (Clemens) is a moth, family Olethreutidae. Larvae were identified by

D. M. Weisman. These larvae also attack the contents of the seed pod. Both larvae of T. sordidus and G. tristegama were commonly found in developing Baptisia seed pods.

The larval stage of another Lepidopteran, Anacampsis sp., family Gelechiidae, attacks the buds and flowers as well as the leaves of Baptisia. D. M. Weisman identified larvae taken from B. australis and B. leucophaea leaves and flowers as Anacampsis sp. (probably new).

A Cleridae (Coleoptera) larva is a parasite on at least G. tristegama. The Cleridae larvae were identified as either Phyllobaenus or Isohydnocera sp. by D. M. Anderson. Anderson noted (personal communication) that larvae of these genera are predaceous on other larvae that burrow in woody and herbaceous plants, as far as is known.

An adult meloid beetle was observed to eat buds, flowers, pods and leaves of Baptisia. It is unknown how host-specific this beetle is. Seedlings per se were not recognized in the field although some very small non-flowering Baptisia were observed. These meloid beetles as well as Anacampsis sp. would be the only likely candidates for seedling predators.

RESULTS AND DISCUSSION

To test Model 1A in Figure 6 and Equation 1 the regression

$$y = B_1 + B_2(\text{DNN}) \quad (\text{from Equation 1})$$

was run for each plot. Plots 13, 14, 15 and 16 were not run since in these plots (all burned plots with B. leucophaea of various densities) none of the flowers successfully produced seed. Table 5B shows that a high percentage of the remaining pods were successfully attacked by insect seed predators. Plot 6 was not run since it had been previously analyzed for a different kind of data. Data on fitness of the plant and efficiency of seed set were not taken on Plot 22 since some pods had already lost seed in the field before being harvested. None of the models were tested with these 6 plots.

In testing Model 1A and the other models, two indices of fitness were used as dependent variables. One was a direct measure of fitness for that season, the total number of filled, unattacked seeds produced. The other was this direct measure corrected for the amount of seeds the plant was able to attempt. This may be called the efficiency of seed production. It was estimated by the number of filled, unattacked seeds produced per flower scar. Seeds attempted was measured by the number of flower scars on a plant because it could be directly determined and the number of ovules a plant produced could not. Each of these measures was transformed with a square root function to help them more closely approximate the assumptions of the underlying statistical model. These indices of fitness used in the analyses do not necessarily vary from zero to 1.0. To get the fitness measure as modelled, each fitness index would have to be divided by a

constant, the largest fitness index in that data set. The B values would be changed by a constant also, which would not alter the signs of their magnitudes. The significance levels would remain the same. Thus the analyses done may be used to test the hypothesized models. Since it was not known whether the seed predators oriented primarily to plants irrespective of reproductive condition or mainly to flowering plants both the distance to the nearest neighbor of the same species with an inflorescence (DSSI) and the distance to the nearest neighbor irrespective of species (B. leucophaea or B. australis) and reproductive condition were used. In testing Models 1A, 1B, 2, 3, 3A and 4, DNN and DSSI had units of 1×10^{-1} meters.

From Model 1A, we expect the estimates of B_1 to be zero or positive and B_2 to be positive. If, however, the relationship is not linear at very short DNN's and DSSI's, B_1 may be negative. Thus the sign of the intercept in this and the other models is not critical since a negative sign probably indicates a lack of linearity at short DNN's and not a negation of other features of the model.

The R^2 and significance level for each plot for Model 1A are given in Table 6. The simple prediction of a significant ($p \ .05$) positive relationship between DNN (or DSSI) and the fitness of the plant, (No. seeds)^{1/2}, was not met in 15 out of the 16 plots tested. This is about the number you would expect to be significant based on chance, $p \ .05$. However, for between DNN (and DSSI) and efficiency of seed set (No. seeds per flower scar)^{1/2} two plots had significant relationships in which 59.8 and 48.7% of the variance in (No. seeds per flower scar)^{1/2} is explained by DSSI alone. This is more plots than I would expect by chance alone. However, since 14 other plots do not show significant relationships of

TABLE 6: Model 1A: $y = B_1 + B_2(\text{DNN})$. Model 1A was tested with regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . Both DNN, the distance from a plant to its nearest Baptisia neighbor, and DSSI, the distance from a plant to its nearest neighbor of the same species with an inflorescence, were used as distance variables. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression are listed for each of the plots.

Plot No.	Efficiency				Fitness			
	$y = (\text{No. seeds per flower scar})^{1/2}$				$y = (\text{No. seeds})^{1/2}$			
	DSSI		DNN		DSSI		DNN	
	R^2	α^*	R^2	α^*	R^2	α^*	R^2	α^*
1	.598	.04	.598	.04	.531	.06	.531	.06
2	.076	.25	.022	.54	.039	.42	.005	.78
3	.094	.33	.005	.82	.031	.58	.016	.70
4	.013	.71	.017	.67	.034	.55	.053	.45
5	.0003	.97	.36	.15	.009	.84	.32	.18
7	.0001	.97	.009	.66	.002	.83	.004	.77
8	.024	.61	.015	.69	.005	.82	.019	.65
9	.0003	.94	.045	.36	.002	.86	.043	.37
10	.001	.87	.00000	.998	.002	.82	.00003	.98
11	.010	.56	.0003	.92	.001	.88	.004	.70
12	.011	.65	.117	.12	.006	.72	.096	.16
17	.008	.65	.00000	.99	.026	.40	.011	.58
18	.487	.001	.314	.0125	.469	.0012	.277	.02
19	.024	.18	.048	.06	.025	.17	.048	.06
20	.007	.55	.003	.68	.004	.68	.001	.83
21	.114	.28	.007	.79	.103	.31	.009	.77

* α is the observed significance level of the F ratio used to test the significance of the regression.

this type, I consider getting 2 significant plots as suggesting that distance measures may be important as part of a larger series of variables.

The values and standard deviations of B_1 and B_2 in Model 1A are given in Table 7. Although the point estimator of B_1 has the predicted sign for a majority of plots, a 95% confidence interval around the B_1 point estimator would include a negative value, for most plots, which is not predicted by Model 1A. A majority of the point estimators of B_2 are themselves negative and thus beyond the lower limits predicted by Model 1A. So our simple predictions of a relationship between number of seed set and distance are not met. The fact that it was the efficiency measure, which attempts to correct for the varying number of flowers different plants produce, that was the dependent variable for a significant regression lends impetus to testing Model 1B in Figure 7 and Equation 3.

$$y = B_1 + B_{2a}(\text{DNN}) - B_{3a}(\text{DNN})(F) \quad (\text{from Equation 3})$$

This model was also tested using both dependent variables and both DSSI and DNN. In this case we expect our estimates of B_1 to be zero or positive, B_{2a} to be positive and B_{3a} to be negative, when consideration is made of the signs in front of the B values in Equation 3. The results are given in Tables 8 and 9.

From Table 8 we can see that 6 or 7 of the 16 plots had their variance in number of unattacked, filled seed set significantly explained by this model. However, from Table 9 we see that the majority of the point estimators of B_{2a} are negative and the majority of the point estimators of B_{3a} are positive. This is the opposite of the signs predicted by Model 1B. This trend is fairly consistent for both distance measures and both fitness measures.

TABLE 7: Values of B_1 and B_2 in Model 1A. See Table 6 for corresponding R^2 and α values. For each B value the corresponding standard deviation is in parentheses to the right of the B value.

Efficiency: $y = (\text{No. seeds per flower scar})^{1/2}$

Plot No.	DSSI		DNN	
	B_1	B_2	B_1	B_2
1	.763 (.192)	-2.357 (.864)	.763 (.192)	-2.357 (.864)
2	.248 (.153)	.638 (.538)	.492 (.187)	-.651 (1.045)
3	.717 (.227)	-.377 (.370)	.631 (.287)	-.267 (1.138)
4	.442 (.399)	.651 (1.731)	.439 (.358)	.711 (1.629)
5	.528 (.331)	.055 (1.409)	.957 (.290)	-3.561 (2.123)
7	.133 (.111)	-.018 (.480)	.092 (.106)	.249 (.559)
8	.083 (.106)	.192 (.368)	.167 (.111)	-.208 (.510)
9	.042 (.058)	-.014 (.195)	.090 (.061)	-.279 (.296)
10	.049 (.032)	-.019 (.115)	.046 (.037)	-.001 (.269)
11	.012 (.033)	.093 (.158)	.027 (.035)	.024 (.239)
12	.012 (.031)	.048 (.104)	-.014 (.027)	.202 (.124)
17	.085 (.077)	-.158 (.343)	.054 (.086)	.004 (.493)
18	-.243 (.097)	1.738 (.433)	-.175 (.112)	1.651 (.591)
19	.426 (.092)	-.828 (.614)	.478 (.095)	-1.321 (.683)
20	.355 (.095)	-.361 (.604)	.342 (.098)	-.302 (.739)
21	.300 (.480)	1.662 (1.463)	.845 (.558)	-.606 (2.227)

Expected sign:

+ or 0

+

+ or 0

+

TABLE 7: Continued

Fitness: $y = (\text{No. seeds})^{1/2}$

Plot No.	DSSI		DNN	
	B ₁	B ₂	B ₁	B ₂
1	5.484 (1.585)	-16.979 (7.135)	5.484 (1.585)	-16.979 (7.135)
2	2.122 (1.354)	3.953 (4.778)	3.416 (1.638)	-2.637 (9.172)
3	5.865 (2.152)	-1.999 (3.511)	4.361 (2.619)	4.180 (10.395)
4	3.154 (3.512)	9.428 (15.254)	2.931 (3.131)	11.228 (14.241)
5	3.253 (1.769)	-1.600 (7.510)	5.068 (1.597)	-18.117 (11.688)
7	.896 (.639)	-.594 (2.756)	.641 (.610)	.965 (3.223)
8	.960 (1.111)	.918 (3.861)	1.631 (1.151)	-2.461 (5.285)
9	.470 (.573)	-.335 (1.909)	.876 (.595)	-2.695 (2.910)
10	.244 (.151)	-.124 (.552)	.226 (.178)	-.040 (1.309)
11	.188 (.272)	.193 (1.294)	.123 (.289)	.756 (1.951)
12	.163 (.365)	.439 (1.228)	-.136 (.326)	2.151 (1.477)
17	1.008 (.703)	-2.670 (3.137)	.884 (.792)	-2.518 (4.529)
18	-1.201 (.527)	9.118 (2.353)	-.781 (.613)	8.272 (3.244)
19	2.819 (.629)	-5.808 (4.190)	3.150 (.645)	-8.980 (4.663)
20	2.603 (.764)	-2.041 (4.864)	2.489 (.785)	-1.308 (5.946)
21	2.280 (2.882)	9.394 (8.782)	5.486 (3.322)	-4.053 (13.266)

Expected sign:

+ or 0

+

+ or 0

+

TABLE 8: Model 1B: $y = B_1 + B_2a(\text{DNN}) - B_3a(\text{DNN})(F)$. Model 1B was tested with regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . Both DNN, the distance from a plant to its nearest Baptisia neighbor, and DSSI, the distance from a plant to its nearest neighbor of the same species with an inflorescence, were used as distance variables. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression are listed for each of the plots.

Plot No.	Efficiency				Fitness			
	$y = (\text{No. seeds per flower scar})^{1/2}$				$y = (\text{No. seeds})^{1/2}$			
	DSSI		DNN		DSSI		DNN	
	R^2	α^*	R^2	α^*	R^2	α^*	R^2	α^*
1	.661	.12	.661	.12	.654	.12	.654	.12
2	.314	.05	.385	.02	.500	.004	.590	.001
3	.106	.60	.226	.32	.168	.44	.468	.06
4	.083	.65	.080	.66	.488	.04	.486	.04
5	.516	.23	.530	.22	.383	.38	.407	.35
7	.002	.97	.024	.76	.002	.98	.007	.93
8	.209	.31	.186	.36	.373	.10	.331	.13
9	.234	.10	.111	.35	.223	.103	.119	.32
10	.001	.99	.0001	.999	.002	.97	.0003	.995
11	.035	.55	.077	.26	.128	.10	.240	.01
12	.288	.04	.413	.01	.318	.03	.460	.003
17	.150	.12	.240	.03	.239	.03	.370	.003
18	.566	.0013	.473	.01	.508	.003	.388	.02
19	.026	.38	.051	.15	.037	.25	.057	.12
20	.098	.09	.105	.07	.214	.004	.252	.001
21	.275	.24	.044	.82	.395	.10	.133	.52

* α is the observed significance level of the F ratio used to test the significance of the regression.

TABLE 9: Estimates of the coefficients in Model 1B. The standard deviation of each coefficient is given in parentheses to the right of the coefficient. See Table 8 for R^2 and t values for each plot.

Plot No.	Fitness measure: (No. seeds per flower scar) ^{1/2} Distance measure: DNN		
	B_1	$+B_{2a}$	$-B_{3a}$
1	.636 (.246)	-4.029 (2.137)	.085 (.098)
2	.533 (.153)	-2.411 (1.028)	.036 (.012)
3	.683 (.268)	-1.820 (1.435)	.017 (.011)
4	.419 (.364)	.091 (1.812)	.009 (.011)
5	.899 (.282)	.107 (3.677)	-.072 (.060)
7	.086 (.108)	.574 (.785)	-.006 (.010)
8	.172 (.106)	-.719 (.600)	.009 (.006)
9	.071 (.062)	-.391 (.309)	.005 (.004)
10	.047 (.041)	.007 (.330)	-.001 (.014)
11	.022 (.035)	-.173 (.261)	.005 (.003)
12	.010 (.024)	-.175 (.160)	.004 (.001)
17	-.012 (.080)	-.518 (.475)	.035 (.012)
18	-.191 (.101)	2.834 (.758)	-.023 (.011)
19	.488 (.097)	-1.121 (.800)	-.006 (.013)
20	.328 (.094)	-1.549 (.890)	.030 (.013)
21	.669 (.650)	-.609 (2.303)	.028 (.048)
Expected sign:	0 or +	+	-

TABLE 9: Continued

Fitness measure: (No. seeds)^{1/2}
 Distance measure: DNN

Plot No.	B ₁	+B _{2a}	-B _{3a}
1	4.120 (1.902)	-34.907 (16.492)	.911 (.762)
2	3.869 (1.088)	-22.067 (7.309)	.396 (.083)
3	5.044 (2.044)	-16.237 (10.925)	.222 (.080)
4	2.479 (2.424)	-3.200 (12.074)	.204 (.070)
5	4.853 (1.697)	-4.417 (22.094)	-.269 (.361)
7	.624 (.626)	1.785 (4.557)	-.016 (.060)
8	1.702 (.998)	-9.632 (5.654)	.129 (.060)
9	.674 (.609)	-3.861 (3.019)	.048 (.039)
10	.219 (.196)	-.120 (.158)	.006 (.065)
11	.050 (.257)	-2.074 (1.936)	.073 (.022)
12	.179 (.274)	-2.769 (1.807)	.048 (.013)
17	.143 (.672)	-8.405 (3.990)	.398 (.103)
18	-.855 (.583)	13.551 (4.369)	-.103 (.060)
19	3.031 (.661)	-11.345 (5.446)	.075 (.089)
20	2.311 (.688)	-17.065 (6.539)	.373 (.094)
21	3.559 (3.689)	-4.086 (13.081)	.307 (.270)
Expected sign:	0 or +	+	-

TABLE 9: Continued

Fitness measure: (No. seeds per flower scar)^{1/2}
 Distance measure: DSSI

Plot No.	B ₁	+B _{2a}	-B _{3a}
1	.636 (.246)	-4.029 (2.137)	.085 (.099)
2	.256 (.136)	-.324 (.629)	.022 (.009)
3	.693 (.248)	-.420 (.406)	.001 (.004)
4	.406 (.405)	.109 (1.857)	.009 (.010)
5	.818 (.294)	2.082 (1.470)	-.098 (.047)
7	.135 (.114)	.049 (.574)	-.002 (.009)
8	.095 (.100)	-.296 (.472)	.008 (.005)
9	-.002 (.056)	-.189 (.190)	.008 (.003)
10	.049 (.039)	-.019 (.142)	-.000 (.009)
11	.009 (.033)	.011 (.181)	.002 (.002)
12	.018 (.027)	-.142 (.114)	.003 (.001)
17	.023 (.078)	-.427 (.349)	.023 (.011)
18	-.232 (.092)	2.321 (.533)	-.014 (.008)
19	.433 (.095)	-.673 (.742)	-.005 (.013)
20	.336 (.092)	-1.315 (.729)	.024 (.011)
21	.135 (.473)	.752 (1.537)	.051 (.036)
Expected sign:	0 or +	+	-

TABLE 9: Continued

Fitness measure: (No. seeds)^{1/2}
 Distance measure: DSSI

Plot No.	B ₁	+B _{2a}	-B _{3a}
1	4.120 (1.902)	-34.907 (16.492)	.911 (.762)
2	2.217 (1.007)	-7.704 (4.670)	.261 (.068)
3	5.098 (2.194)	-3.329 (3.600)	.043 (.035)
4	2.336 (2.694)	-2.874 (12.352)	.205 (.069)
5	4.576 (1.776)	7.652 (8.894)	-.446 (.286)
7	.894 (.655)	-.645 (3.307)	.002 (.051)
8	1.137 (.928)	--	--
9	.050 (.551)	-2.009 (1.881)	.072 (.032)
10	.235 (.186)	-.156 (.677)	.004 (.045)
11	.126 (.259)	-1.331 (1.404)	.043 (.019)
12	.240 (.311)	-1.931 (1.317)	.032 (.011)
17	.303 (.685)	-5.704 (3.041)	.257 (.095)
18	-1.159 (.524)	11.309 (3.033)	-.053 (.047)
19	2.691 (.643)	-8.471 (5.035)	.083 (.086)
20	2.373 (.689)	-13.754 (5.472)	.293 (.083)
21	.951 (2.574)	2.073 (8.371)	.408 (.195)
Expected sign:	0 or +	+	-

The consistency of this unpredicted result suggests a pattern. A negative B_{2a} and a positive B_{3a} is that expected if pollination is the important variable which varies with isolation and whose probability is modified by the number of flowers a plant has. This is the model displayed graphically in Figure 12 and stated mathematically in Equation 8.

Since it appears that pollinators might be affected by plant isolation, I looked at a combined model of both Fitness(Pollination) and Fitness(Escape). This model (Model 2) is displayed graphically in Figure 11 and stated mathematically in Equation 6.

$$y = B_7 + B_8(\text{DNN}) - B_9(\text{DNN})^2 \quad (\text{from Equation 6})$$

Note that with this model we expect B_7 to be 0 or positive, B_8 to be negative, zero or positive, and $-B_9$ to be negative as noted in the section on Model Development.

Since this model does not take into account the number of flowers when fitness is the dependent variable, we would not expect this model to do too well. The model with efficiency as the dependent variable should do better. The results are shown in Tables 10 and 11.

Only one plot, Plot 18, shows a significant regression for this model. For both DSSI and DNN and the efficiency and fitness measures, the sign of B_9 is not negative as expected. From 77.1 - 89.7% of the variance of the dependent variable is explained, however, by the variance in the independent variables. In about two-thirds of the other plots the point estimator of the critical B value, B_9 , is negative as predicted by Model 2. A 95% confidence interval about each of these point estimators does, however, in general include zero, and positive numbers, which is not predicted by Model 2.

TABLE 10: Model 2: $y = B_7 + B_8(\text{DNN}) - B_9(\text{DNN})^2$. Model 2 was tested with regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . Both DNN, the distance from a plant to its nearest Baptisia neighbor, and DSSI, the distance from a plant to its nearest neighbor of the same species with an inflorescence, were used as distance variables. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression are listed for each of the plots.

Plot No.	Efficiency				Fitness			
	$y = (\text{No. seeds per flower scar})^{1/2}$				$y = (\text{No. seeds})^{1/2}$			
	DSSI		DNN		DSSI		DNN	
	R^2	α^*	R^2	α^*	R^2	α^*	R^2	α^*
1	.712	.08	.712	.08	.642	.13	.642	.13
2	.195	.18	.053	.65	.080	.51	.080	.51
3	.094	.64	.184	.40	.105	.61	.184	.40
4	.224	.28	.411	.07	.137	.48	.267	.21
5	.116	.78	.451	.30	.130	.76	.414	.34
7	.009	.90	.034	.68	.007	.92	.020	.80
8	.039	.82	.124	.52	.005	.97	.090	.62
9	.004	.96	.045	.66	.002	.98	.043	.67
10	.034	.62	.077	.32	.029	.66	.078	.32
11	.051	.41	.014	.79	.028	.62	.032	.57
12	.089	.41	.217	.10	.081	.45	.202	.12
17	--	--	.00001	.9999	--	--	.013	.84
18	.897	.0000	.860	.0000	.796	.0000	.771	.0000
19	.025	.39	.048	.16	.027	.37	.048	.17
20	.008	.83	.023	.58	.005	.89	.025	.55
21	.444	.07	.122	.56	.409	.09	.148	.49
All of the above plots together:								
	.001	.81	.004	.453	.000	.95	.005	.355

* α is the observed significance level of the F ratio used to test the significance of the regression

TABLE 11: Estimates of the coefficients in Model 2. The standard deviation of each coefficient is given in parentheses to the right of the coefficient. See Table 10 for R^2 and α values for each plot.

Fitness measure: (No. seeds per flower scar)^{1/2}
Distance measure: DNN

Plot No.	B_7	B_8	B_9
1	1.140 (.350)	-8.980 (5.330)	16.298 (12.960)
2	.687 (.332)	-3.918 (4.677)	9.576 (13.352)
3	1.214 (.497)	-7.348 (5.163)	11.713 (8.348)
4	-1.080 (.655)	18.236 (6.900)	-40.101 (15.496)
5	.606 (.526)	4.542 (10.211)	-32.162 (39.580)
7	-.035 (.197)	2.350 (2.791)	-5.189 (6.751)
8	.002 (.184)	1.891 (1.952)	-4.665 (4.190)
9	.091 (.116)	-.293 (1.132)	.030 (2.444)
10	-.032 (.062)	1.476 (.992)	-4.182 (2.706)
11	-.013 (.067)	.552 (.807)	-1.429 (2.085)
12	-.094 (.058)	.923 (.480)	-1.218 (.785)
17	.052 (.167)	.030 (2.401)	-.082 (7.373)
18	.538 (.104)	-7.468 (1.185)	22.046 (2.788)
19	.459 (.175)	-.980 (2.692)	-1.128 (8.612)
20	.227 (.154)	1.539 (2.047)	-4.599 (4.771)
21	-.114 (1.044)	8.883 (9.038)	-15.578 (14.388)
Expected sign:	0 or +	-, 0 or +	-

TABLE 11: Continued

Fitness measure: (No. seeds)
Distance measure: DNN

Plot No.	B ₇	B ₈	B ₉
1	8.331 (2.983)	-67.060 (45.409)	123.235 (110.415)
2	6.084 (2.847)	-47.196 (40.112)	130.595 (114.507)
3	9.550 (4.566)	-58.924 (47.424)	104.377 (76.680)
4	-7.026 (6.508)	126.137 (68.567)	-262.938 (153.990)
5	3.195 (2.913)	25.076 (56.504)	-171.449 (219.021)
7	.065 (1.141)	10.479 (16.178)	-23.495 (39.126)
8	.252 (1.946)	15.174 (20.659)	-39.190 (44.353)
9	.857 (1.135)	-2.489 (11.113)	-.463 (24.131)
10	-.145 (.298)	6.979 (4.753)	-19.878 (12.965)
11	-.338 (.546)	6.967 (6.539)	-16.808 (16.889)
12	-1.105 (.686)	10.923 (5.696)	-14.822 (9.319)
17	1.187 (1.529)	-7.548 (22.052)	15.765 (67.573)
18	2.844 (.712)	-38.081 (8.107)	112.066 (19.066)
19	3.018 (1.192)	-6.645 (18.372)	-7.723 (58.776)
20	1.454 (1.236)	15.275 (16.440)	-41.438 (38.312)
21	-.807 (6.134)	58.222 (53.103)	-102.242 (84.540)
Expected sign:	0 or +	-, 0 or +	-

TABLE 11: Continued

Fitness measure: (No. seeds per flower scar)^{1/2}
 Distance measure: DSSI

Plot No.	B ₇	B ₈	B ₉
1	1.140 (.350)	-8.980 (5.330)	16.298 (12.960)
2	.536 (.238)	-1.705 (1.615)	2.974 (1.941)
3	.724 (.325)	-.415 (1.446)	.021 (.753)
4	-.934 (.912)	15.254 (8.992)	-32.245 (19.534)
5	.820 (.534)	-3.520 (5.166)	7.319 (10.132)
7	.066 (.186)	.944 (2.183)	-2.115 (4.677)
8	.134 (.170)	-.366 (1.457)	.988 (2.485)
9	.014 (.124)	.171 (.734)	-.227 (.868)
10	.015 (.047)	.323 (.368)	-.381 (.389)
11	-.047 (.059)	.743 (.559)	-1.408 (1.162)
12	-.060 (.064)	.594 (.438)	-.818 (.447)
17	--	--	--
18	.286 (.080)	-3.510 (.686)	9.887 (1.237)
19	.469 (.161)	-1.519 (2.186)	2.007 (6.085)
20	.335 (.166)	-.071 (2.067)	-.657 (4.470)
21	1.880 (.793)	-11.992 (6.038)	17.439 (7.552)
Expected sign:	0 or +	-, 0, or +	-

TABLE 11: Continued

Fitness measure: (No. seeds)
Distance measure: DSSI

Plot No.	B ₇	B ₈	B ₉
1	8.331 (2.983)	-67.060 (45.409)	123.235 (110.415)
2	3.607 (2.216)	-8.130 (15.014)	15.341 (18.046)
3	4.142 (2.965)	8.900 (13.201)	-5.887 (6.868)
4	-5.431 (8.565)	100.569 (84.448)	-201.243 (183.465)
5	4.857 (2.840)	-21.216 (27.461)	40.156 (53.857)
7	.609 (1.070)	3.548 (12.576)	-9.102 (26.937)
8	1.044 (1.792)	.011 (15.269)	1.604 (26.257)
9	.340 (1.220)	.509 (7.210)	-1.038 (8.527)
10	.097 (.226)	1.360 (1.769)	-1.649 (1.868)
11	-.204 (.487)	4.498 (4.624)	-9.331 (9.621)
12	-.663 (.756)	6.696 (5.178)	-9.367 (7.536)
17	--	--	--
18	1.318 (.602)	-15.879 (5.170)	47.091 (9.318)
19	3.147 (1.096)	-11.031 (14.903)	15.160 (41.489)
20	2.316 (1.333)	2.161 (16.652)	-9.507 (35.985)
21	11.363 (4.875)	-69.126 (37.123)	100.286 (46.433)
Expected sign:	0 or +	-, 0, or +	-

Model 3, which is a modification of Model 2, was tested with both Fitness(Pollination) and Fitness(Escape) curves allowed to vary with the number of flowers as shown graphically in Figure 15 and mathematically in Equation 12.

$$y = B_7 + B_{14}(\text{DNN}) + B_{15}(\text{F})(\text{DNN}) - B_{16}(\text{DNN})^2 + B_{17}(\text{F})(\text{DNN})^2 - B_{18}(\text{F})^2(\text{DNN})^2 \quad (\text{from Equation 12})$$

Regressions were run for both DSSI and DNN and dependent variables, (No. seeds per flower scar)^{1/2} and (No. seeds)^{1/2}. These results are shown in Table 12.

Note that R^2 , the amount of variance in (No. of seeds)^{1/2}, the fitness measure, that is explained by the independent variables including DNN is greatly increased for Model 3 over Model 1B, its nearest competitor. The six significant R^2 values range from 31.6% to 83.5% with most lying in the 60's. The significance levels remain high, in some cases decreasing and in some cases increasing. However, due to the high correlation between certain of the independent variables there was rounding error in many of the plots. Thus the signs of the B values are not reliable. To alleviate this problem, I attempted to use the procedure of ridge regression. Model 3 was tested on Plot 2 using ridge regression. For Plot 2 using regular regression analysis the R^2 for (No. seeds/scar)^{1/2} is .581 with a significance level of .029 and the R^2 for (No. seeds)^{1/2} is .666 with a significance level of .008. With Model 3, point estimates of B_7 are expected to be zero or positive, point estimates of B_{14} and B_{15} are expected to be negative, zero, or positive, point estimates of $-B_{16}$ and $-B_{18}$ are expected to be negative, and point estimates of B_{17} are expected to be positive.

TABLE 12: Model 3: $y = B_7 + B_{14}(\text{DNN}) + B_{15}(\text{F})(\text{DNN}) - B_{16}(\text{DNN})^2 + B_{17}(\text{F})(\text{DNN})^2 - B_{18}(\text{F})^2(\text{DNN})^2$. Model 3 was tested with regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . Both DNN, the distance from a plant to its nearest Baptisia neighbor, and DSSI, the distance from a plant to its nearest neighbor of the same species with an inflorescence, were used as distance variables. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression are listed for each of the plots.

Plot No.	Efficiency $y = (\text{No. seeds per flower scar})^{1/2}$				Fitness $y = (\text{No. seeds})^{1/2}$			
	DSSI		DNN		DSSI		DNN	
	R^2	α^*	R^2	α^*	R^2	α^*	R^2	α^*
1	.996	.11	.996	.109	.995	.12	.995	.12
2	.581	.03	.501	.08	.666	.01	.690	.01
3	.365	.65	.444	.51	.581	.28	.636	.20
4	.457	.41	.729	.06	.629	.15	.738	.0507
5	.912	.48	.944	.39	.896	.52	.952	.36
7	.035	.98	.062	.93	.050	.96	.054	.95
8	.575	.21	.504	.32	.749	.04	.696	.08
9	.300	.32	.251	.45	.262	.42	.263	.41
10	.209	.29	.157	.48	.217	.26	.152	.50
11	.191	.23	.262	.08	.403	.005	.613	.0000
12	.363	.16	.600	.01	.419	.09	.695	.001
17	--	--	.348	.06	--	--	.659	.0001
18	.912	.0000	.920	.0000	.816	.0002	.835	.0001
19	.036	.76	.055	.54	.043	.68	.058	.51
20	.128	.29	.190	.09	.233	.03	.316	.004
21	.594	.26	.510	.39	.622	.22	.535	.35
All of the above plots together:								
	.048	.0019	.042	.0053	.138	.0000	.173	.0000

* α is the observed significance level of the F ratio used to test the significance of the regression.

However, using ridge regression analysis, the signs of the point estimators of $-B_{16}$ and $-B_{18}$ for Plot 2 are positive, which is not as predicted (Table 13).

A modification of Model 3 in which the number of stalks was also allowed to vary with isolation for both pollinators and seed predators was also tested on a few plots. This model, Model 4, is mathematically stated in Equation 19.

$$\begin{aligned}
 y = & B_{25} + B_{26}(\text{DNN}) + B_{27}(\text{F})(\text{DNN}) + B_{28}(\text{Size})(\text{DNN}) - B_{29}(\text{DNN})^2 \\
 & + B_{30}(\text{F})(\text{DNN})^2 - B_{31}(\text{F})^2(\text{DNN})^2 + B_{32}(\text{Size})(\text{DNN})^2 \\
 & - B_{33}(\text{F})(\text{Size})(\text{DNN})^2 - B_{34}(\text{Size})^2(\text{DNN})^2 \quad (\text{from Equation 19})
 \end{aligned}$$

Several plots were analyzed for Model 4 using regular as well as ridge regression. As in Model 3 rounding error due to highly correlated independent variables made the B values not reliable. The R^2 and significance level for each plot analyzed with regular regression are found in Table 14. The B values and their standard deviations for the plot for which the ridge regression was properly performed are shown in Table 15. The expected sign of each B value is shown in the column to the right. The signs of the estimates of the B values are generally not as predicted by Model 4.

Since the signs of the coefficients for Models 3 and 4 from the ridge regression analysis were not as predicted, yet the R^2 values were high, I tried a simplified Model 3, called Model 3A in the section on Model Development and in Appendix II. This model basically assumes pollinators are affected both by a plant's isolation and the number of flowers it bears. Since the expected reaction of weevils to the number of flowers is counteracted in part by an increased opportunity for ovules

TABLE 13: Model 3: $y = B_7 + B_{14}(\text{DNN}) + B_{15}(\text{F})(\text{DNN}) - B_{16}(\text{DNN})^2 + B_{17}(\text{F})(\text{DNN})^2 - B_{18}(\text{F})^2(\text{DNN})^2$.

Model 3 was tested on Plot 2 using ridge regression. The distance variable DSSI = DNN. The K values chosen from the ridge trace are .4 for (No. seeds per flower scar)^{1/2} and .3 for (No. seeds)^{1/2}. The B values at the respective K values are listed with their standard deviations in parentheses to the right.

B Number	(No. seeds per flower scar) ^{1/2}	(No. seeds) ^{1/2}	Predicted signs
B ₇	.479 (.217)	3.866 (1.683)	0 or +
B ₁₄	-.324 (.672)	-4.714 (6.048)	?
B ₁₅	.008 (.010)	.107 (.092)	?
-B ₁₆	.341 (.805)	.792 (7.296)	-
B ₁₇	.012 (.020)	.095 (.182)	+
-B ₁₈	.000 (.000)	.001 (.002)	-

TABLE 14: Model 4: $y = B_{25} + B_{26}(\text{DNN}) + B_{27}(\text{F})(\text{DNN}) + B_{28}(\text{Size})(\text{DNN})$

$$- B_{29}(\text{DNN})^2 + B_{30}(\text{F})(\text{DNN})^2 - B_{31}(\text{F})^2(\text{DNN})^2 + B_{32}(\text{Size})(\text{DNN})^2$$

$$- B_{33}(\text{F})(\text{Size})(\text{DNN})^2 - B_{34}(\text{Size})^2(\text{DNN})^2.$$

Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . In this case $\text{DNN} = \text{DSSI}$. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression for Model 4 are given below.

Efficiency			Fitness		
$y = (\text{No. seeds per flower scar})^{1/2}$			$y = (\text{No. seeds})^{1/2}$		
Plot No.	R^2	α^*	R^2	α^*	Degrees of freedom
2	.78	.035	.91	.001	(9,9)
8	.85	.335	.92	.158	(9,3)
11	.25	.458	.44	.039	(9,27)
17	.45	.153	.78	.0001	(9,19)
18	.95	.0001	.89	.003	(9,9)
20	.21	.312	.33	.044	(9,40)
$y = \text{seeds per flower scars}$			$y = \text{No. seeds}$		
4	.996	.002	.997	.001	

* α is the observed significance level of the F ratio used to test the significance of the regression.

TABLE 15: Model 4. Model 4 was tested on Plot 2 using ridge regression analysis. The distance variable DSSI = DNN in this plot. The K values chosen from the ridge trace are .2 for (No. seeds per flower scar)^{1/2} and .1 for (No. seeds)^{1/2}. The B values at the respective K values are listed with their standard deviations in parentheses to the right. The predicted signs of the B estimates are shown.

Plot No. 2

B	(No. seeds per flower scar) ^{1/2}	(No. seeds) ^{1/2}	Predicted signs
B ₂₅	.540 (.238)	3.407 (1.336)	0 or +
B ₂₆	-.511 (1.057)	-7.989 (10.602)	?
B ₂₇	.014 (.017)	.215 (.169)	?
B ₂₈	-.360 (.662)	-3.251 (6.728)	?
-B ₂₉	.464 (1.294)	2.744 (13.630)	-
B ₃₀	.018 (.033)	.157 (.349)	+
-B ₃₁	.000 (.000)	.001 (.004)	-
B ₃₂	.078 (1.246)	-.295 (13.457)	+
-B ₃₃	.001 (.015)	.008 (.161)	-
-B ₃₄	-.123 (.566)	-1.443 (6.056)	-

to become seeds due to an increase in ovules per se, the escape from predation curve is not shown as being affected by the number of flowers. Model 3A is shown graphically in Figure 14 and expressed mathematically in Equation 10.

$$y = B_7 + B_{10}(DNN) + B_{11}(F)(DNN) - B_{12}(DNN)^2 + B_{13}(F)(DNN)^2 \quad (\text{from Equation 10})$$

With this model, estimates of B_7 are expected to be zero or positive, estimates of B_{10} are expected to be negative, zero or positive, estimates of B_{11} are expected to be zero or positive, estimates of B_{12} are expected to be negative, and estimates of B_{13} are expected to be positive.

I ran the ridge regression using Model 3A for the plots listed in Table 16. The R^2 values and the significance levels for Model 3A for these plots using regular regression analysis are shown in Table 16. They should be very similar to values calculated using ridge regression. Both dependent variables were used and DSSI instead of DNN was used. The efficiency measure was significantly predicted by Model 3A in only 2 out of the nine plots tested. The fitness measure was significantly predicted in six of the nine plots tested. The point estimators of the B values and their standard deviations are listed in Table 17. For both the fitness and efficiency of seed production measures, the signs of the point estimators of the critical B's (B_{11} , B_{12} , and B_{13}) are as expected in four of the nine plots tested. However, of these four plots, only one, Plot 20, had a significant R^2 for at least one of the dependent variables. Thus the significant regressions did not in general give the predicted signs of the B values. Also, the 95% confidence interval around the point

TABLE 16: Model 3A: $y = B_7 + B_{10}(\text{DNN}) + B_{11}(\text{F})(\text{DNN}) - B_{12}(\text{DNN})^2 + B_{13}(\text{F})(\text{DNN})^2$.

Model 3A was tested with regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . DSSI was the only distance variable tested. The R^2 values and the observed significance levels of the F ratio used to test the significance of the regression are listed for each of the plots.

Plot No.	(No. of seeds per flower scar) ^{1/2}		(No. seeds) ^{1/2}	
	R^2	α^*	R^2	α^*
1	.921	.151	.978	.044
2	.539	.021	.663	.003
4	.423	.298	.626	.068
8	.800	.014	.823	.009
9	.280	.235	.247	.309
11	.129	.338	.282	.027
12	.363	.089	.402	.056
17	.294	.069	.558	.0004
20	.100	.304	.218	.023

* α is the observed significance level of the F ratio used to test the significance of the regression.

TABLE 17: Model 3A: $y = B_7 + B_{10}(\text{DNN}) + B_{11}(\text{F})(\text{DNN}) - B_{12}(\text{DNN})^2 + B_{13}(\text{F})(\text{DNN})^2$

Model 3A was tested using ridge regression analysis. Measures of both efficiency of seed production and reproductive fitness of a plant that year were used as the dependent variable y . DSSI was the only distance variable tested. The point estimators of the B values for the best K value for each plot are listed. The standard deviation of the point estimator of each B value is in parentheses to the right of the B value. The K value used for each plot and the predicted signs of the B estimates are listed.

(No. of seeds per flower scar)^{1/2}

Plot No.	B_7	B_{10}	B_{11}	$-B_{12}$	B_{13}	K
1	1.142 (.511)	-1.873 (3.683)	.031 (.128)	-.247(8.193)	-.088 (.407)	.1
2	.579 (.200)	-.656 (.819)	.011 (.010)	.535(.991)	.016 (.024)	.2
4	-.875 (.881)	1.803 (4.117)	.000 (.021)	-4.980(9.005)	.030 (.069)	.3
8	.290 (.096)	-.355 (.826)	.009 (.008)	.461(1.521)	-.006 (.022)	.1
9	.011 (.125)	-.083 (.263)	.005 (.004)	-.151(.320)	.004 (.010)	.3
11	-.049 (.058)	.065 (.178)	.002 (.002)	-.067(.376)	-.002 (.007)	.5
12	-.028 (.059)	-.008 (.108)	.001 (.001)	-.075(.158)	.000 (.002)	.6
17	-.049 (.121)	-.133 (.539)	.025 (.014)	-.032(1.125)	-.040 (.049)	.2
20	.312 (.165)	-.362 (.629)	.010 (.009)	-.791(1.386)	.010 (.028)	.6

Predicted sign:

0 or + ? 0 or + - +

TABLE 17: Model 3A: Continued

(No. of seeds) ^{1/2}							
Pilot No.	B ₇	B ₁₀	B ₁₁	-B ₁₂	B ₁₃	K	
1	6.561 (2.077)	-15.165 (29.389)	.403 (1.023)	-1.899 (65.255)	-.808 (3.250)	.1	
2	4.122 (1.491)	-6.493 (6.635)	.147 (.084)	1.123 (8.035)	.132 (.195)	.2	
4	-4.239 (6.312)	7.431 (27.894)	.088 (.142)	-35.173 (61.013)	.369 (.470)	.1	
8	2.543 (.959)	-3.471 (8.219)	.117 (.078)	.070 (15.202)	-.072 (.216)	.1	
9	.197 (1.257)	-.947 (2.604)	.044 (.035)	-1.340 (3.167)	.038 (.094)	.3	
11	-.257 (.434)	.267 (1.959)	.046 (.024)	-1.669 (4.249)	-.054 (.075)	.2	
12	-.243 (.671)	-.147 (1.138)	.013 (.009)	-.763 (1.656)	.006 (.020)	.8	
17	-.170 (.887)	-2.673 (4.693)	.301 (.119)	1.814 (9.790)	-.543 (.426)	.2	
20	2.276 (1.236)	-2.763 (4.407)	.109 (.062)	-6.379 (9.651)	.076 (.196)	.8	
Predicted signs							
0 or +		?	0 or +	-	+		

estimators in each plot generally include values which are not predicted by Model 3A.

This leaves me with the conclusion that for many of the Baptisia plots studied on Konza Prairie and the Dewey Ranch I am able to predict quite well how many seeds a plant will produce, but that the relationships within the models are not the entire story. Because of the significant high R^2 values attained for some of the plots I feel I did measure some of the important variables.

For every relationship assumed in the model development, another assumption was that all other things were equal. Perhaps the lack of fit between expected and fitted B values is an indication that all other things were not equal. Varying degrees of chemical and/or mechanical defenses by individual plants and habitat differences would be possible examples of other things not equal. The existence of possibly less host-specific herbivores such as the meloid beetles, which consumed many an inflorescence or parts thereof, could also interfere with the possibly quite real relationships hypothesized.

It is also a possibility that the foraging strategies by the pollinators and seed predators are not as hypothesized but that the measured variables interact in other ways to predict fairly accurately the number of unattacked, filled seeds a plant will produce in a single season.

With the latter idea in mind, I used a backward elimination procedure to find the best subset of linear and quadratic combinations of three of the variables measured, F(number of flowers per plant), S(number of stalks per plant), and DNN(distance to the nearest neighbor of the same species with an inflorescence). The full model was $y = S + F + DNN + S^2 + F^2 + (DNN)^2 + SF + S(DNN) + F(DNN)$. Only those variables whose

contribution to the model was significant ($p < .05$) were left in the model. Due to the variability among plots indicated in previous models, I made a dummy variable for each plot number. These dummy variables were both forced into the regression equation or left out entirely. Due to limitations on the number of variables which could be forced, plots with predominantly B. australis (Plots 1-4 and 17-21) were analyzed separately from plots with predominantly B. leucophaea (Plots 7-12). Only B. australis plants were used in the analysis of Plots 1-4 and 17-21 and only B. leucophaea were used in the analysis of Plots 7-12.

In the B. australis plots, the same variables (except for the dummy plot variables) yielded the best model whether the dummy variables for plot number were forced into the regression equation or not. The "best" models for the B. australis plots are:

Plots forced:

$$\begin{aligned}
 (\text{No. seeds per flower scar})^{1/2} = & .872 - .274 (\text{Plot 1}) - .270 (\text{Plot 2}) \\
 & - .097 (\text{Plot 3}) - .032 (\text{Plot 4}) - .523 (\text{Plot 17}) - 0.518 (\text{Plot 18}) \\
 & - .326 (\text{Plot 19}) - .350 (\text{Plot 20}) + .084 (S)^2 + .045 (DNN)^2 \\
 & - .002 (S)(F) - .231 (DNN) - .321 (S) + .009 (F)
 \end{aligned}$$

where $R^2 = .258$, $\alpha = .0000$.

$$\begin{aligned}
 (\text{No. seeds per plant})^{1/2} = & 4.387 - 1.464 (\text{Plot 1}) - 1.355 (\text{Plot 2}) \\
 & - .067 (\text{Plot 3}) + .114 (\text{Plot 4}) - 3.094 (\text{Plot 17}) - 3.582 (\text{Plot 18}) \\
 & - 2.302 (\text{Plot 19}) - 2.076 (\text{Plot 20}) + .583 (S)^2 + .261 (DNN)^2 \\
 & - .017 (S)(F) - 1.262 (DNN) - 2.142 (S) + .084 (F)
 \end{aligned}$$

where $R^2 = .368$, $\alpha = .0000$.

Plots not included:

$$\begin{aligned}
 (\text{No. seeds per flower scar})^{1/2} &= .503 + .079 (S)^2 + .050 (DNN)^2 \\
 &- .002 (S)(F) - .243 (DNN) - .289 (S) + .009 (F) \\
 \text{where } R^2 &= .178, \quad \alpha = .0000.
 \end{aligned}
 \tag{Equation 22}$$

$$\begin{aligned}
 (\text{No. seeds per plant})^{1/2} &= 2.100 + .556 (S)^2 + .294 (DNN)^2 \\
 &- .016 (S)(F) - 1.325 (DNN) - 1.986 (S) + .085 (F) \\
 \text{where } R^2 &= .296, \quad \alpha = .0000.
 \end{aligned}$$

The "best" models for the B. leucophaea plots are:

Plots forced:

$$\begin{aligned}
 (\text{No. seeds per flower scar})^{1/2} &= -.021 + .132 (\text{Plot 7}) \\
 &+ .121 (\text{Plot 8}) + .034 (\text{Plot 9}) + .063 (\text{Plot 10}) \\
 &+ .014 (\text{Plot 11}) + .0000063 (F)^2 \\
 \text{where } R^2 &= .104, \quad \alpha = .034.
 \end{aligned}$$

$$\begin{aligned}
 (\text{No. seeds per plant})^{1/2} &= -.333 + .865 (\text{Plot 7}) \\
 &+ 1.124 (\text{Plot 8}) + .359 (\text{Plot 9}) + .476 (\text{Plot 10}) \\
 &+ .197 (\text{Plot 11}) + .000089 (F)^2 \\
 \text{where } R^2 &= .219, \quad \alpha = .0000.
 \end{aligned}$$

Plots not included:

$$\begin{aligned}
 (\text{No. seeds per flower scar})^{1/2} &= .043 + .0000053 (F)^2 \\
 \text{where } R^2 &= .032, \quad \alpha = .041.
 \end{aligned}$$

$$\begin{aligned}
 (\text{No. seeds per plant})^{1/2} &= .170 + .000083 (F)^2 \\
 \text{where } R^2 &= .150, \quad \alpha = .0000.
 \end{aligned}$$

For B. leucophaea in plots 7-12, DNN and stalk number are clearly not related to the fitness indices. The square of the number of flowers

was the only variable to significantly effect R^2 . This R^2 is low but significant. Other factors not included in the full model tested are clearly more important in determining the fitness indices tested.

For B. australis in Plots 1-4 and 17-21, DNN as well as stalk and flower number in a nonlinear fashion contribute significantly to explaining the variance in the fitness indices tested. While the R^2 values are low they are very significant. By forcing plot number into the equation, the R^2 value was significantly increased from .296 to .368. The F value is 3.090 with d.f. 8,217. Mean values for stalk and flower number for flowering plants in these plots were inserted into the "best" regression equation predicting (No. seeds per plant)^{1/2} when plot number was not forced (Equation 22). DNN was varied from 0 to 5 meters in increments of .1 m. (No. seeds per plant)^{1/2} is 2.1 at DNN = 0 m, decreases to a minimum of .608 at DNN = 2.3 m and thereafter increases within the range of DNN tested.

A similar process may be done for Models 3 and 4, using mean values of S and F from Plot 2 and the point estimators of the B values shown in Tables 13 and 15. (No. seeds per plot)^{1/2} for both Models 3 and 4 decrease to a minimum and then increase again with increasing DNN. This type of F(Success) curve could be derived from either curves for Fitness(Pollination) and for Fitness(Escape) such as shown in Figures 4 and 11 or for the appropriate exponential curve for each, if in either case both curves crossed in the asymptotic parts of their range.

This area of research merits further exploration. It would be particularly useful to measure changes in Fitness(Pollination) and Fitness(Escape) with changes in DNN, F, and S.

APPENDICES

APPENDIX I

Model 2

$$\text{Fitness(Success)} = \text{F(Pollination)} \text{ F(Escape)}$$

$$\text{F(Pollination)} = B_4 - B_5(\text{DNN})$$

$$\text{F(Escape)} = B_1 + B_2(\text{DNN})$$

$$\text{F(Success)} = [B_4 - B_5(\text{DNN})] [B_1 + B_2(\text{DNN})]$$

$$B_4 - B_5(\text{DNN})$$

$$B_1 + B_2(\text{DNN})$$

$$B_1 B_4 - B_1 B_5(\text{DNN})$$

$$+ B_2 B_4(\text{DNN}) - B_2 B_5(\text{DNN})^2$$

$$B_1 B_4 + (B_2 B_4 - B_1 B_5) \text{DNN} - B_2 B_5(\text{DNN})^2$$

(Equation 5)

APPENDIX II

Model 3A

Fitness(Success) = F(Pollination) F(Escape)

Where flowers affect pollination:

$$F(\text{Pollination}) = B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})$$

$$F(\text{Escape}) = B_1 + B_2(\text{DNN})$$

$$F(\text{Success}) = [B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})] [B_1 + B_2(\text{DNN})]$$

$$B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})$$

$$B_1 + B_2(\text{DNN})$$

$$B_1 B_4 - B_1 B_{5a}(\text{DNN}) + B_1 B_{6a}(F)(\text{DNN})$$

$$+ B_2 B_4(\text{DNN}) - B_2 B_{5a}(\text{DNN})^2 + B_2 B_{6a}(F)(\text{DNN})^2$$

$$B_1 B_4 + (B_2 B_4 - B_1 B_{5a})(\text{DNN}) + B_1 B_{6a}(F)(\text{DNN}) - B_2 B_{5a}(\text{DNN})^2 + B_2 B_{6a}(F)(\text{DNN})^2 \quad (\text{Equation 9})$$

APPENDIX III

Model 3

$$\text{Fitness}(\text{Success}) = F(\text{Pollination}) \quad F(\text{Escape})$$

Where the number of flowers affects both pollination and seed predation:

$$F(\text{Pollination}) = B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN}) \quad (\text{Equation 8})$$

$$F(\text{Escape}) = B_1 + B_{2a}(\text{DNN}) - B_{3a}(F)(\text{DNN}) \quad (\text{Equation 3})$$

$$F(\text{Success}) = [B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})] [B_1 + B_{2a}(\text{DNN}) - B_{3a}(F)(\text{DNN})]$$

$$B_4 - B_{5a}(\text{DNN}) + B_{6a}(F)(\text{DNN})$$

$$B_1 + B_{2a}(\text{DNN}) - B_{3a}(F)(\text{DNN})$$

$$B_1 B_4 - B_1 B_{5a}(\text{DNN}) + B_1 B_{6a}(F)(\text{DNN})$$

$$B_{2a} B_4(\text{DNN}) - B_{2a} B_{5a}(\text{DNN})^2 + B_{2a} B_{6a}(F)(\text{DNN})^2$$

$$-B_{3a} B_4(F)(\text{DNN}) + B_{3a} B_{5a}(F)(\text{DNN})^2$$

$$- B_{3a} B_{6a}(F)^2(\text{DNN})^2$$

$$B_1 B_4 + (B_{2a} B_4 - B_1 B_{5a})(\text{DNN}) + (B_1 B_{6a} - B_{3a} B_4)(F)(\text{DNN}) - B_{2a} B_{5a}(\text{DNN})^2$$

$$+ (B_{2a} B_{6a} + B_{3a} B_{5a})(F)(\text{DNN})^2 - B_{3a} B_{6a}(F)^2(\text{DNN})^2 \quad (\text{Equation II})$$

APPENDIX IV

$$F(\text{Escape}) = B_1 + B_2(\text{DNN}) \quad (\text{Equation 1})$$

$$B_2 = B_{2a} - B_{3a}(\text{F}) \quad (\text{Equation 2})$$

$$B_2 = B_{2b} - B_{3b}(\text{Size}) \quad (\text{Equation 13})$$

$$2B_2 = B_{2a} + B_{2b} - B_{3a}(\text{F}) - B_{3b}(\text{Size})$$

$$B_2 = \frac{B_{2a} + B_{2b}}{2} - B_{3a}(\text{F}) \frac{1}{2} - B_{3b}(\text{Size}) \frac{1}{2}$$

$$\text{Let: } B_{19} = \frac{B_{2a} + B_{2b}}{2}$$

$$B_{20} = B_{3a} \frac{1}{2}$$

$$B_{21} = B_{3b} \frac{1}{2}$$

Then

$$B_2 = B_{19} - B_{20}(\text{F}) - B_{21}(\text{Size}) \quad (\text{Equation 15})$$

APPENDIX V

$$F(\text{Pollination}) = B_4 - B_5(\text{DNN}) \quad (\text{Equation 4})$$

$$B_5 = B_{5a} - B_{6a}(\text{F}) \quad (\text{Equation 7})$$

$$B_5 = B_{5b} - B_{6b}(\text{Size}) \quad (\text{Equation 16})$$

$$2B_5 = B_{5a} + B_{5b} - B_{6a}(\text{F}) - B_{6b}(\text{Size})$$

$$B_5 = \frac{B_{5a}}{2} + \frac{B_{5b}}{2} - \frac{B_{6a}(\text{F})}{2} - \frac{B_{6b}(\text{Size})}{2}$$

$$\text{Let: } B_{22} = \frac{B_{5a}}{2} + \frac{B_{5b}}{2}$$

$$B_{23} = \frac{B_{6a}}{2}$$

$$B_{24} = \frac{B_{6b}}{2}$$

Then

$$B_5 = B_{22} - B_{23}(\text{F}) - B_{24}(\text{Size}) \quad (\text{Equation 17})$$

APPENDIX VI

Model 4

$$\text{Fitness}(\text{Success}) = F(\text{Pollination}) \quad F(\text{Escape})$$

Where flower number and plant size affect pollination and seed predation:

$$F(\text{Escape}) = B_1 + B_2(\text{DNN}) \quad (\text{Equation 1})$$

$$\text{where } B_2 = B_{19} - B_{20}(F) - B_{21}(\text{Size}) \quad (\text{Equation 15})$$

so that

$$F(\text{Escape}) = B_1 + B_{19}(\text{DNN}) - B_{20}(F)(\text{DNN}) - B_{21}(\text{Size})(\text{DNN}) \quad (\text{Equation 20})$$

$$F(\text{Pollination}) = B_4 - B_5(\text{DNN}) \quad (\text{Equation 4})$$

$$\text{where } B_5 = B_{22} - B_{23}(F) - B_{24}(\text{Size}) \quad (\text{Equation 17})$$

so that

$$F(\text{Pollination}) = B_4 - B_{22}(\text{DNN}) + B_{23}(F)(\text{DNN}) + B_{24}(\text{Size})(\text{DNN}) \quad (\text{Equation 21})$$

APPENDIX VI - Model 4: Continued

Fitness(Success) equals the product of Equations 20 and 21.

$$B_1 + B_{19}(\text{DNN}) - B_{20}(\text{F})(\text{DNN}) - B_{21}(\text{Size})(\text{DNN}) \quad (\text{Equation 20})$$

$$B_4 - B_{22}(\text{DNN}) + B_{23}(\text{F})(\text{DNN}) + B_{24}(\text{Size})(\text{DNN}) \quad (\text{Equation 21})$$

$$B_1 B_4 + B_4 B_{19}(\text{DNN}) - B_4 B_{20}(\text{F})(\text{DNN}) - B_4 B_{21}(\text{Size})(\text{DNN})$$

$$- B_1 B_{22}(\text{DNN}) - B_{19} B_{22}(\text{DNN})^2 + B_{20} B_{22}(\text{F})(\text{DNN})^2 + B_{21} B_{22}(\text{Size})(\text{DNN})^2$$

$$B_1 B_{23}(\text{F})(\text{DNN}) + B_{19} B_{23}(\text{F})(\text{DNN})^2 - B_{20} B_{23}(\text{F})(\text{DNN})^2 - B_{21} B_{23}(\text{F})(\text{Size})(\text{DNN})^2$$

$$B_1 B_{24}(\text{Size})(\text{DNN}) + B_{19} B_{24}(\text{Size})(\text{DNN})^2 - B_{20} B_{24}(\text{F})(\text{Size})(\text{DNN})^2 - B_{21} B_{24}(\text{Size})^2(\text{DNN})^2$$

$$B_1 B_4 + (B_4 B_{19} - B_1 B_{22})\text{DNN} + (B_1 B_{23} - B_4 B_{20})(\text{F})(\text{DNN}) + (B_1 B_{24} - B_4 B_{21})(\text{Size})(\text{DNN})$$

$$- B_{19} B_{22}(\text{DNN})^2 + (B_{19} B_{23} + B_{20} B_{22})(\text{F})(\text{DNN})^2 - B_{20} B_{23}(\text{F})^2(\text{DNN})^2$$

$$+ (B_{21} B_{22} + B_{19} B_{24})(\text{Size})(\text{DNN})^2 - (B_{21} B_{23} + B_{20} B_{24})(\text{F})(\text{Size})(\text{DNN})^2$$

$$- B_{21} B_{24}(\text{Size})^2(\text{DNN})^2$$

(Equation 18)

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PLANT DISPERSION, SEED PREDATION, POLLINATION,
AND THEIR EFFECT ON THE FECUNDITY OF
BAPTISIA SPP. (LEGUMINOSAE)

by

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Graphical and mathematical models were developed for the relationship between fitness as a function of success in producing seed and the isolation of a plant in outcrossing plant species which are attacked by host-specific seed predators. A measure of isolation was assumed to be the distance from a plant to its nearest neighbor (DNN). Fitness as a function of success in producing seed was assumed to be the product of fitness as a function of pollination and fitness as a function of escape from seed predation. Both the relationships between pollination and isolation and between escape from seed predation and isolation were modeled. These models were then combined to form the model for success in producing seed. This model predicted that an optimum distance between nearest neighbors exists. The manner in which the number of flowers a plant produces and the plant size affect this optimum distance is modeled.

To test the models, study sites were selected on tallgrass prairie which included areas that were burned, unburned, grazed, ungrazed, of Florence soil type and of Benfield soil type in various combination. All study sites contained single species populations of Baptisia australis or B. leucophaea or mixtures of the two species. Data on the distance from a plant to its nearest neighbor of either species, the distance from a plant to its nearest neighbor of the same species with an inflorescence, number of stalks and number of inflorescences were taken. The number of flowers on each inflorescence and the number of seed which had not been attacked and which were filled were counted. Using regression analysis and ridge regression analysis the models were tested. Some of the models significantly predicted the dependent variables. However, the fitted coefficients of the independent variables were not consistent with the signs expected.

Thus the relationships are not as hypothesized in the model or other factors not measured obscure these relationships.

I also used a backward elimination procedure to find the best subset of linear and quadratic combinations of F(number of flowers per plant), S(number of stalks per plant) and DNN to predict fitness. For the combined B. australis plots, the variables which significantly contribute to predicting fitness are S^2 , $(DNN)^2$, $(S)(F)$, DNN, S, and F. Mean values for S and F were inserted into this regression equation. DNN values were then varied. As DNN increased from zero, the value of (No. seeds per plant)^{1/2} decreased, reached a minimum and then increased again. This suggests that plants "near" and "far" from each other are more likely to produce filled, unhit seeds. This relationship would be derived if fitness as a function of pollination and fitness as a function of escape from seed predation curves crossed at a DNN in the asymptotic parts of their range. For the combined B. leucophaea plots only $(F)^2$ was useful.