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VERTEBRATE POLLINATION AND THE MAINTENANCE OF DIOECISM IN *FREYCINETIA*

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Increasing attention recently has been directed toward the role that ecological forces play in the evolution of plant breeding systems. Within the past 20 years a variety of explanations have been proposed for the evolution of dioecism in flowering plants (Ornduff 1966; Baker 1976; Freeman et al. 1976; Lloyd and Webb 1977; Charlesworth and Charlesworth 1978; Onyekwelu and Harper 1979; Webb 1979; Willson 1979; Bawa 1980*a*, 1980*b*; Beach and Bawa 1980; Givnish 1980; Lloyd 1980; Cox 1981*b*). Several recent theoretical models have examined in some detail possible conditions which can favor the evolution of dioecism in a hermaphroditic population (Smouse 1971; Charnov et al. 1976; Charnov and Bull 1977; Maynard Smith 1978).

The Charnov-Maynard Smith-Bull model can be adapted to describe the fitnesses of sexual phenotypes in a plant population, as long as the sexual type is not determined by cytoplasmic factors. Let m, f, and h be the numbers of males, females, and hermaphrodites within a population. A single male produces N pollen grains, a female n seeds, and an hermaphrodite αN pollen and βn seeds. According to the fitness set model, if R is the total number of offspring produced by the population, and Wm, Wf, and Wh is the expected number of offspring produced by males, females, and hermaphrodites, respectively, then total pollen $= N(m + \alpha h)$, and total seeds $= n(f + \beta h)$, and therefore

$$Wm = R\left(\frac{1}{m + \alpha h}\right); \; Wf = R\left(\frac{1}{f + \beta h}\right); \; Wh = R\left(\frac{\alpha}{m + \alpha h} + \frac{\beta}{f + \beta h}\right). \quad (1)$$

Under what conditions could the hermaphroditic population be vulnerable to invasion by a dioecious mutant? A dioecious mutant could invade if $Wf = Wm > Wh$, which from equation (1) reduces to $\alpha + \beta < 1$. This is equivalent to saying that if the fitness set is concave (i.e., $\alpha + \beta < 1$) then dioecism is evolutionarily stable, but if the fitness set is convex ($\alpha + \beta > 1$) dioecism is not stable and hermaphrodites will be favored. It follows, then, that an ecological factor which can lead to the evolution of dioecism in an otherwise hermaphroditic population must alter the topology of the fitness set from convexity to concavity.

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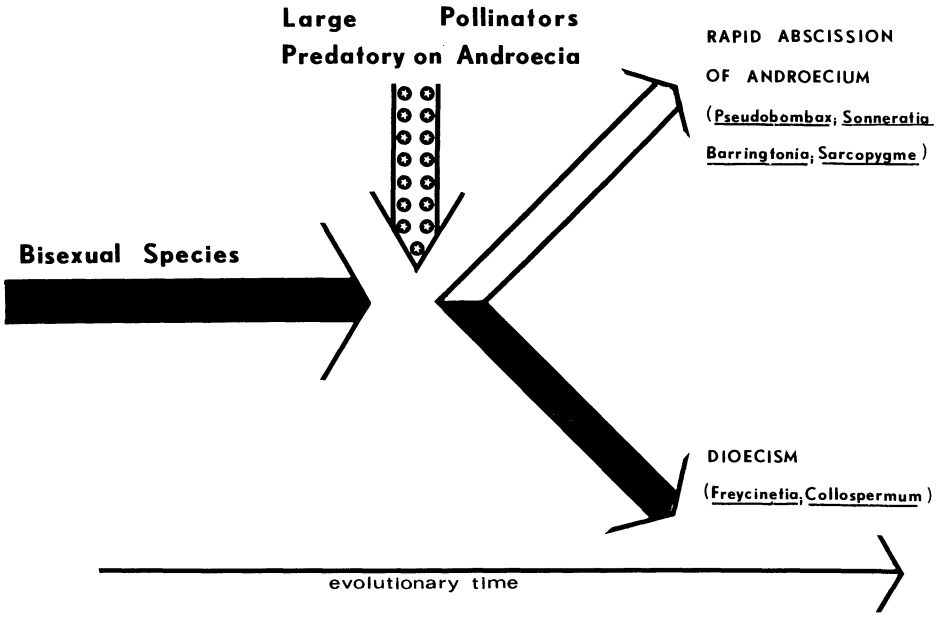


FIG. 1.—Graphical representation of hypothesis.

Here I will attempt to fit empirical data from a real population to the fitness set model. Specifically I will suggest that the fitness sets generated by the model are a useful way of visualizing the selective forces that are acting to maintain dioecism in Samoan populations of *Freycinetia reineckei*, a dioecious liana in the Pandanaceae. In addition I will present my own model of a generalized force which can in some instances lead to the evolution of dioecism in otherwise hermaphroditic flowering plant species: the destructive actions of large vertebrate pollinators which are attracted primarily to solid floral rewards rather than nectar.

Baker (1976) has suggested that the absence of nectar rewards in pistillate flowers of the Caricaceae functions to reduce the visits of dangerous floral visitors (hummingbirds, *Trigona* bees, etc.) which might damage the large superior succulent ovary. Extending this idea that gynoecial structures risk incidental damage from certain types of floral visitors, I suggest that a bisexual plant species with a superior ovary may face a fork in the evolutionary road if it is pollinated by a large vertebrate, such as a bird or a bat (fig. 1). On the one hand selection may favor the rapid postfertilization abscission of the stamens, petals or septals (tepals), and any other structures surrounding the gynoecium which may invite a chewing or pecking behavior from the pollinator.

Assume, for example, that the large vertebrate pollinator is attracted not only to nectar, but also to solid floral organs such as stamens, bracts, or tepals as a reward. Even though chewing or pecking the floral parts entails a risk of incidental damage to the superior ovary, the plant still benefits by the pollination effected by the visitor. The plant gains no further benefit through female reproductive functions from subsequent visits, however, if all of the ovules are fertilized in the initial

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visit. Indeed further visitation increases the risk that the ovary will be damaged by pollinator activity near the gynoecium, even if the ovary itself is not attractive to the pollinator. Thus in such a case selection would favor plants which abscise attractive floral parts soon after fertilization. Such rapid abscission of stamens and petals, often as a fused unit, seems to be common in tropical plants pollinated by large bats and birds. Striking examples of this phenomenon can be found in several different plant families including the Lecythidaceae, Myrtaceae, Barringtoniaceae, Bombacaceae, and Sonneretiaceae (table 1).

On the other hand, pollination by large vertebrates may alternatively favor in some cases the evolution of dioecism, particularly if the probability of incidental ovary damage is proportional to both the frequency and duration of visitation. In such a case, any mechanism which reduces the amount of chewing or pecking near the ovary would be favored by selection. Assume, for example, that inheritable variability in the time of abscission of floral parts did not exist in the population, but variability in the allocation of resources to stamens and ovaries did occur. Thus some individuals produce flowers with many stamens but fewer or smaller ovaries than other members of the population. Because of this imbalance in allocation of resources, these individuals are more male than hermaphrodite and have in the fitness set model a high α but a low β value. At the other end of the spectrum are individuals which produce flowers with few stamens, but with many ovaries or large ovaries. Such individuals resemble females in that they have low α values but high β values.

Individuals leaning toward maleness might tend to attract more pollinators by virtue of their numerous stamens, and the pollinators would tend to make visits of a longer duration, particularly if they consumed the stamens. Such plants would therefore stand excellent chances of having their pollen carried to other plants, but their ovaries would be in great danger of incidental damage from the pollinators. Thus natural selection would favor increasing investments in stamens and decreasing investments in ovaries in such individuals, because every transfer of resources allocated from ovaries to stamens would result in a disproportionate increase in fitness. Thus through evolutionary time, α would approach a value of 1 and β would approach a value of 0. On the other hand, individuals leaning toward femaleness would also be favored over strict hermaphrodites because they would not suffer as much damage to their ovaries and would tend to transmit more genes via ovules. In such individuals every decrease in the allocation to staminal production would increase fitness because it would increase the probability that the ovules would escape destruction. Since reduction of the number of stamens would reduce the amount of chewing or pecking by pollinators near the ovary, natural selection would favor in these individuals decreasing investments in stamens and increasing investments in ovaries, and through time α would approach 0 and β would approach 1. Such individuals could persist in the population, however, only if their flowers mimicked the male flowers to such a degree that the pollinators were deceived into visiting. Pollination could then occur but masticatory behaviors of the pollinator would be less likely to be triggered, and the visitor would possibly leave before any ovary damage occurred. In this scenario, then, the effect of large vertebrate pollinators in terms of the fitness set model would be to

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TABLE 1

PLANTS POLLINATED BY LARGE VERTEBRATES WHERE A POSSIBILITY OF GYNOECIAL DAMAGE EXISTS

Plant	Pollinator	Floral Abscission/ Dioecism	Authority
Kigelia africana	Bat (*Micropteropus pusillus*)	Abscission	Harris and Baker 1958
Blakea sp.	Rodent (*Oryzomus devius*)	Abscission	Lumer 1980
Collospermum sp.	Bat (*Mystacina tuberculata*)	Dioecism	Daniel 1976
Durio sp.	Bat (*Cynopterus* sp.)	Abscission	Corner 1952
Oroxylum indicum	Bats	Abscission	Corner 1952
Adansonia digitata	Bush baby (*Galago crassicaudatum*)	Abscission	Coe and Isaac 1965
Banksia attenuata	Rat (*Rattus fuscipes*)	Abscission	Faegri & van der Pijl 1979
Leucadendron sp.	Bird?	Dioecism	Hutchinson 1967; Rao, 1971
Freycinetia funicularis	Bird (*Psycnonotus* sp.)	Dioecism	Faegri & van der Pijl 1979
Osmoxylon insidiator	Bird (*Reinwardtoena reinwardtii*)	Abscission	Beccari 1877
Sonneretia sp.	Bat	Abscission	Corner 1952 Faegri & van der Pijl 1979
Ceiba acuminata	Bat (*Leptonycteris sanborni*)	Abscission	Baker et al. 1971
Calceolaria uniflora	Bird	Corolla withers	Vogel 1974

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change the shape of the fitness set from convexity to concavity, rendering hermaphroditism evolutionarily unstable. Under such conditions, the evolution of dioecism would be favored.

In situations where a plant with a superior ovary is pollinated by large, sometimes destructive pollinators, it is difficult to predict what specific factors would favor one evolutionary pathway over another. Phylogenetic constraints would probably be important in determining whether dioecism, or, alternatively the abscission of floral parts would be favored. In general one might expect the abscission of attractive floral parts to be more advantageous for a flower isolated temporally or spatially from other flowers than for a flower produced in aggregation with many others, since an isolated flower would not suffer predation because of the proximity of other flowers. Thus rapid postfertilization shedding of attractive floral parts would result in an immediate decrease in the probability of ovary damage. One might also expect that abscission would be of greater benefit to flowers which produce roughly equivalent shares of pollinator rewards within an inflorescence, than for flowers produced in inflorescences in which a large fraction of the reward is localized in specialized structures such as bracts subtending the inflorescence. Flower size could also be an important constraint since large flowers would have a proportionately higher gain in fitness by abscising attractive organs than would small flowers in which the entire inflorescence serves as a unit of attraction. It could be therefore that rapid floral abscission would be more likely to evolve in vertebrate-pollinated taxa with large, solitary flowers, or with inflorescences of widely spaced flowers with asynchronous anthesis. Alternatively, dioecism would probably be more frequent in vertebrate-pollinated taxa with small flowers in congested inflorescences with synchronous anthesis and some localization of floral rewards in large bracts or modified flowers. It should be noted, however, that in both cases I am considering only taxa which are pollinated by large vertebrates which chew or peck at solid rewards such as bracts, tepals, or stamens.

I suggest, then, that the actions of large vertebrate pollinators can function to maintain dioecism in some plant species, and in others create conditions favorable for the evolution of dioecism. To explore the plausibility of this hypothesis, I made several field investigations of the dioecious liana *F. reineckei* in Samoa and examined the results to see if they fit the fitness set model.

METHODS

Several populations of *Freycinetia reineckei* were studied on Mt. Fia Moe and in the mountains of Tapatapaō on the large island of Upolu, Western Samoa. During the study, all of the data recorded as percentages were transformed to degrees using the angular transformation $\phi = \text{arc sin } \sqrt{p}$, where p is the percentage expressed in decimal form (Fisher and Yates 1953; Bliss 1967). Statistical tests were made on the transformed data and the means were then reexpressed as percentages by reversing the transformation. In 1979, a survey of inflorescence destruction in the Mt. Fia Moe population was made. The sex of each inflorescence surveyed was recorded together with a destruction index. This index was

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calculated by estimating the percent destruction of the total surface area of each inflorescence physically occupied by androecial or gynoecial structures. During this survey, the existence of bisexual inflorescences was discovered (Cox 1981*a*) but only male and female scores were recorded. The difference between the mean destructions for the two sexes were tested with a *t*-test. A 2 × 2 contingency table was constructed by comparing inflorescences which had been completely destroyed to those which had suffered no or only partial destruction. The hypothesis that probability of complete destruction is independent of sex was tested with a chi-squared statistic. Also in 1979 an experiment was conducted to study pollinator/predator bias towards the different sexes of inflorescences. Completely randomized blocks in the form of large grids were laid out in the mature rain forest of Tapatapaō. Each 4,096 square meter grid had four rows of four presentation points, each point being at a 16-m interval from the previous point. At each point a floral part excised from either a male or a female inflorescence was displayed, the choice of sex determined by reference to a sequence of random binary digits. Periodically each presentation point was visited and a percentage index of the destruction of the inflorescence part displayed there was recorded. The final scores, derived from visits made after 18 days subsequent to the initiation of the experiment, were used for the analysis. Two sets of these experiments were conducted, each involving several blocks. One set of four blocks involved displaying uniform (16 cm^2) pieces of the fleshy bracts which subtend *Freycinetia* involucres, while the other set of three blocks involved displaying uniform sized spikes. The transformed data from each experimental series were analyzed with a two-way analysis of variance using Yates' (1933) approximate analysis to deal with the disproportionate class frequencies and nonorthogonality inherent in the completely randomized block design. For both experimental series an *F* statistic was used to test the hypothesis that the mean destruction of the sexes was equivalent. A *t*-test was used to test the difference between the means for significance.

Seven bisexual inflorescences of *F. reineckei* near anthesis were preserved in FAA. The total surface area of each spike occupied respectively by anthers and ovaries was measured. Means and variances for these areas were calculated and a ratio of the mean area occupied by anthers to the mean area occupied by ovaries was calculated.

In 1980 a population of *F. arborea* was studied in the mountains above Kealakekua on the island of Hawaii, Hawaii. A survey was conducted in which the sex of each inflorescence together with its destruction index was recorded. The difference between the mean destruction for both sexes was tested for significance with a *t*-test. A 2 × 2 contingency table was constructed comparing the number of inflorescences which had been completely destroyed to the number of inflorescences which had suffered only partial, or no destruction. The hypothesis that probability of destruction is independent of sex was tested for significance with a chi-square statistic. Also in 1980 a random survey of postanthesis *F. reineckei* inflorescences at Tapatapaō, Samoa was made for 92 inflorescences. The sex of male, female, and bisexual inflorescences was recorded together with a destruction index. The transformed data were analyzed with a one-way analysis of

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TABLE 2

PERCENT *Freycinetia reineckei* INFLORESCENCE DESTRUCTION, 1979 SURVEY

	n	Mean Surface Area Destroyed	*t*	*P*
Female	29	18%	2.24	.05
Male	32	55%		
	Total Destruction	Incomplete Destruction	χ^2	*P*
Female	5	24	6.06	.05
Male	15	17		

variance and an *F* statistic was used to test the hypothesis that inflorescence destruction probability is independent of sex. The difference between each pair of means was tested for significance with a *t*-test.

RESULTS

The results of the 1979 *Freycinetia reineckei* inflorescence survey are shown in table 2. The *t*-test showed that male inflorescences suffer significantly more destruction than females. The chi-square test indicates that there is a 95% probability that male inflorescences face a higher chance of complete destruction. The randomized block experiments (table 3) fail to support the hypothesis that staminate and pistillate spikes have equal probabilities of destruction; the mean destruction of male spikes was 72.5% of their surface area and for the females, 43.0%. The difference between mean male and female spike destructions was also found to be significant within each block. However, the analysis of variance of the four blocks displaying bracts indicates that male and female bracts do not differ significantly in the probability of their destruction since the *F* statistic did not permit rejection of the null hypothesis at the 0.05 level. The mean destructions for the bract experiment for all blocks were 41.9% for males and 24.4% for females.

The 1980 *F. reineckei* destruction survey, unlike the 1979 survey, included male, female, and bisexual inflorescences. The *F* test of the analysis of variance allows rejection of the null hypothesis (level of destruction is independent of sex) at the 0.01 level. The *t*-tests for each pair of means indicate that all pairs differ significantly (fig. 2). The mean destructions were found to be 96.2% for the males, 69.1% for the bisexuals, and 6.3% for the females (fig. 2).

The seven bisexual inflorescences of *F. reineckei* collected near anthesis were found to have a mean area of 24.5 cm^2 occupied by anthers and 16.2 cm^2 occupied by ovaries. The mean percentage of the reproductive surface occupied by anthers is therefore 60% and that by ovaries 40%.

The results of the 1980 *F. arborea* survey conducted in Hawaii are shown in table 4. Male inflorescences were found to suffer significantly greater mean destruction than females, and the chi-square statistic showed that the probability of

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TABLE 3

ANALYSIS OF VARIANCE OF PREDATION EXPERIMENTS

Source of Variation	df	Sum of Squares	Mean Square
Bracts (four completely randomized blocks)			
Between means of eight classes	7	1843.36	
Between sexes	1	690.06	690.06
Between blocks	3	700.58	233.53
Sex × block interaction	3	452.72	150.90
Experimental error	59		25.09
F (sexes) = 4.57 [NS]; F (blocks) = 1.55 [NS]			
Spikes (three completely randomized blocks)			
Between means of six classes	5	3947.67	
Between sexes	1	1084.61	1084.61**
Between blocks	2	2712.10	1356.05**
Sex × block interaction	2	150.96	8.98
Experimental error	41		5.85
F (sexes) = 120.78 [$P < .01$]; F blocks = 151.00 [$P < .01$]			

** Significant at the .01 level.

an inflorescence being completely destroyed is not independent of sex: males face a significantly higher probability of destruction.

DISCUSSION

Grant (1950) has examined several possible morphological adaptations which serve to protect ovules from damage incidental to bird or bat pollination. These include the development of an inferior ovary, positioning the ovary on a stipe above the nectary, the interposition of fused staminal bases between the ovary

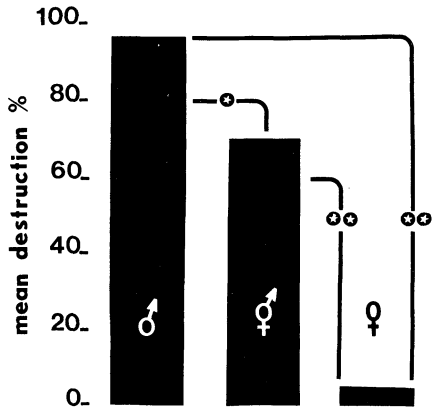


FIG. 2.—*Freycinetia reineckei* inflorescence destruction, 1980 survey. Mean male destruction = 96.19%, bisexual destruction = 69.13%, female destruction = 6.32%. Stars indicate level of significance for differences between means. F statistic for analysis of variance = 59.9, $P < .01$, $n = 91$.

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TABLE 4

PERCENT *Freycinetia arborea* INFLORESCENCE DESTRUCTION IN HAWAII, 1980 SURVEY

	n	Mean Surface Area Destroyed	*t*	*P*
Female	18	6%	6.5	.001
Male	28	87%		
	Total Destruction	Incomplete Destruction	χ^2	*P*
Female	1	17	9.9	.0005
Male	14	14		

and the nectary, or storing the nectar in a spur which passes to one side of the ovary. With the exception of positioning the ovary in an inferior position or raising it on a stipe, such adaptations will poorly protect the ovules if floral organs, such as bracts, stamens, or tepals, rather than nectar, are the principal pollinator reward. Here I have suggested two additional adaptations which might serve to protect ovules in such vertebrate-pollinated species with superior ovaries: rapid abscission of floral organs, or dioecism.

Lianas of the genus *Freycinetia* have appropriate floral morphologies and pollination ecologies for an examination of the hypothesis that pollination by large vertebrates can favor the evolution of dioecism. Nectar is not produced in *Freycinetia* inflorescences; the principal pollinator rewards are the hexose-rich sweet fleshy bracts which subtend each spike, the fleshy bracts (Bekös-tigungsköper) produced at the termination of the flowering axis, and the pollen which is embedded in a waxy matrix of highly saturated lipids. Three or four (sometimes more) spikes and their subtending bracts are produced in each inflorescence, with the internode distance being so reduced that the entire involucre has the appearance of a single large flower with the bracts superficially resembling large fleshy petals. The true flowers are exceedingly tiny and at maturity are devoid of both tepals and subtending bracts. The spike is so congested at maturity that individual flowers are nearly impossible to distinguish, and an accurate description of the floral unit has been obtained only by scanning electron microscopy of floral primordia of early developmental inflorescence stages (Cox 1981*c*). The large, showy inflorescences have been noted to attract a variety of vertebrates including bats, birds, and rodents (Cunningham 1842; Burck 1892; Perkins 1902; Knuth and Loew 1904; Guppy 1906; Porsch 1915, 1923; Heide 1927; van der Pijl 1956; Daniel 1976) which consume the bracts and staminate spikes causing severe damage to the reproductive surfaces (Burck 1892; Porsch 1915; 1923; Cammerloher 1923; Jaeger 1954; van der Pijl 1956). Heide (1927) found staminate spikes to suffer more damage than pistillate spikes. The present study confirms that male and bisexual inflorescences, both of which produce viable pollen (Cox 1981*a*), suffer much greater destruction than female inflorescences (fig. 2). The randomized block experiments indicate that this difference in probability of destruction results from differences in the spikes, rather than any dif-

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ference in the bracts (table 3). The waxy matrix containing the pollen, which functions both to adhere the pollen to the pollinator and to offer a high-value food resource, is undoubtedly a major factor in the disproportionately greater destruction of male and bisexual inflorescences.

I suggest that these observed differences in probability of destruction for different sexes of *F. reineckei* inflorescences in Samoa are due in large part to the feeding behavior of the endemic flying fox, *Pteropus samoensis*. *Pteropus samoensis,* one of the largest known bats, with a wing span approaching 2 m, and is a major pollinator of *F. reineckei* as determined by field observations, exclusion experiments, SEM analysis of facial hairs, palatability studies, and comparative nutritional analysis of inflorescences (Cox 1981*c*). Two captive individuals of *P. samoensis* which were presented with random sequences of food items including *Freycinetia* inflorescences were found to devour any *F. reineckei* inflorescence placed in their cage. They would eat the fleshy outer and inner bracts and then, if the inflorescence was staminate or bisexual, they would eat the spike, frequently biting if off at the base and chewing and licking it in a manner similar to the way a small child eats a Fudgesicle. During this process most of the gynoecial structures on bisexual spikes were severely damaged. I never observed a flying fox eating a pistillate spike, although they devoured the sweet bracts subtending it.

There is also circumstantial evidence which suggests that birds which pollinate *Freycinetia* damage pollen-bearing spikes more frequently than pistillate spikes. In Hawaii, I witnessed *Zosterops japonica,* the primary extant pollinator of *F. arborea* (Cox 1981*c*) snipping off pieces of staminate spikes with its beak and devouring them. After witnessing *Z. japonica* visits, I frequently found beneath the visited inflorescence bits and pieces of staminate spikes which the birds had dropped; any staminate spike remaining in the inflorescence was severely damaged. I never witnessed, however, any animal attempting to eat the green, mucilaginous pistillate spike. These observations of greater damage by pollinators to staminate spikes are confirmed by the Kealakekua survey (table 4). In Samoa I have observed another major pollinator of *F. reineckei,* the endemic starling *Aplonis atrifuscus,* eating staminate spikes both in the field and in captivity, but again never witnessed a bird eating a pistillate spike.

In Samoa, *F. reineckei* lianas produce only a single inflorescence each year, the growth consisting of an unbranched linear sympodium of hapaxanthic axes. Therefore the contribution of any single flowering season to a plant's fitness is determined entirely by the success of its single inflorescence. Monoecism, in the sense of a single plant producing in the same year inflorescences of different sexes, is impossible because of the architecture (Chamberlain's model) and phenology. Information from the present study of *F. reineckei* inflorescences therefore can be used to estimate the parameters of a fitness set in an attempt to determine if predation can influence the topology of the fitness set. In a modification of the fitness set model, it is assumed that a male disperses N pollen, a female produces n seed, and a hermaphrodite disperses αN pollen and produces βn seed. It is assumed that the amount of pollen deposited on flying fox or bird faces by any single pollen-bearing inflorescence is proportional to the amount of inflorescence destruction caused by the pollinator up to some threshold value, T, beyond which

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an increase in destruction of the spikes does not indicate an increase in the pollen load deposited on the face of the pollinator. Different values of T were used for the subsequent analysis; varying the value of T had no effect on the ultimate convexity or concavity of the fitness set, but resulted only in a small change in shape. The effects of using maximum or minimum values of T are shown in figure 2.

It is also assumed that the percent seed set of an ovary-bearing spike is inversely related to the amount of reproductive surface destroyed by the pollinator so that the percent seed set is given by $(1 - d)$; where d is the percent reproductive surface destroyed (undamaged *F. reineckei* inflorescences almost always have a high seed set if they are pollinated).

The value of α can then be approximated by

$$\frac{(m)\ (P_h)}{(P_m)} \tag{2}$$

where m is the mean percent of the reproductive surface of hermaphrodites occupied by anthers, P_h is the mean amount of pollen dispersed by hermaphrodites, and P_m is the mean amount of pollen dispersed by males.

Setting T at a minimum (or 0%), $P_h = P_m = 1$ since $d_h = 69.1\%$ and $d_m = 96.2\%$, both of which are greater than T. Using the values obtained in the present study, α at $T_{\min}$ is therefore approximately

$$\frac{(0.6)\ (1)}{(1)} = 0.6. \tag{3}$$

If, however, T is set at a maximum so that $T = 100\%$, then α is decreased and at $T_{\max}$ is therefore approximately

$$\frac{(0.6)\ (0.691)}{(0.962)} = 0.43. \tag{4}$$

The value of β is independent of T and can be approximated by

$$\frac{(f)\ (1 - d_h)}{(1 - d_f)} \tag{5}$$

where f is the mean percent reproductive area of bisexual spikes occupied by ovaries, d_h is the mean percent reproductive surface of hermaphrodites which is destroyed, and d_f is the mean reproductive surface destroyed of females. Using values from the present study, β can be approximated as

$$\frac{(0.4)\ (1 - 0.692)}{(1 - 0.064)} = 0.13. \tag{6}$$

Therefore

$$\alpha + \beta = 0.73 \tag{7}$$

when T is set at a minimum. When T is set at a maximum,

$$\alpha + \beta = 0.56. \tag{8}$$

Since $\alpha + \beta < 1$, the fitness set is concave (fig. 3) and the model predicts that as

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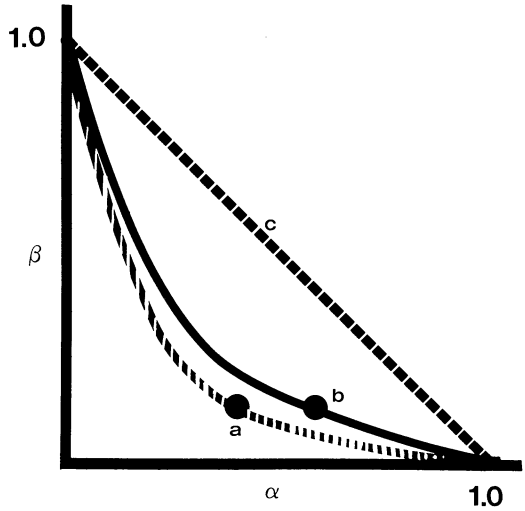


FIG. 3.—Approximate fitness set of sexual phenotypes of *F. reineckei* in Samoa. *a*, Dotted curve illustrates approximate fitness set when T is set at a maximum value. The point shown is (0.43, 0.13). *b*, Solid curve shows approximate fitness set when T is set at a minimum value. The point shown is (0.60, 0.13). *c*, Dotted line is a plot of the equation $\alpha + \beta = 1$. For fitness sets above this line (convex) hermaphroditism is the evolutionarily stable strategy; for fitness sets below the line (concave), dioecism is the evolutionarily stable strategy.

long as predation continues, dioecism is an evolutionarily stable strategy in *F. reineckei*. The experimental results therefore lend credence to the fitness set model.

Clearly, however, showing that the data fit the model is not tantamount to proving that the model or theory is true; the data only show that in this case the model has not been falsified. It is possible that the differential predation of the inflorescences and the entire syndrome of vertebrate pollination is but a recent occurrence in the evolutionary history of *Freycinetia* and that vertebrates have yet to have had a significant effect on the evolution of the genus. Several pieces of evidence suggest that this latter alternative is not likely, however. First, the pollination of *Freycinetia* species by bats and birds of various species in diverse locales such as Indonesia, Samoa, Hawaii, and New Zealand suggests that vertebrate pollination is not a recent or novel occurrence in the genus. Second, the inflorescence of *Freycinetia* appears to have several features adapted to vertebrate pollination. The spicate inflorescence of *Freycinetia* is quite different from the paniculate inflorescence of *Sararanga* and the racemose or paniculate inflorescence of *Pandanus* in that *Freycinetia* inflorescences are usually (but not always, cf. *F. angustifolia* or *F. jagorii*) severely telescoped into a pseudoumbellate structure forming an involucre. This telescoping permits the food bodies and bracts to be clustered into a single anthecological unit which seems well adapated for vertebrate pollination. The inflorescence is large and showy, no nectar is produced (the pollinator rewards are pollen and the fleshy bracts), and the floral structures lack the specializations usually associated with anemophily. Third, fossil remains of

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the Pteropidae have been found as early as the Oligocene (Allen 1939) suggesting that the potential for flying fox pollination has long existed, although this does not indicate how long flying fox pollination of *Freycinetia* may have occurred.

Another alternative to my hypothesis is that differential predation of the sexes is but a consequence of dioecism (Bawa and Opler 1978) and that dioecism itself evolved as a result of different selective pressures. This alternative is difficult to reject because it is indeed very likely that many varied forces have shaped the breeding system in the genus, and that the pollination syndrome is but one of a multitude of different factors which may have selected for dioecism. This alternative hypothesis is in fact strengthened by the fact that the other two genera of the Pandanaceae are believed to be strictly dioecious; it is possible that dioecism is a very primitive condition in the Pandanaceae. Were this to prove to be true, however, the data from the current study strongly indicate that vertebrate pollination is a force which maintains dioecism in *Freycinetia* by effectively reducing the fitness of any bisexual mutants; by extrapolation it could be speculated that a similar force may have played an evolutionary role in other taxa. However, it now appears likely that bisexuality is the ancestral condition in the Pandanaceae. Support for the suggestions of previous workers (Stone 1968, 1972; Vaughan and Wiehe 1953) has recently come from field studies of extant bisexuality in the family (Cox 1981*a*) and studies of floral organogenesis in which rudimentary bisexual flowers can be detected in early developmental stages of *Freycinetia* inflorescences (Cox 1981*c*).

As more information becomes available on this family, it is possible that the hypothesis suggested here may have to be revised or even discarded. Presently, however, the data are consistent with the hypothesis that large vertebrates which function as pollinators can maintain dioecism in populations of flowering plants and can act as a selective force in the evolution of the breeding system. Other genera in which these effects might be found include *Astelia* and *Collospermum,* dioecious members of the Liliaceae which in some cases appear to be bat pollinated. Recent evidence (Daniel 1976) suggests that the bat *Mystacina tuberculata* feeds on the pollen of *Collospermum hastatum,* a striking analogue of the bat-plant relationship here described for *Freycinetia. Astelia* may also offer an interesting analogue of *Freycinetia* because hermaphrodites which produce seed are known (Moore 1966). It is also possible that selection by large vertebrate pollinators may lead to the evolution of breeding systems different from either the dioecism or abscission paths which I have presented in my dichotomous model (fig. 1). One such alternative outcome might be the evolution of dicliny where a single individual produces flowers of both sexes, but separates them in time or space. An example of this may be found in the genus *Musa* in which pistillate flowers are first produced at the basal portion of the inflorescence while staminate flowers are produced last at the distal end. Although most cultivars are known to be visited by bats, they are not truly chiropterophilous since pollination is not necessary for fruit development. *Musa textilis, M. truncata,* and *M. malaccensis* can truly be said to be chiropterophilous, however, since they are pollinated (and require pollination) by bats of the genera *Macroglossus* and *Eonycteris* (Purseglove 1972; Start 1974). It is possible that gynoecial damage from pollinators to

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earlier monoclinous forms may have been one of the factors favoring the evolution of dicliny in the genus. It is also possible that pollinator-induced gynoecial damage favored the evolution of andromonoecy in the bat-pollinated *Parkia clappertonia* which produces staminate or sterile nectar-producing flowers above the inflorescence depression which acts as a nectar reserve (Baker and Harris 1957). This is the precise area where the feeding behavior of the bats would be most likely to cause gynoecial destruction.

In conclusion, I suggest that sex-specific predation by animals has the potential to influence the evolution of plant breeding systems. Here I have concentrated on the role of incidental ovary damage caused by the visits of large vertebrate pollinators, but clearly similar evolutionary trends could be generated by sex-specific predation from nonpollinating organisms including destructive invertebrates (Baker 1976). Although such pollinator/predator pressure can probably be implicated only in a very small minority of cases of the evolution of dioecism in plants, I suggest the situation I have described in *Freycinetia,* a dioecious liana which is both pollinated and plundered by large vertebrates, may prove not to be unique, particularly as more cases of dystropic or destructive pollination are studied at the population level.

SUMMARY

The hypothesis that pollination by large, nonnectivorous vertebrates can in some cases favor the evolution of dioecism was explored through a series of surveys and experiments with *Freycinetia reineckei,* a dioecious liana in Samoa, which is primarily pollinated by the flying fox *Pteropus samoensis* and the starling *Aplonis atrifuscus*. Staminate and bisexual inflorescences were found to face a far higher probability of destruction than pistillate inflorescences. Although destruction of staminate spikes is not deleterious to the fitness contribution of staminate spikes since the pollen is carried on the bat's face or bird's feathers, destruction of the bisexual spike is deleterious since the investment in gynoecial structures is forfeited. The data from the study were found to generate a concave fitness set, indicating that dioecism rather than hermaphroditism is an evolutionarily stable strategy. The relevance of these findings to other taxa is briefly discussed.

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Sigma Xi. This paper is dedicated to the memory of Harold G. Moore Jr., tropical botanist, teacher, and friend.

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