



On the Function of Flowers

G. Bell

Proceedings of the Royal Society of London. Series B, Biological Sciences, Vol. 224, No. 1235.
(Apr. 22, 1985), pp. 223-265.

Stable URL:

<http://links.jstor.org/sici?sici=0080-4649%2819850422%29224%3A1235%3C223%3AOTFOF%3E2.0.CO%3B2-Z>

Proceedings of the Royal Society of London. Series B, Biological Sciences is currently published by The Royal Society.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/rsl.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

On the function of flowers

BY G. BELL†

*Biology Department, McGill University, 1205 Avenue Dr Penfield, Montreal,
Québec, Canada H3A 1B1*

(Communicated by W. D. Hamilton, F.R.S. – Received 4 October 1984)

Most flowers are bisexual in function, but counting secondary allocation to attractive structures such as the corolla as equally male and female leads to the paradoxical conclusion that plants bearing perfect flowers invariably allocate much more to female than to male function. A method of calculating the gender of secondary floral allocation is described, and it is speculated that this allocation is predominantly male. Observations and experiments with natural populations of herbs, designed to test this hypothesis gave the following major results. (i) Insects visit larger flowers more frequently (*Fragaria*), and removal of floral biomass causes a reduction in the frequency of insect visits proportional to the fraction of biomass removed (*Impatiens*). (ii) Removal of attractive structures may cause a decline in the probability that a fruit will be formed but has no effect on the number of seeds set per fruit; thus, mutilation of essentially solitary flowers has no effect on seed-set per fruit (*Impatiens*), while removal of flowers from inflorescences in a species that forms several many-seeded fruits per inflorescence reduces fruit-set per inflorescence but has no effect on seed-set per fruit (*Asclepias*), and removal of sterile flowers from an inflorescence in which the fertile flowers yield one-seeded fruits is effective in reducing seed-set per inflorescence (*Viburnum*). (iii) Larger flowers may disperse a greater fraction of their pollen in unit time (*Impatiens*) and the removal of flowers from inflorescences causes a steep reduction in total pollen exported and a weak decline in the quantity of pollen exported per flower (*Asclepias*). These results are consistent with the hypothesis that a single insect visit (or a very few visits) suffices to fertilize almost all available ovules and is procured by a very small allocation to attractive structures, while much greater allocation is necessary to procure the numerous visits required to disperse a large fraction of the pollen. This inference is supported by a comparative survey of sexually dimorphic plants, in which male flowers are generally larger than female flowers, male inflorescences bear more flowers, and male plants bear more inflorescences. It is concluded that the flower is primarily a male organ, in the sense that the bulk of allocation to secondary floral structures is designed to procure the export of pollen rather than the fertilization of ovules. This conclusion may be sensitive to whether it is the flower or the inflorescence as a whole that represents the primary unit of attraction to insects. It was found that the performance of a given flower was substantially affected by other flowers in the same compact inflorescence (*Asclepias*), though not by other inflorescences on

† Present address: The University of Sussex, Biology Building, Falmer, Brighton, Sussex BN1 9QG, U.K.

the same plant nor by those borne by nearby plants (*Fragaria*, *Impatiens*). A general quantitative theory of flower and inflorescence design is outlined, and used to organize the extensive experimental results for *Asclepias*.

INTRODUCTION: PARADOX OF SECONDARY ALLOCATION TO FLOWERS
IN PLANTS

Most flowers are hermaphroditic, bearing both male and female sexual organs. These organs (anthers and pistils) are themselves of unequivocal gender, but they are usually rather small. The bulk of the flower, especially in insect-pollinated plants, is made up of tissues to which no definite gender can be ascribed *a priori*. In particular, the corolla contributes to the success of both male and female gametes by attracting insects which import pollen to fertilize the flower's own ovules and export pollen to fertilize ovules elsewhere. Is the material allocated to the construction of the corolla then equally male and female, or can we better describe it as being predominantly one or the other?

I encountered this problem when studying the theory of gender allocation. The major goal of this theory is to explain why the sexes are united or divided in different groups of organisms. An important secondary goal, and the only way in which the theory can be tested quantitatively, is to specify what proportion of the total quantity of resources available for reproduction should be spent on male function: on the production, storage and dissemination of male gametes. For instance, it has often been suggested that hermaphroditism evolves because it increases the chance of encountering a compatible mate in organisms that are sluggish or rare. This might explain why plants and sessile animals are often hermaphroditic, while motile animals are more often gonochoric (dioecious); it might even explain why some groups of plants have an abnormally high proportion of dioecious species. The most satisfactory way to test the hypothesis, however, would be to use its quantitative prediction: that the expenditure on male function should increase with local population density to an asymptote at 50% (Charnov 1980; Bell 1982). To perform the test involves measuring the proportional allocation to male function. This might be done straightforwardly in one of two ways. First, we could choose to ignore secondary structures and instead measure allocation to primary structures only: the pollen and the mature seeds. Since the seeds would greatly outweigh the pollen, the allocation ratio calculated in this way would be strongly biased towards female function. Secondly, we could choose to include secondary structures, interpreting their gender according to some *a priori* scheme. The fruit seems clearly female; the flowers, since they serve both male and female function, we shall say are equally male and female. Even if fruit and flower are of comparable bulk, counting the former as purely female and the latter as both male and female implies that the overall allocation ratio will again be strongly skewed towards femaleness. Thus, either ignoring secondary allocation to the flower or treating it as being equally male and female results in the interpretation of plants with hermaphroditic flowers as spending far more on female than on male function.

This is a paradoxical conclusion, for nothing we know about plants leads us to expect such a proposition to hold as an empirical generalization. It must be resolved before the theory of gender, which has had such striking success elsewhere (see, for example, Wenner 1981; Charnov 1982) can make any progress with the interpretation of flowering plants. Its resolution will require the construction of a new theory of floral function, expressed in terms of measurable quantities. It is the purpose of this paper to advance such a theory, and then to describe a series of observations and experiments which were performed to investigate its validity.

The empirical basis of a theory of secondary allocation must be a knowledge of its effects on the success of primary allocation. We must therefore be able to measure the curves illustrated in figure 1, which relate variation in secondary

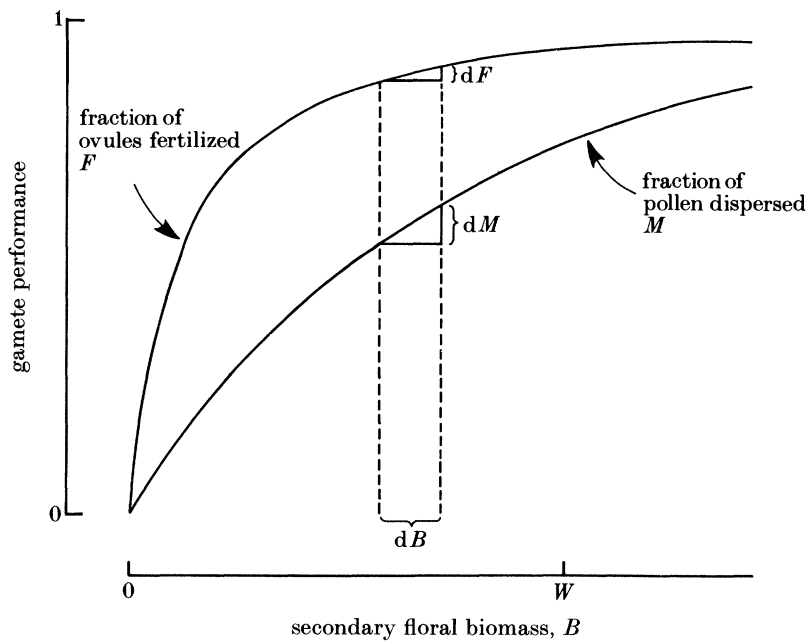


FIGURE 1. Measurement of floral function. See text.

allocation to the fraction of ovules fertilized and the fraction of pollen removed. Further, we must be able to use this information to partition the secondary allocation into male and female components. Suppose that the fraction of ovules fertilized, F , and the fraction of pollen removed, M , are functions of flower size, B . I assume that both F and M are zero when B is zero; this simplifies the treatment, but a more general expression for the case in which some degree of male or female success is possible with zero secondary allocation is easily obtained. We are required to find how the secondary allocation B is divided between male and female function in flowers of some given size W ; the proportion of secondary allocation devoted to male function is termed α .

Consider the effect of a small increment in secondary allocation from B to $B + dB$. This will be associated with an increment in the fraction of ovules fertilized of dF ,

and with an increment in the fraction of pollen dispersed of dM . The gender of this increment dB in secondary allocation is thus $dM/(dM + dF)$. If it has no effect on the fraction of ovules fertilized ($dF = 0$), its function is wholly male (gender is 1); if it has no effect on the fraction of pollen dispersed ($dM = 0$) its function is wholly female (gender is 0); if it has some effect on both male and female function then it has intermediate gender. By summing the gender of all the increments of B between $B = 0$ and $B = W$ we can obtain the overall gender of the secondary allocation of the flower:

$$\alpha = \frac{1}{W} \int_0^{B=W} \frac{dM}{dM + dF} dB.$$

Thus, if all increments of B increase male and female function by the same amount ($dM = dF$ for any B), the gender of the secondary allocation is $\alpha = (1/W) \int_0^W \frac{1}{2} dB = \frac{1}{2}$, and we conclude, as we obviously should, that in this case the secondary allocation is equally male and female. But if the responses of male and female function differ, then secondary allocation will be judged to be male-biased or female-biased, depending on the shapes of the curves relating M and F to B . To estimate α from data, we would fit the data to functions describing F and M , then use the parameters of the fitted functions to obtain the derivatives $M' = dM/dB$ and $F' = dF/dB$. Integrating $M'/(M' + F')$ over B between zero and W , then dividing the result by W , gives the estimate of α .

The particular hypothesis I shall attempt to test in the body of this paper is very simple: it states that secondary floral allocation is almost exclusively male ($\alpha \approx 1$). This will be the case if a very small corolla suffices to ensure that almost all the ovules become fertilized, while any further increase in corolla size procures the dispersal of a greater quantity of pollen; thus $dF \approx 0$ but $dM > 0$ for B greater than some minimum value, and consequently $\alpha \approx 1$ for flowers that substantially exceed some minimal size. The reason for choosing this hypothesis is that it removes the paradox that stimulated the research; if flowers are almost exclusively male while fruits are entirely female, then the overall gender of the plant will be given as a first approximation by the ratio of flower mass to the sum of flower mass and fruit mass, which might easily vary between being almost exclusively female (flower very small relative to fruit, plant gender *ca.* 0) and almost exclusively male (flower very large relative to fruit, plant gender *ca.* 1). In practice, complications such as fruit abortion (which will skew the plant gender towards maleness) and self-fertilization (which introduces a male component to the fruit and a female component to the flower) will mean that so simple a rule cannot be entirely satisfactory, but will not alter, and may strengthen, the conclusion that the gender of hermaphroditic plants is expected to vary around an average of about $\frac{1}{2}$, rather than being strongly female biased in all cases. Failure to falsify the hypothesis therefore resolves an important paradox, and provides us with the conceptual foundation necessary for quantitative tests of theories of gender in flowering plants.

1. THE SITE AND THE STUDY ORGANISMS

Organization of the paper

The primary object of the paper is to show how (and of course whether) increase in secondary allocation affects floral function. The next section therefore deals with the relation between flower size and the number of visits made by insects in unit time. The third and fourth sections attempt to show how the response by the insects to variation in flower size is translated into effects on female function (fraction of ovules fertilized) and male function (fraction of pollen dispersed), respectively. The fifth section deals with an important complication, the effects of neighbouring flowers on a target flower of given size, and introduces a general quantitative theory of overall floral function. The sixth section reviews comparative material on allocation to male and female flowers in dimorphic plants.

Each section, whenever possible, is divided into three parts. The first part is comparative and describes correlates of flower size between different species of plants. The second and third parts are largely original and comprise observations and experiments respectively; by 'observations' I mean measurements made on unmanipulated flowers which varied naturally in size, whereas 'experiments' concern situations in which variance in flower size was created according to a predefined protocol. Directly relevant results obtained by other authors are also described briefly, though a great deal of indirectly relevant information has been omitted to keep the text to a reasonable length. Each section concludes with a brief summary and is to that extent self-contained; the final section of the paper is a general summary in which the performance of the hypothesis under test is evaluated.

Study organisms

The five plants used in this work are briefly described here to avoid excessive repetition in the main text.

(a) Fragaria virginiana Duchesne (Rosaceae)

Strawberry. A creeping stoloniferous perennial herb. The flowers have five white petals and bear numerous stamens and pistils; several occur together in a loose corymbiform cluster. Gynodioecious, with female and perfect (hermaphroditic) flowers on separate stocks.

(b) Chrysanthemum leucanthemum L. (Compositae)

Daisy. Erect perennial herb, about 1 m in height, head terminal or stem bears several heads. Heads up to about 5 cm in diameter; white ray florets female, yellow disc-florets perfect.

(c) Impatiens capensis Meerb. (Balsaminaceae)

Jewelweed. Glabrous annual herb about 1 m in height. Large, pendant, orange-red, zygomorphic flowers in few-flowered axillary racemes. Petals fused; large petaloid sepal saccate and prolonged into a nectariferous spur (for simplicity, I have called all corolla parts 'petals' in the text). Flowers strongly protandrous, with five stamens united into a mass around the stigma, which is entirely concealed

during the initial male stage of flower life, later exposed when the androecium withers and falls away. Cleistogamous flowers common, but not discussed here. Ovary five-celled with one or a few ovules in each cell; fruits explosively dehiscent and usually bearing four to seven mature seeds.

(d) *Asclepias syriaca* L. (Asclepiadaceae)

Milkweed. Perennial herb, usually single-stemmed, arising from a stout rhizome. Flowers strongly scented, nectariferous, arranged in many-flowered pedunculate umbels. Pollen contained in pollinia, connected in pairs by a translator easily visible to the naked eye, five pairs in each flower; both pollinia removed as a unit by insects. Only one or a few flowers in each umbel set seed; fruit a large follicle bearing about 100–200 wind-dispersed seeds.

(e) *Viburnum alnifolium* Marsh (Caprifoliaceae)

Small shrub. Fertile flowers pentamerous, perfect, white, borne in many-flowered cymes; each inflorescence also bears a marginal ring of large white sterile flowers. Fruit a one-seeded drupe.

Study sites

All the work described below was done at the McGill University Field Station at Mont St Hilaire, southern Quebec. The mountain is a mass of intrusive rocks rising from the St Lawrence valley floor to a height of about 1300 feet (400 m). It is at the northern limit of eastern deciduous forest, dominated by beech and maple but with a diverse flora catalogued by Maycock (1961). The particular study sites used were as follows. For strawberry, a highly disturbed area of sand and gravel soils, exposed or in the partial shade of sumac bushes, on a southeastern exposure in the eastern corner of the estate. For daisies, a nearby woodland ride, in full sunlight or dappled shade. For jewelweed, wet hollows close to the above sites and to a small laboratory building, at the edge of the forest or in gaps. For milkweed, an abandoned orchard in the centre of the estate; the milkweeds grow in exposed situations away from the forest edge, in an old-field assemblage otherwise dominated by *Apocynum*, *Rubus* and *Solidago*. For *Viburnum*, a north-facing slope at the northern edge of the estate, close to permanent water in a closed beech–maple forest.

2. FLOWER SIZE AND INSECT VISITS

Comparative evidence

Although most people would accept that larger flowers are visited more often by insects, the evidence is widely scattered and largely anecdotal. Knuth (1906) reports several cases in which the larger flowers of one species are visited more often than the smaller flowers of a closely related species; naming the larger species first, these are *Anemone sylvestris* (*nemorosa*), *Adonis vernalis* (*aestivalis*), *Stellaria holostea* (*graminea*), *Cerastium arvense* (*triviale*), *Hypericum* spp. (*humifusum*), *Malva* spp. (*rotundifolia*), *Linum usitatissimum* (*catharticum*), *Geranium* spp. (*rotundifolium*), *Geranium molle* (*pusillum*), *Potentilla aurea* (*salisburgensis*),

P. salisburgensis (minima), *Ulmaria pentapetala (filipendula)* and *Tofieldia calyculata (palustris)*. More generally, the larger-flowered species of Umbelliferae, Boraginaceae and Polygonaceae are said to be more frequently visited. No cases are given to the contrary.

Mulligan & Kevan (1973) related the frequency of visits to a series of Canadian herbs to their size, odour and photometric brightness. Their data are unsuitable for statistical analysis, but the brief summary given in table 1 shows that larger and more odorous flowers attract more visits, with colour having little effect.

I have found no other broad surveys.

TABLE 1. INSECT RESPONSE TO FLORAL CHARACTERISTICS OF CANADIAN WEEDS

insect visits†	mean size‡ mm	frequency of odour§	mean photometric brightness (%)¶			number of species in category
			u.v.	blue	yellow	
none	2.9	0.00	21.8	35.3	39.8	6
rare	12.0	0.25	14.6	14.4	41.7	9
occasional	34.8	0.33	21.5	37.7	46.6	23
frequent	63.9	0.80	20.1	26.9	52.9	13

† Frequency of insect visits, as judged by original authors.

‡ Mean length in millimetres of flower, head or inflorescence.

§ Fraction of species having an obvious odour.

¶ Where several different values are available, that of the most peripheral flower part is chosen.

Source: Mulligan & Kevan (1973; table 3).

Observations

Obs. 1: *Fragaria*

Strawberries grow thickly in an area of disturbed ground about 50000 m² in extent on the southeastern face of Mont St Hilaire. Four observers censused insect visits throughout this area by choosing a location haphazardly and watching two flowers for 2 min. This period of time was chosen because preliminary observations suggested that the probability of observing a visit within 2 min was about one third. At the end of the observation period both flowers were stored in vials and later taken back to the laboratory, where their petals were removed and weighed; no more than 1 h elapsed between picking and weighing. All observations were made between 10h00 and 15h00 on 2 and 3 June 1983, both warm and sunny days. A total of 515 flowers were watched and 166 visits recorded. About 90% of all visits were made by syrphid flies, most of the remainder being by muscids, solitary bees and ichneumonids.

Petal mass varied over an order of magnitude, roughly between 2 and 25 mg. The data were divided at 1 mg intervals, within each of which the total number of flowers $N(x)$ and the total number of these that were visited $V(x)$ are known. The conditional probability that a flower of size x will be visited within a 2 min period is then estimated by $V(x)/N(x)$. The data show that the probability of being visited increases steeply and linearly with petal mass (figure 2). Large flowers with

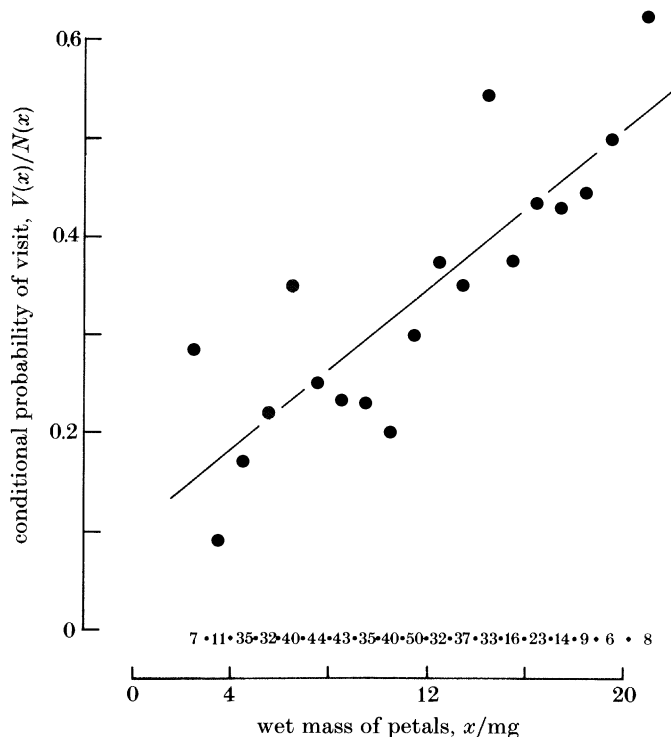


FIGURE 2. Flower size and rate of visits in *Fragaria*. Unweighted least-squares regression is $y = 0.100 + 0.021x$ ($r^2 = 0.72$, $p < 0.001$). For design, see text. Numbers along bottom are sample sizes, $N(x)$.

petals weighing about 20 mg will be visited about 100 times each day (of 8 h) while small flowers about 2 mg in mass will receive only about 10 visits.

This strawberry population was gynodioecious, with the smaller flowers being predominantly female; the relation between sex, size and visits is described in §5.

Obs. 2: Chrysanthemum

Four patches of daisies growing along a woodland ride were each watched for 30 min by two observers. Heads were tagged according to whether or not they were visited during this period, and the disc diameter, ray diameter (that is, total head diameter less disc diameter) and stem height were subsequently measured. Sites could not be pooled because of differences both in plant size and in rate of visits. Very few visits were seen at two of the sites, and both have been omitted from the analysis; in neither case did the visited differ significantly from the non-visited heads with respect to any of the characters measured. Data for the other two sites are given in table 2. Almost all the visits were made by syrphid flies or honeybees, which were about equally frequent; they did not differ with respect to any of the characters measured and have been pooled for analysis. In both sites the heads that were visited exceed those that were not visited in disc diameter, ray diameter, overall diameter and stem height. The effect is a small one; when both sites are

TABLE 2. SIZE OF *CHRYSANTHEMUM* HEADS VISITED AND NOT VISITED BY INSECTS AT TWO SITES

site	visited?	N	mean \pm s.d. of measurement/mm			
			disc	ray	head	stem height
1	yes	50	1.363 ± 0.26	2.462 ± 0.49	3.825 ± 0.67	37.23 ± 10.4
		41	1.285 ± 0.27	2.283 ± 0.54	3.575 ± 0.74	35.27 ± 9.4
		$t =$	1.40	1.65	1.71	0.93
		$P_1 =$	0.085	0.050	0.045	0.18
2	yes	58	1.488 ± 0.18	2.478 ± 0.37	3.966 ± 0.49	42.26 ± 10.3
		123	1.431 ± 0.25	2.400 ± 0.50	3.823 ± 0.70	39.35 ± 12.4
		$t =$	1.54	1.05	1.39	1.55
		$P_1 =$	0.065	0.145	0.085	0.065
pooled		$\chi^2_3 =$	10.4	9.85	11.1	8.90
		$P_1 =$	0.04	0.05	0.03	0.06

P_1 is the one-tailed probability for rejection of the directional hypothesis that larger (or taller) heads are visited more frequently.

taken together the effects are significant at about $p = 0.05$, if the one-tailed hypothesis that plants that allocate more to these structures will be visited more often, is allowed.

Obs. 3: *Impatiens*

Bumble bees foraging in a patch of *Impatiens* were followed until a flower was visited. After the visit this flower and the two nearest open flowers were picked and weighed. In 26 out of 40 observations the mass of the visited flower exceeded the average of its two unvisited neighbours, giving goodness-of-fit $\chi^2_1 = 3.60$ and $p < 0.05$ for the one-tailed hypothesis that larger flowers are more likely to be visited than their smaller neighbours. The mean (\pm s.d.) mass of visited flowers was 53.8 ± 14.3 mg and of their unvisited neighbours 49.4 ± 14.0 mg, yielding $t = 1.62$ and $p < 0.05$ for the one-tailed hypothesis.

In conclusion, although the *Chrysanthemum* and *Impatiens* observations are consistent with the hypothesis that larger flowers are visited more frequently, only the *Fragaria* observations were decisive, with the largest flowers receiving about ten times more visits than the smallest. Comparable observations are difficult to find in the literature. Knuth remarks that larger flowers are visited more frequently than smaller flowers in *Echium officinalis*, but says that this is not the case in *Stellaria graminea*. Willson & Price (1977) found that larger inflorescences of *Asclepias syriaca* received more visits, and Schaffer & Schaffer (1977) obtained similar results for several species of *Yucca*.

*Experiments**Exp. 1: Impatiens*

Designated petals were removed with scissors from the corolla of an experimental flower, which was then marked with a very short length of coloured thread round the peduncle. A nearby flower in the same sexual phase and of similar size was also tagged. All flowers used were male and had still been closed on the previous evening. Five such pairs of flowers, each representing a different treatment, were constructed by an observer and watched for 500 s. The observers (five or six in number) then rotated around the patch so that each group of flowers was watched by each observer. Three groups of observers were used; all observations were made at the same site, in late August 1981 and 1982. The fraction of floral biomass removed by the treatments (assessed by weighing the flowers, giving very closely similar results in 1981 and 1982) was then related to the number of visits received by the flowers. These results are given in figure 3. Removal of parts of the corolla causes a reduction in the frequency of visits, more or less in proportion to the quantity of material removed. There was no indication that removal of any particular part had a greater effect than the removal of any other part or parts of equal mass, though the number of visits involved is too small for this observation to be conclusive. The mass measured in this experiment is the total mass of the flower, including the sexual parts; the most extreme mutilations shown in figure 3 involved the excision of the entire corolla, but a few visits were nevertheless observed. The total effect of the corolla is thus to raise the frequency of visits by a factor of about ten, an effect comparable with that associated with the difference between the largest and smallest flowers of *Fragaria*.

Exp. 2: Asclepias

Flowers were removed systematically from milkweed inflorescences in connection with an experiment to measure the effect of inflorescence size on the removal and reception of pollinia which will be described below (exp. 7). Before the inflorescences were collected, the number of insect visits to each during a 5 min observation period was recorded. Results are given in table 3. They show quite clearly an effect of target size, with larger inflorescences attracting more visitors, and, therefore, conform to the observations using natural variation of inflorescence size made by Willson & Price (1977). The frequency of visits per flower is minimal for very small inflorescences of 1–10 flowers, much greater for inflorescences with 11–30 flowers, but remains constant or even falls for inflorescences close to the mean size ($49.8 \pm \text{s.d. } 14$ flowers) of unmanipulated inflorescences in this population.

Similar experiments are described by Plateau (1896), who also refers to scattered observations in the earlier literature, including one made by Darwin (1876). Plateau claimed that mutilation, even as extreme as the complete removal of the corolla, did not drastically reduce the visits received by flowers. His results were vigorously attacked by Knuth (1906, vol. 1, p. 204 ff). Since Plateau does not give quantitative comparisons between experimental and control plants, his work is difficult to evaluate; the sole exception was a *Lobelia* from which all the petals had

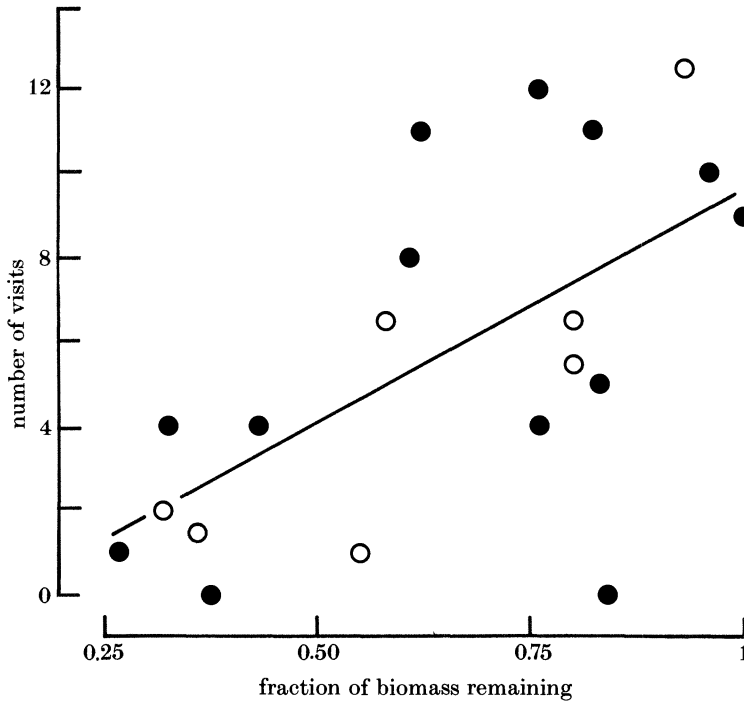


FIGURE 3. Effect of floral mutilation on the frequency of insect visits in *Impatiens*. The figure is illustrative; twice as many visits were recorded in 1981 as in 1982, so that numbers of visits for 1981 (open circles) have been divided by two to plot them on the same figure as the results for 1982 (solid circles). The equation of the regression line drawn is

$$y = 1.39 + 11.0x \quad (r^2 = 0.39)$$

and a parametric and non-parametric analysis of the raw data for the two years is given below. For regression analysis the x -variate is arcsin square-root of fraction of floral biomass remaining, the y -variate being number of visits observed.

	1981	1982	pooled
Pearson			
intercept	0.643	0.771	—
slope	0.0276	0.0353	—
correlation	0.861	0.503	$\chi^2_4 = 13.76$
p	0.013	0.08	$p = 0.01$
Spearman			
correlation	0.773	0.374	$\chi^2_4 = 9.48$
p	0.042	0.208	$p = 0.05$

Probabilities cited are two-tailed; if a one-tailed hypothesis is allowed the non-parametric analysis for the two years pooled yields $p < 0.02$. Excluding the 1982 outlier with most of corolla remaining but no visits observed produces much more highly significant results.

been removed, which received in all 41 visits during 3.5 h while a nearby unmutated plant received 62 visits. Much more thorough and careful work was described by Knoll (1922) and Kugler (1943), though both used paper models and were more concerned with colour, odour and form than with size. The most extensive experiment reported by Knoll concerns the attractiveness of coloured paper discs to the hawk-moth *Macroglossum*, and his results are summarized in figure 4. The number of visits increased more or less proportionately with the area of the disc

TABLE 3. INFLORESCENCE SIZE AND RATE OF VISITS IN *ASCLEPIAS*

numbers of flowers per inflorescence	number of inflorescences	number of flowers	number of visits	number of visits per inflorescence	number of visits per flower
1-10	59	283	39	0.661	0.138
11-20	39	554	158	4.051	0.285
21-30	39	944	256	6.564	0.271
31-60	38	1505	328	8.632	0.218
pooled	175	3286	781	4.498	0.238

A 'visit' is contact with a flower; insects may make several or many consecutive visits to different flowers on the same inflorescence. All comparisons of visits per inflorescence or visits per flower for inflorescences with different numbers of flowers are significant at $p = 0.01$ except that visits per flower does not differ between inflorescences with 11-20 flowers and those with 21-30 flowers.

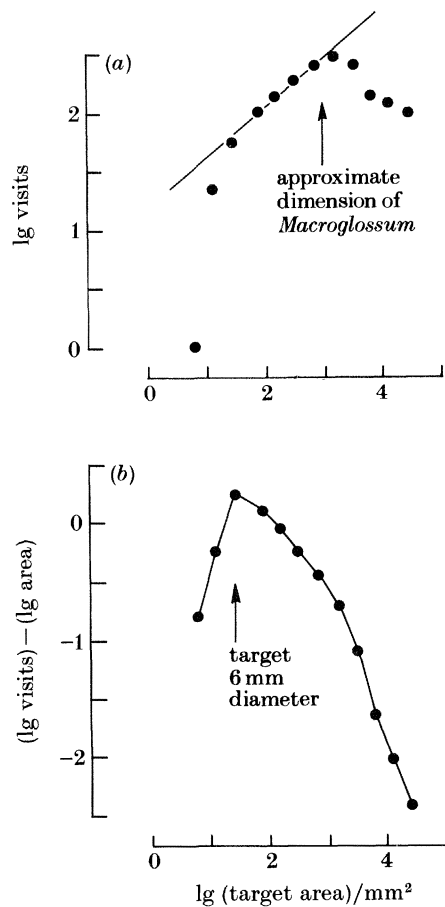


FIGURE 4. Visits by *Macroglossum* to target discs. Note that axes of both graphs are logarithmic. (a) Total visits. Line is not a regression, but is drawn in to guide the eye (see text); it has a slope of about 0.2. *Macroglossum* fits inside a circle of 40 mm diameter. (b) Visits per unit area. This function is maximized by targets of about 6 mm diameter. Source of data: Knoll (1922; table 2).

for discs between 3 and 22 mm radius. The upper end of this range corresponds roughly with the size of *Macroglossum*, and larger discs received fewer visits. Very small discs of 1.4 mm radius received hardly any visits. When we calculate the number of visits received per unit area, a very clear picture emerges (figure 4*b*): there is a well-defined maximum at a radius of about 3 mm, with visits per unit area falling off steeply for smaller and for larger discs. This implies that, given a fixed quantity of paper, the total number of visits per unit time would be maximized by dividing it into discs of intermediate size, in this case 3 mm. Other, less extensive experiments gave similar results (Knoll tables 3 and 4). The inference that subdividing floral biomass may maximize floral function receives some support from Kugler's experiments. He, too, found that larger models (in the range 1–4 cm radius) received more visits, but also reports that a cluster of small models receives more visits than a single target of comparable area (Kugler 1943, p. 261).

In my own work, neither the observations on *Fragaria* nor the experiments with *Impatiens* show any effect of flower size on the rate of visits per unit size; in both cases the total number of visits increases with flower size but the regressions of visits per unit mass on flower size have slopes indistinguishable from zero. Only for *Asclepias* does an intermediate number of flowers per inflorescence, well below that of the average number for the population procure a greater number of visits per flower.

3. FLOWER SIZE AND OVULE FERTILIZATION

I do not know any comparative or observational evidence that the proportion of ovules fertilized increases with flower size, and this section will be limited to a discussion of experimental results. Indirect evidence might come from studies of fruit abortion, since if the proportion of ovules fertilized increases with inflorescence size then the number of fruits initially formed should be disproportionately greater for inflorescences with more flowers. I have found no direct test of this hypothesis, but the scatter plots given by Aker (1982) for *Yucca whipplei* show no sign of the expected curvilinearity. The increased number of insect visits to larger inflorescences of *Yucca* did not cause a disproportionately larger number of fruits to be initiated (Schaffer & Schaffer 1977).

Experiments

Exp. 3: Asclepias (inflorescence removal)

This experiment was designed to test the hypothesis that stems that bear more inflorescences set more seeds as the result of being more conspicuous and thus receiving more insect visits. It is important to recall that although the inflorescence of *Asclepias* bears many flowers, only a very few of these set fruit: removal of flowers, therefore, has no necessary effect on seed production by an inflorescence, so long as a few flowers remain. Like all the milkweed experiments, it was located in an abandoned orchard, surrounded by second-growth woodland, at Mont St Hilaire. Forty-seven stems matched for height and number of leaves were mutilated so as to form a series bearing from one to seven inflorescences; stems with one remaining inflorescence were created by removing six inflorescences from a stem originally bearing seven inflorescences, five inflorescences from a stem

originally bearing six, and so forth. The results for the 38 stems subsequently recovered are given in table 4. There was no effect of the initial number of inflorescences on any of the measurements. The effect of the manipulation is clear. There is no relation between the number of seeds per pod and the number of inflorescences, whether the data are analysed by regression or by calculating t for

TABLE 4. EFFECT OF INFLORESCENCE REMOVAL ON SEED AND FRUIT PRODUCTION IN *ASCLEPIAS*

	number of inflorescences remaining per stem						
	1	2	3	4	5	6	7
stems	12	8	8	5	2	2	1
Pods	17	15	20	14	9	6	7
seeds	2751	2108	3002	2049	1331	867	791
aborted seeds	192	9	35	875	42	4	152
Pods per inflorescences	1.42	0.94	0.83	0.50	0.90	0.50	1.00
seeds per pod	161.8	140.5	150.1	146.4	147.9	144.5	113.0
seeds per inflorescence	229.3	131.8	125.1	146.4	133.1	83.3	113.0
Pods per stem	1.42	1.88	2.50	2.80	4.50	3.00	7.00
seeds per stem	229.3	263.5	375.3	409.8	665.5	433.5	791.0
filled seeds per stem	213.3	262.4	370.9	234.8	644.5	431.5	639.0

Explanation in text.

pairwise comparisons. Analyses were performed both for total seeds and for filled seeds only, with the same negative outcome in both cases. On the other hand, there is clearly an increase in the number of pods formed per stem when more inflorescences are present. The regression equation (for the raw data) relating pods per stem to inflorescence number is $y = 0.68 + 0.61x$, with $r^2 = 0.32$ ($p < 0.001$). Since the slope of the regression is less than unity, the number of pods per stem increases despite a fall in the number of pods formed per inflorescence. The effect of inflorescence removal on seed production per stem is, therefore, due wholly to an effect through total pod production and not to any effect through the number of seeds produced per pod or per inflorescence.

Exp. 4: Asclepias (flower removal)

In a second series of experiments the number of pods per stem was held constant while the number of flowers per inflorescence was manipulated by removing flower buds. Two experiments were performed.

In the first experiment (exp. 4A, August 1981), three sets of eight stems each, matched for height and leaf number, were chosen, stems being allocated to sets at random. The first set comprised unmanipulated controls; the second set manipulated controls, in which all inflorescences except one were removed; and the third set experimentals, in which all inflorescences except one were first removed and 20–90% of the flower buds on this remaining inflorescence were then excised to create a range of inflorescence sizes. The design was replicated twice to give a total of 48 stems, of which 42 were subsequently recovered and analysed.

The mean (\pm s.d.) number of seeds set per pod did not respond to the treatment: for the unmanipulated controls 176.7 ± 38.1 ($N = 44$ pods); for the manipulated controls 161.8 ± 40.3 ($N = 15$); and for the experimentals 149.8 ± 55.5 ($N = 12$). Despite the negative trend, no pairwise comparison yields a value of t significant at $p = 0.05$ for the one-tailed hypothesis that the manipulation reduces seeds set per pod. In contrast, there was a clear effect of the manipulation on pod number (table 5). All the unmanipulated controls set at least one pod, while total reproductive failure was frequent among both the manipulated controls and the experimental group. The experimentals set even fewer pods than the manipulated controls, but the difference was not significant. This experiment, therefore, confirms the effect of inflorescence removal on pod production per stem, but fails to show any effect of the manipulation on pods per inflorescence or on seeds per pod. However, in view of the negative trends in both measurements a more extensive experiment designed to test the effect of flower removal on seed and pod production was run in 1982.

In this experiment (exp. 4b), all inflorescences except two were removed from each of 48 matched stems, 42 of which were subsequently recovered. Each inflorescence received one of seven treatments: removal of 0%, 5%, 20%, 50%, 80%, 95% or 100% of flower buds, giving a total of 49 pairwise combinations of treatments (one of which, total removal of flower buds from both inflorescences, is obviously superfluous). Because of the labour of counting seeds, only a single replicate was used. The results are presented and analysed in figure 5 and table 5. Total reproductive failure is again more frequent among inflorescences with few flowers; the effect is not significant when the data are divided at the median and analysed by χ^2 (table 5), but inflorescences with few remaining flowers produce on average fewer pods (table 5) and the disproportionate number of very small inflorescences that fail to produce any pods is obvious (figure 5). When these inflorescences are omitted, the average effect of removing flowers is to lower expected seed production per inflorescence from 295 for an unmanipulated inflorescence of 50 flowers to 195 for the minimal inflorescence comprising a solitary flower. This effect is wholly due to a decrease in pod production from about 1.5 in inflorescences with 50 flowers to about 1 in very small inflorescences. There is no sign of any effect of removing flowers on the number of seeds set per pod.

These experiments yield results that are consistent with one another and with the observation of Willson & Price (1977), who used unmanipulated plants, that small inflorescences bear relatively few pods. They show that the removal of flower buds reduces the number of mature fruits but has no effect on the number of seeds set in each fruit. It is inferred, but not directly proven, that these effects are caused by the reduction in the number of insect visitors documented in the previous section. If so, then insects have an all-or-none effect on female function; either a fruit is formed, in which case almost all ovules are fertilized and there is little variance in seed number between fruits, or no fruit is formed and consequently no seeds set. Two further experiments were designed to investigate the validity and generality of this interpretation. One concerned *Impatiens*, in which the flowers are essentially solitary and the fruit bears several seeds; the other involved *Viburnum*, which bears an infructescence of single-seeded fruits. To be consistent

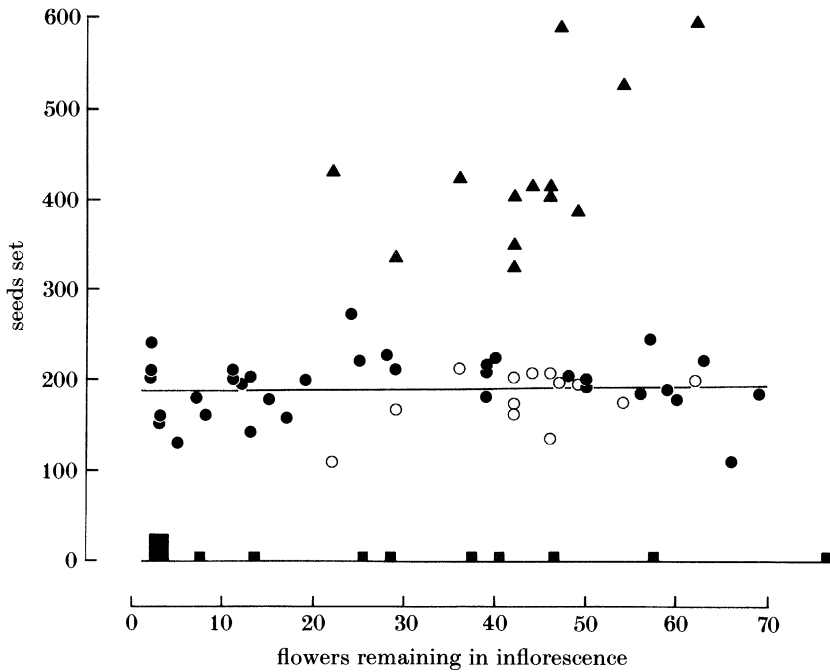


FIGURE 5. Response of seed production to removal of flowers from inflorescence in *Asclepias*. Plotted points are: ● total seeds set in inflorescences bearing a single pod (= seeds set per pod for these inflorescences); ▲ total seeds set in inflorescences bearing more than one pod; ○ seeds per pod for inflorescences bearing more than one pod. Histogram at bottom shows numbers of inflorescences that failed to set fruit. Regression line is for seeds per pod, excluding inflorescences that set no pods. Parametric and non-parametric correlation analyses gave the results shown below. o.l.s., Ordinary least squares.

	total seeds set	pods	seeds per pod
parametric (o.l.s. regression)			
intercept	192.6	1.081	187.4
slope	2.05	0.0098	0.093
correlation	+0.351	+0.271	+0.058
<i>t</i>	2.51	1.89	0.39
<i>p</i>	0.008	0.032	0.35
non-parametric (Kendall rank)			
τ	+0.211	+0.258	-0.005
<i>z</i>	2.09	2.56	-0.05
<i>p</i>	0.018	0.005	0.48

with the *Asclepias* results, floral mutilation, with its implied reduction of insect visits, should reduce seed set per infructescence in *Viburnum* but should have no effect on seeds per fruit in *Impatiens*.

Exp. 5: *Impatiens*

Flowers were mutilated by removing parts of the corolla with scissors. Spur, back petal, lower right and lower left petals, and upper petal were treated as separate units, with 24 of the 31 possible combinations of treatments forming a single

TABLE 5. EFFECT OF FLOWER AND INFLORESCENCE REMOVAL ON FRUIT PRODUCTION IN *ASCLEPIAS*

	steams bearing		$\bar{x} \pm \text{s.d. pods}$	χ^2_1	p	t	p
	1 pod	0 pods					
1981 (exp. 4a)							
unmanipulated controls	13	0	3.385 ± 2.60	9.58	0.01	2.70	0.01
manipulated controls	6	7	1.154 ± 1.46				
experimentals	5	11	0.750 ± 1.29	0.73	0.41	0.79	0.43
1982 (exp. 4b)							
more than 30 flowers per inflorescence	25	5	1.335 ± 0.92	1.79	0.19	2.63	0.01
fewer than 30 flowers per inflorescence	22	10	0.774 ± 0.76				

Explanation in text. Compare values for pods per stem in exp. 3, table 4. See figure 5.

experimental series. Two replicate series were constructed, at sites some 100 m apart. Each experimental flower was paired at the time of mutilation with a randomly chosen control nearby. Experimental flowers were marked with short lengths of coloured cotton thread; each control received the same tag as the corresponding experimental flower, plus a white thread. All flowers had opened in the morning preceding the afternoon on which the manipulations were performed, and would not enter their female phase for at least one more day. Because of the paired design of the experiment, it was possible to predict that the experimental flowers should tend to set fewer seeds than the corresponding controls. The results are given in full in table 6. Controls exceed experimentals in only 10 cases, whereas the experimentals actually exceed the controls in 14 cases, there being no difference in 13 cases. The remaining 11 pairs cannot be put into any of these three categories since one or both flowers were lost. When these unpaired observations are included in the calculation of mean seed set, however, the conclusion from the paired analysis is undisturbed: the mean seed set per fruit by experimentals and controls respectively was 4.7 and 4.6 at one site, and 5.3 and 5.2 at the other. Nor is there any indication that the most severe mutilations, involving the removal of most or all of the corolla, had any effect on seed set.

Exp. 6: Viburnum

The inflorescence of *Viburnum alnifolium* is a cyme whose central flowers are small and fertile while the outermost flowers are much larger and sterile. It has often been speculated that the function of the sterile flowers is to attract insect visitors, since they can have no direct reproductive role. The experimental design was paired, with all the sterile flowers being removed from a randomly chosen inflorescence whose nearest neighbour on the same shrub was unmanipulated and served as a control. All manipulations were performed in early May, when the fertile flowers were still in bud. A total of 68 pairs were constructed and marked with metal tags, 66 being subsequently recovered.

The pairwise data yielded an unambiguous result: the control inflorescences

TABLE 6. EFFECT OF FLORAL MUTILATION ON SEED SET IN *IMPATIENS*

N	structures removed				site 1		site 2	
	B	R	L	U	exp.	control	exp.	control
*	—	—	—	—	5	0	5	4
—	*	—	—	—	0	6	5	5
—	—	*	—	—	6	5	6	6
—	—	—	*	—	—	6	7	6
—	—	—	—	*	—	4	6	—
*	*	—	—	—	4	4	5	—
*	—	*	—	—	7	7	6	0
*	—	—	*	—	6	5	7	7
*	—	—	—	*	0	4	6	6
—	—	*	*	—	5	8	6	5
—	—	*	—	*	6	6	7	6
—	—	—	*	*	6	0	5	5
*	—	*	*	—	6	6	6	7
*	—	*	—	*	5	6	6	5
*	—	—	*	*	—	0	5	5
*	*	*	—	—	5	4	7	—
*	*	—	*	—	5	5	3	4
*	*	—	—	*	—	4	6	6
—	—	*	*	*	7	5	6	6
*	—	*	*	*	0	6	6	—
*	*	*	*	—	5	4	0	6
*	*	*	—	*	6	5	6	—
*	*	—	*	*	—	—	0	5
*	*	*	*	*	5	7	—	—
mean \pm s.d. seeds set					4.7	4.6	5.3	5.2
					± 2.2	± 2.1	± 1.9	± 1.6

Structures are: N, nectary; B, back 'petal'; R, lower right petal; L, lower left petal; U, upper petal. Figures in body of table are seeds in fruits; a dash indicates that the fruit could not be found.

yielded more fruits than the experimentals in 46 out of 66 cases, for which $\chi_1^2 = 10.2$ and $p < 0.001$ for the null hypothesis that the removal of sterile flowers has no effect on fruit production. However, a more powerful parametric analysis can also be used, since the fertile flowers on experimental and control inflorescences were counted at the time of manipulation. The fraction of these flowers forming fruits can then be calculated, and we can test the hypothesis that the difference between experimental and control is zero. The observed difference is -0.0283 ± 0.059 , for which $t_{65} = 3.89$ and $p < 0.001$.

An analysis of the pooled data is shown in table 7. The experimental and control series do not differ with respect to the initial number of either sterile or fertile flowers, but the controls bear more fruit, so that removal of the sterile flowers causes a reduction in the fraction of fertile flowers that set fruit.

The indirect manipulation of the *Viburnum* inflorescence, in such a way as to reduce the likelihood of insect visits without damaging the fertile flowers, is therefore associated with a 20% reduction in the fraction of fertile flowers forming fruits, or equivalently a decline in fruit production from about 25 to about 20 per inflorescence.

TABLE 7. EFFECT OF REMOVING STERILE FLOWERS ON FRUIT PRODUCTION IN *VIBURNUM*

	mean \pm s.d. value of			fruit set
	sterile	fertile	fruits	
control	11.05 ± 5.43	190.8 ± 44.7	25.12 ± 14.09	0.1329 ± 0.072
experimental	10.68 ± 5.13	191.6 ± 47.8	19.59 ± 10.99	0.1044 ± 0.061
test				
$t =$	0.40	-0.10	2.51	2.46
$p =$	0.7	0.9	0.015	0.018

The experiments with *Impatiens* and *Viburnum* are therefore consistent with the *Asclepias* result, showing that the effect of removing material from flowers or inflorescences is to reduce fruit set without altering the number of seeds per fruit, and suggesting that floral allocation has a discontinuous effect on female function by increasing the probability that a flower is visited once.

If this proposition is true, we expect to find that the number of fruits per stem will generally be more variable than the number of seeds per fruit. Since both variances are likely to scale with the mean, this prediction must be tested by regressing the variance on the mean, both being appropriately transformed, and measuring the difference in elevation of the two fitted curves. This has been done for the extensive data published by Salisbury (1942). The appropriate transforms turn out to be the logarithm of the standard deviation and the logarithm of the mean, which yield linear homoscedastic graphs. The slopes do not differ from one another or from unity, showing that the coefficient of variation remains the same as the mean changes. The elevations are different, with the number of fruits per stem being more variable than the number of seeds per fruit for any given mean value. The predictive equations for the regressions of log standard deviation on log mean are:

(i) fruits per stem: $y = -0.10 + 1.04 x$ ($r^2 = 0.89$, $p < 0.0001$);

(ii) seeds per fruit: $y = -0.59 + 1.02 x$ ($r^2 = 0.95$, $p < 0.0001$),

the sample sizes being 92 and 87 species respectively. This gives comparative support to the experimental results.

A second line of argument is provided by experimental studies of factors affecting seed production. These have been reviewed very recently by Willson & Burley (1983), whose main conclusion is that resource availability very often limits seed production while pollen availability is seldom a limiting factor. This is entirely consistent with the hypothesis that most floral allocation serves male function, with very little material being enough to ensure the one or two insect visits sufficing to fertilize almost all the ovules.

4. FLOWER SIZE AND POLLEN DISPERSAL

Male function is much more difficult to measure than female function. Unless the pollen is organized into pollinia, as in milkweeds, the technical difficulties involved in measuring its rate of removal are considerable, and I have not been able to solve them satisfactorily. This section therefore describes only two studies, which I hope will spur more able experimenters to work on the problem.

*Observations**Obs. 4: Impatiens*

If the bulk of floral allocation is designed to serve male function, we expect larger flowers to be more successful in dispersing pollen. I have measured the allometry of androecium mass in *Impatiens*. In a series of observations, flowers were located on the evening before anthesis, some being bagged while others were left open. On the following evening all the flowers were collected and later dissected, the corolla and the androecium being weighed separately. It was found that in the bagged flowers corolla mass and androecium mass vary together, the slope of the fitted linear regression describing the allometric increase in the mass of male structures with increase in attractive structures. In the open flowers, insects should remove pollen and thus reduce androecium mass during the course of the day. We expect that both the total quantity and the proportion of pollen removed will increase as corolla mass increases. By measurement, we find that androecium mass (y) and corolla mass (x) are related by two linear regressions:

(i) bagged flowers: $y_B = b_0 + b_1 x$;

(ii) open flowers: $y_A = a_0 + a_1 x$.

Our predictions can therefore be formulated as follows:

(i) the total quantity of pollen removed increases with corolla mass: $b_1 > a_1$;

(ii) the proportion of pollen removed increases with corolla mass: $(b_1/b_0) > (a_1/a_0)$.

The results for each series of observations are shown in table 8, and the pooled results illustrated in figure 6. In all cases the mean androecium mass is lower in the open flowers, while mean corolla mass does not differ consistently between the treatments. This establishes that flowers that are exposed to insect visits lose on average about 12% of the mass of the androecium during the course of a day, presumably as the result of pollen export. The pooled data yield the following estimates of the regression parameters: $b_0 = 0.51$, $b_1 = 0.111$, $a_0 = 0.76$, $a_1 = 0.095$. There is therefore a tendency for flowers with larger corollas to export both more pollen, since $b_1 > a_1$, and a greater proportion of their pollen, since $(b_1/b_0) > (a_1/a_0)$ (figure 7b).

This conclusion must be treated with some reserve. Although the pooled results support the hypothesis, this is due very largely to the contribution of the 1981 data, while the 1982 observations show no clear pattern. More extensive observations and more sophisticated methods of measuring pollen export are needed before the hypothesis can be tested decisively.

TABLE 8. ALLOMETRY OF ANDROECIUM MASS IN BAGGED AND OPEN FLOWERS OF *IMPATIENS*

date	site	N	bagged flowers				open flowers						
			b_0	b_1	r	x_{fir}	x_{and}	b_0	b_1	r	x_{fir}	x_{and}	
2 September 1982	Dorm	38	-0.082	+0.134	0.78	53.1	6.31	44	+0.61	+0.092	0.76	54.5	5.62
15 August 1983	Charb	27	+3.1	+0.073	0.42	69.4	8.2	23	-0.24	+0.105	0.79	64.1	6.7
15 August 1983	Dorm	26	+1.7	+0.102	0.67	63.3	8.2	26	+2.9	+0.079	0.63	58.6	7.5
16 August 1983	Charb	21	-0.48	+0.120	0.56	65.1	7.3	20	-3.0	+0.147	0.64	67.3	7.0
17 August 1983	Dorm	30	+4.0	+0.061	0.55	76.4	8.7	24	+3.8	+0.066	0.57	72.9	8.6
18 August 1983	Charb	26	+4.3	+0.061	0.37	66.1	8.3	27	+1.7	+0.076	0.61	61.4	6.4
1983	pooled	130	+3.1	+0.075	0.52	68.4	8.19	120	+1.6	+0.087	0.61	64.6	7.24
1982 + 1983	pooled	168	+0.51	+0.111	0.97	64.9	7.76	164	+0.76	+0.095	0.97	61.9	6.81

The six data columns for each of the two treatments are: N, sample size; b_0 , intercept and b_1 , slope of linear regression of androecium mass on corolla mass; r, correlation coefficient, x_{fir} , mean corolla mass, x_{and} , mean androecium mass. All data are fresh masses in milligrams.

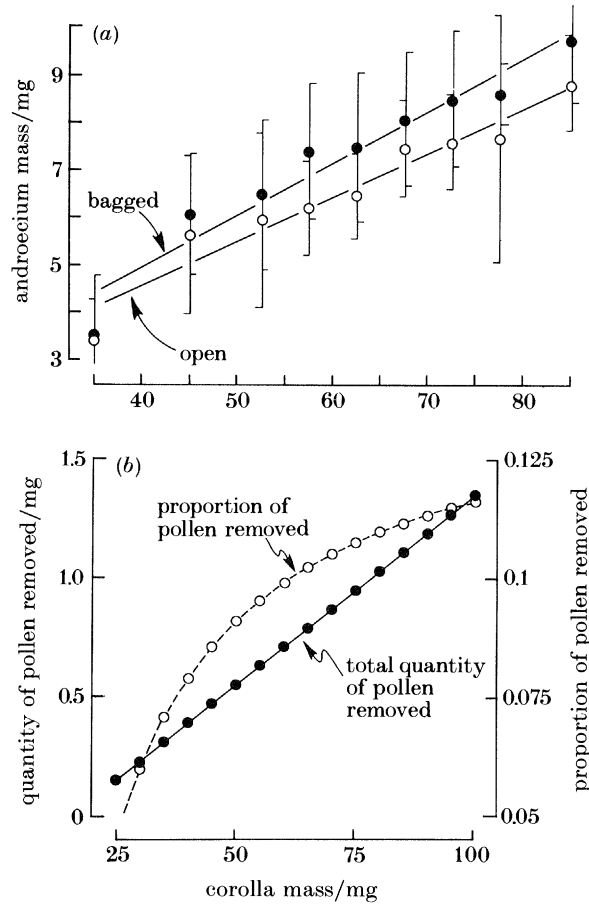


FIGURE 6. Allometry of androecium mass in bagged and open flowers of *Impatiens*. (a) Linear regressions of means for bagged and open flowers on pooled 1982 and 1983 data, summarizing the results given in table 8. (b) Curves of floral function derived from the allometry regressions. Total quantity of pollen removed is the difference between the expected androecium masses of bagged and open flowers, for given corolla mass; proportion of pollen removed is the same quantity, divided by the expected androecium mass of the bagged flowers, for given corolla mass.

Experiments

Exp. 7: Asclepias

Milkweeds are exceptionally suitable for quantitative studies of flower function because the pollen is borne within easily countable pollinia which are removed as units. This experiment was designed to test the hypotheses that the total number and the proportion of pollinia removed from flowers increase with inflorescence size. The design of the manipulations is similar to that of exp. 4: 49 stems matched for height and leaf number were selected and all but two inflorescences removed from each, after which all pairwise combinations of inflorescences with 0%, 5%, 20%, 50%, 80%, 95% and 100% of flower buds removed were constructed. This experiment was replicated twice at different locations within the abandoned

orchard; both series were run at the same time and have been pooled for analysis. The total number of inflorescences constructed was thus 49 combinations of treatments \times 2 inflorescences per stem \times 2 replicates = 196, less the 14 inflorescences from which all flowers had been removed, giving a total of 182, of which 175 were recovered and scored. Each inflorescence was mutilated while the flowers were still in bud, bagged for two days to allow the remaining flowers to open, exposed for two days (three days in some cases) and then collected and taken back to the laboratory. Here the number of pollinia remaining in place and the number inserted were counted, giving a measure for each flower of male function (pollinia exported) and female function (pollinia received). Pollinia lying loose on the surface of the flower were also observed and counted, but these are very unlikely to achieve fertilization and the analysis is restricted to legitimate insertions.

The results of this experiment are given in tables 9 and 10 and figure 7.

At the level of the inflorescence, the effect of the manipulation is very clear; the number of pollinia dispersed and the number received increase proportionately and nearly deterministically with the number of flowers in the inflorescence. From the results of exp. 4*b*, it is clear that the enhanced reception of pollinia is translated only loosely into enhanced female function, through a roughly 50% increase in fruit numbers over the extreme range of inflorescence sizes. An increase in inflorescence size from one to about 50 flowers therefore enhances female function by a factor of about 1.5 but male function by a factor of about 50.

At the level of the flower, the effects of the manipulation are much weaker. Table 9 and figure 7 show that each flower, in very small inflorescences of five or fewer flowers, exports and receives relatively few pollinia, while there is little effect for larger inflorescences. A more extensive regression analysis is given in table 10. I constructed four variables to express the performance per flower of the manipulated inflorescences:

- (i) the mean number of pollinia removed per flower;
- (ii) the mean number of pollinia received per flower;
- (iii) the mean number of pollinia received, as a fraction of the number of spaces left vacant by the removal of pollinia from the flower;
- (iv) the total flux of pollinia, as the sum of removals and insertions per flower.

All four measures increased with inflorescence size, supporting the one-tailed hypothesis that the removal and reception of pollinia per unit of inflorescence increases with inflorescence size at the $p = 0.03$ level or better. The effects, however, were both weak (log-log slopes about 0.05–0.10) and very variable (coefficients of determination 0.05 or less). The design of the experiment allows the results to be analysed for the effect of four other factors which might contribute to pollinium flux:

- (i) the number of flowers in the neighbouring inflorescence on the same stem, which might attract insects who would then visit the nearby target inflorescence;
- (ii) the mean number of pollinia removed per flower from the neighbouring inflorescence, which will reflect the intensity of pollinator activity near the target;
- (iii) the position of the target inflorescence on the stem, above or below its neighbour;
- (iv) the number of days (two or three) that the target inflorescence was exposed to visits.

TABLE 9. EFFECT OF INFLORESCENCE SIZE ON REMOVAL AND INSERTION OF POLLINIA IN *ASCLEPIAS*

number of flowers per inflorescence	total inflorescences	total flowers	number of pollinia						<i>I/R</i> per flower	total flux per flower
			removed (<i>R</i>)			inserted (<i>I</i>)				
			mean per inflorescence	s.d. per flower	mean per inflorescence	mean per flower	s.d. per flower			
1-5	35	85	5.30	1.182	2.66	1.094	0.897	0.501	3.276	
6-10	24	198	22.84	0.704	14.82	1.796	0.615	0.649	4.565	
11-15	28	365	35.16	0.803	22.13	1.698	0.748	0.630	4.395	
16-20	11	189	49.05	0.618	31.27	1.820	1.066	0.637	4.675	
21-25	25	584	63.31	0.710	42.96	1.839	0.689	0.679	4.549	
26-30	14	386	74.75	0.625	53.41	1.937	0.717	0.714	4.648	
31-35	14	464	99.03	0.605	74.51	2.248	0.688	0.752	5.236	
36-40	8	305	98.74	0.555	63.94	1.677	0.580	0.647	4.267	
41-45	9	378	119.78	0.423	89.25	2.125	0.581	0.745	4.977	
46-60	7	358	141.67	0.764	99.68	1.949	0.658	0.704	4.719	

Sample sizes involved are 175 inflorescences, 3312 flowers and about 12000 pollinia. Description of experiment in text; see figure 8.

TABLE 10. REGRESSION ANALYSIS OF EXPERIMENT 7

dependent variable	independent variable	coefficient	s.e.	<i>t</i>	<i>p</i>	<i>r</i> ²
REM	FLO	+0.0527	0.0276	1.92	0.057	0.02
INS	FLO	+0.137	0.0484	2.82	0.005	0.05
FIL	FLO	+0.0839	0.0388	2.16	0.032	0.03
FLX	FLO	+0.0714	0.0293	2.43	0.016	0.04
REM	FLO	+0.0485	0.0258	1.88	0.062	0.17
	NEI	-0.0093	0.0244	0.38	0.70	
	NRM	+0.0320	0.0723	4.43	0.0001	
	POS	-0.0445	0.0210	2.12	0.036	
	EXP	-0.0376	0.0232	1.62	0.11	
INS	FLO	+0.135	0.0469	2.87	0.0046	0.13
	NEI	+0.0581	0.0445	1.31	0.19	
	NRM	+0.314	0.132	2.39	0.018	
	POS	-0.0747	0.038	1.95	0.053	
	EXP	-0.0585	0.042	1.39	0.017	
FIL	FLO	+0.0863	0.0388	2.22	0.028	0.06
	NEI	+0.0673	0.0368	1.83	0.069	
	NRM	-0.0059	0.109	0.05	0.96	
	POS	-0.0302	0.0317	0.95	0.34	
	EXP	-0.0209	0.0349	0.60	0.55	
FLX	FLO	+0.0677	0.0274	2.47	0.0145	0.19
	NEI	+0.0132	0.0259	0.51	0.61	
	NRM	+0.312	0.0767	4.07	0.001	
	POS	-0.0520	0.0223	2.33	0.021	
	EXP	-0.0476	0.0246	1.93	0.055	

Variables are: REM, number of pollinia removed per flower; INS, number of pollinia inserted per flower; FIL, number of pollinia inserted per flower divided by number of spaces available; FLX, sum of removals and insertions per flower; NEI, number of flowers borne by neighbouring inflorescence on same stem; NRM, pollinia removed per flower on neighbouring inflorescence; POS, position of inflorescence on stem (0, upper; 1, lower); EXP, exposure between removal of bag and collection of inflorescence (0, 2 days; 1, 3 days). All values are logarithms resulting in exclusion of zeros; sample size for all regressions is 161 inflorescences.

Multiple regression shows that the effect of the number of flowers in the target inflorescence retains the same sign and about the same magnitude and level of significance when these other factors are included. Flowers lower on the stem tend to be visited somewhat more frequently, but neither the duration of exposure nor the number of flowers in the neighbouring inflorescence had any consistently significant effect. The number of pollinia removed per flower from the neighbouring inflorescence, however, was strongly correlated with the number removed from the target inflorescence, and rather less strongly with the number received. Even with all five factors in the regression model, the proportion of variation in pollinium flux explained was no greater than 20%.

In conclusion, the flux of pollinia into and out of flowers is due in large part to unexplained variation, is affected fairly strongly by very local differences in pollinator activity, and is weakly (though significantly) related to the number of flowers in the inflorescence and the position of the inflorescence on the stem.

These results should be compared with the less extensive data obtained from

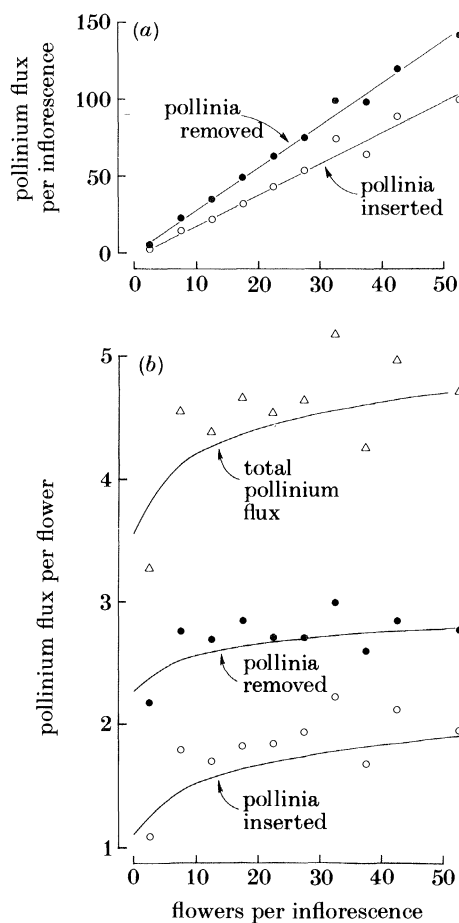


FIGURE 7. Import and export of pollinia from inflorescences of different sizes in *Asclepias*. (a) Pollinium flux per inflorescence as a function of inflorescence size. Regressions fitted to plotted means (see table 9) are:

$$\text{pollinia removed: } y = -0.14 + 2.73x \quad (r^2 = 0.99);$$

$$\text{pollinia inserted: } y = -2.42 + 2.00x \quad (r^2 = 0.97).$$

(b) Pollinium flux per flower as a function of inflorescence size. Fitted curves are log-log regressions on individual observations (not plotted means) and exclude zeros; including zeros would steepen the curves somewhat, since all zeros are from small inflorescences. For regression equations, see table 10.

similar experiments with milkweeds by Willson & Rathke (1974). They also found that very small inflorescences (consisting of a single flower) exported few pollinia per flower, and observed a similar but much weaker effect for inflorescences of up to 20 flowers.

5. THE EFFECT OF NEIGHBOURS

This section represents a short but necessary deviation from the main argument. The object of the experiments and observations I have described above has been to show how floral function is affected by the material allocation made to a

particular flower or inflorescence. This approach is sufficient only for plants that bear a single flower and grow alone. In any other circumstances, the reproductive return on any given quantity of floral investment will depend to some extent on two other factors: first, on whether all the material available is invested in a single flower, or partitioned between a number of separate flowers; and secondly, on the effect of the allocation made by neighbouring plants on the performance of flowers borne by some given target plant. The first problem points to the desirability of an optimization theory of the inflorescence; the second to the possibility of an evolutionarily stable strategy theory of floral function in which plants growing in stands might better spend less on flowers than plants growing alone. Neither theory exists except in the most rudimentary form at present. The results described below are an attempt to demonstrate such social effects in the species I have studied. They are organized according to the level of comparison: between flowers within the same inflorescence, between flowers (or inflorescences) on the same plant, and between flowers on different plants.

Flowers in the same inflorescence

Experiments 2, 4 and 7 show how the size (flower number) of the inflorescence of *Asclepias* affects its performance. They show that an intimate association with other flowers raises the number of visits received, the number of pollinia removed and received, and the probability of fruit production by a given target flower, though the number of seeds set in the fruit, if one is formed, is unaffected. We can use the results of exp. 4b and exp. 7 to calculate the total rate of return on unit floral investment yielded by inflorescences of different size.

The empirical basis of the calculation is that performance per flower and the number of flowers per inflorescence are logarithmically related:

(i) seeds set per flower: $\lg S = a_0 + a \lg n$;

(ii) pollinia removed per flower: $\lg R = b_0 + b \lg n$,

where n is the number of flowers per inflorescence. Our problem is to optimize n , given values for a_0 and a (from exp. 4b), and b_0 and b (from exp. 7). Let \bar{n} be the mean value of n for the population; then we can define the mean performances

$$\lg \bar{S} = a_0 + a \lg \bar{n}, \quad \lg \bar{R} = b_0 + b \lg \bar{n}.$$

Since the mean seed set per flower is \bar{S} , the mean number of ovules successfully fertilized by each pollinium removed is \bar{S}/\bar{R} , and the mean number of seeds descending from pollinia removed from any given flower is $R(\bar{S}/\bar{R})$. Total reproductive success per flower is thus

$$E = S + R(\bar{S}/\bar{R}).$$

Now suppose that each flower costs F units of resource to make, while the inflorescence as a whole has a fixed overhead cost (for example, for the peduncle, common to all flowers in the inflorescence) of C , irrespective of n . Then the reproductive output per unit allocation of an inflorescence with n flowers is

$$w = nE/(nF + C).$$

The optimal value of n is that that maximizes w . To find this value, which I shall call \hat{n} , we differentiate w with respect to n , set the result equal to zero, substitute

$n = \bar{n}$, and solve for \hat{n} . To check that w is maximized rather than minimized, ascertain the sign of the second derivative evaluated at $n = \hat{n}$. These procedures show that

$$\hat{n} = -(C/F)(1 + 2/(a+b))$$

and

$$\frac{d^2w}{dn^2} \Big|_{n=\hat{n}} = \frac{4C^2}{(a+b)} \left[1 + \frac{a^2+b^2}{a+b} \right].$$

From the upper sentence, it is clear that $n > 0$ requires $0 > (a+b) > -2$. Hence for $d^2w/dn^2 < 0$ we need $1 + (a^2+b^2)/(a+b) > 0$, or $a(a+1) + b(b+1) < 0$. This quadratic has real solutions in $X > a, b > Y$, where $X = -(4 - \sqrt{32})/8$ and $Y = -(4 + \sqrt{32})/8$, or roughly $X = 0.207$ and $Y = -1.207$.

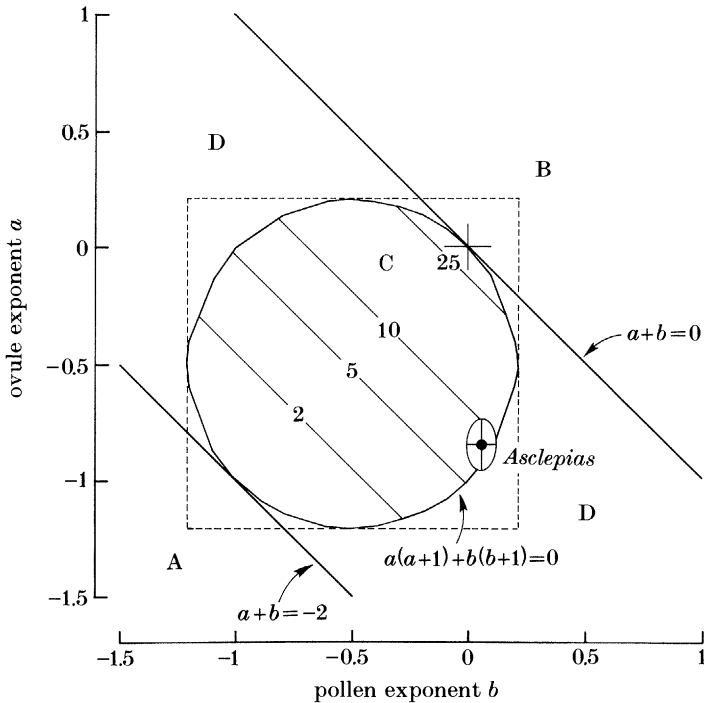


FIGURE 8. A quantitative theory of the inflorescence. See text for explanation; the different zones indicated are: A, directional selection for solitary flowers; B, directional selection for many-flowered inflorescences; C, stabilizing selection for inflorescences of moderate size; the contours indicated are for optimal numbers of flowers per inflorescence; D, disruptive selection, either for solitary flowers or for many-flowered inflorescences. Note that the observed result for *Asclepias* is shown in the figure, with an ellipse at ± 2 standard errors of the exponents a and b .

These algebraic results are shown geometrically in figure 8. They can be used to divide the (a, b) plane into four regions:

- (i) a lower region in which $a + b < -2$. Here, w always decreases with n and selection will favour solitary flowers;
- (ii) an upper region in which $a + b > 0$. Here, w always increases with n , and selection will favour inflorescences with very many flowers;

(iii) a central region, ellipsoidal in shape, which approximates a circle of unit diameter with its centre at $a = b = -0.5$. It is in this region that inflorescences of intermediate size are optimal, and will be maintained by stabilizing selection. Within this region the optimal value of n will be set by the value of C/F . The locus of points (a, b) that produce the same optimal value of n is a straight line with slope -1 .

(iv) In the remaining space, to either side of this central region, $d^2w/dn^2 > 0$ and n therefore defines the inflorescence whose w is minimal. In this region selection will be disruptive, and will cause the evolution of one of the two extreme phenotypes, solitary flowers or many-flowered inflorescences, depending on the initial state of the population.

In the zone separating the central region of stabilizing selection from the peripheral regions of disruptive selection, numerical studies indicate that more complex behaviour is possible, with both local maxima and local minima of w , but this complication seems unlikely to be of much empirical interest and will not be considered further here.

From the experimental work, we have the estimates $a = -0.854$ (exp. 4*b*) and $b = +0.053$ (exp. 7). *Asclepias* is therefore located in the central region of stabilizing selection. To calculate the expected number of flowers per inflorescence, 56 flowers from eight inflorescences were collected, oven-dried and weighed. The mean dry masses of different structures were: flower 11.3 mg, pedicel 5.1 mg and peduncle 86.9 mg, leading to estimates of $F = 11.3 + 5.1 = 16.4$ and $C = 86.9$. This suggests that $\hat{n} = 7.9$, from the expression given above. The observed mean value is $\bar{n} = 49.8$ (s.d., 14; $N = 119$; from material for exp. 4*b*). There is therefore no doubt that prediction and observation are quantitatively different. However, the confidence ellipse defined by ± 2 s.e. from the estimate of a, b projects into the region of disruptive selection, in which the evolution of a many-flowered inflorescence is unsurprising. A rigorous test of the hypothesis requires the regression of observed on predicted values of n for a series of species or populations, all of which fall unequivocally within the central region of stabilizing selection. The hypothesis would then be qualitatively falsified if the correlation coefficient were not positive and significant, and quantitatively falsified unless the regression coefficient did not differ significantly from $+1$.

Until such a test is performed, the value of the theory lies in its capacity to organize information from experiments such as those performed with *Asclepias* by showing how it relates to a general quantitative account of inflorescence design. This account also leads to comparative predictions, which organize information about inflorescence structure in widely different plants. The chief predictions that seem to follow straightforwardly from the expression for \hat{n} are as follows:

- (i) the overhead cost C often represents the cost of a common supporting structure, the peduncle; then sessile flowers with $C \approx 0$ should be solitary;
- (ii) larger flowers (large F) should be in smaller inflorescences (small n);
- (iii) in wind-pollinated species, it seems unlikely that either male or female success per unit allocation is a function of the total allocation to a flower, since the flowers have no attractive function. Such flowers will have $a = b = 0$ and thus \hat{n} large, and should be organized into many-flowered inflorescences such as catkins or cones. A more extensive comparative account will be given elsewhere.

Finally, this theory of the inflorescence can be translated directly into a quantitative theory of the flower by using corolla size (in units of mass) in the place of inflorescence size (in units of flower numbers). Such a theory has the same geometry as figure 9, with selection favouring very small flowers, very large flowers, or flowers of some intermediate size according to the way in which male and female success per unit allocation vary with total allocation to the corolla.

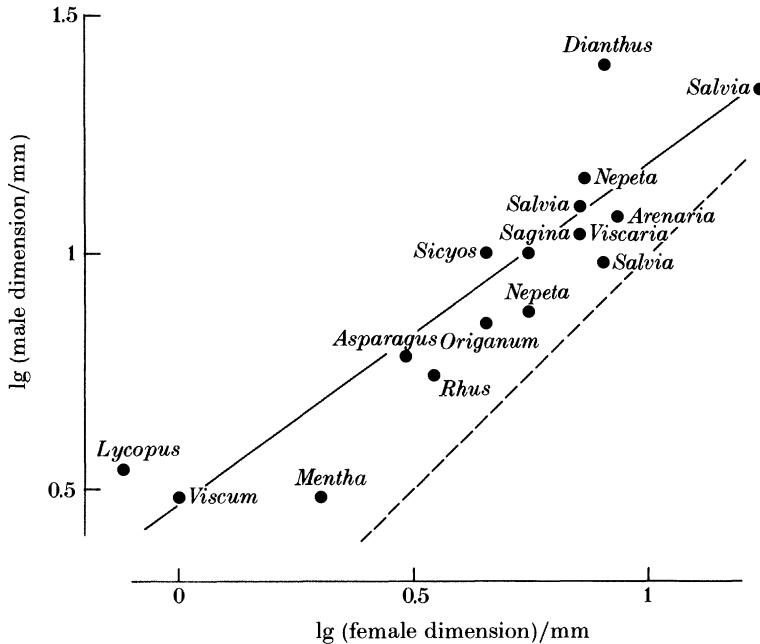


FIGURE 9. Linear measurements of male and female flowers in dimorphic herbs. Plotted points are midpoint of range of greatest linear dimension, in millimetres. Both axes are logarithmic. Solid line is regression of data; broken line is line of equality. Regression equation is:

$$y = 0.46 + 0.71x \quad (r^2 = 0.81, p < 0.001).$$

Source is Knuth (1906), who gives relative but not absolute measurements for three other herbs: *Calamintha alpina* (male is $1.3 \times$ female), *Bryonia dioica* (male is $2 \times$ female) and *Urtica urens* (male is $4 \times$ female). Including these three species, the mean value of the ratio of male length to female length is 2.06 (s.d., 0.96, $N = 16$).

Flowers or inflorescences on the same plant

The milkweed experiments can be analysed further to investigate the effect of neighbouring inflorescences on one another. Any such effect seems to be very small. The multiple regression analysis described in table 10 shows that the null hypothesis of no effect cannot be rejected at the $p = 0.05$ level for any of the pollinium export or import variables measured, though there is some evidence (at $p = 0.07$) for a positive effect of the number of flowers in a neighbouring inflorescence on the fraction of vacated sites into which pollinia were inserted in the target inflorescence. A similar multiple regression analysis was performed for exp. 4*b*; it was found that the size of the neighbouring inflorescence had no effect

(at $p = 0.50$) on the seeds per pod, the total seeds set or the number of pods on the target inflorescence. I conclude that the two inflorescences on each stem in these experiments were independent with respect to reproductive success.

Flowers on the same or on different plants in the same site

When the relation between petal mass and the rate of insect visits was studied in *Fragaria* (obs. 1), the number of flowers within a 5 cm radius of each target flower was measured at the same time. Since *Fragaria* has extensive vegetative propagation, some of these flowers would be borne by the same stock. Petal mass and the number of neighbours were found to be uncorrelated, so we can use these data straightforwardly to test the hypothesis that flowers with more neighbours are visited more often. The observations are summarized in table 11. They show that there is no effect of local flower density on the rate of visits to target flowers.

TABLE 11. VISITS TO TARGET FLOWERS AS A FUNCTION OF THE NUMBER OF NEIGHBOURS IN *FRAGARIA*

number of neighbours	visits				total observations	total visits	visits per 2 min mean \pm s.e.
	0	1	2	3			
0	40	17	2	0	59	21	0.356 \pm 0.072
1	74	24	2	0	100	28	0.280 \pm 0.049
2	58	19	7	1	85	36	0.424 \pm 0.076
3	52	21	2	0	75	25	0.333 \pm 0.061
4	36	17	4	0	57	25	0.439 \pm 0.083
5	24	17	3	0	44	23	0.523 \pm 0.095
6	22	4	4	0	30	12	0.400 \pm 0.132
7	17	6	1	1	25	11	0.440 \pm 0.154
8-9	14	7	1	0	22	9	0.409 \pm 0.126
10+	11	5	1	0	17	7	0.412 \pm 0.150
pooled	348	137	27	2	514	207	0.4027 \pm 0.027

Data obtained during obs. 1. The regression equation relating number of visits per 2 min observation to the number of neighbouring flowers is $y = 0.365 + 0.0076x$ ($r^2 = 0.176$, $p > 0.10$).

Exp. 8: Fragaria

This observation was then checked by experiment. A 2 m \times 2 m square was laid out with thin cord in the middle of a large patch of strawberry flowers, and a grid then constructed at 50 cm intervals within the square. All flowers were then removed from the grid and for a strip 50 cm wide on all sides. In the centre of each 50 cm \times 50 cm area within the grid a small glass jar filled with water was buried in the soil. Strawberry flowers were picked and placed in these jars, strawberry leaves being used to cover and conceal the jars themselves. One, two, four or eight flowers were put in each jar, in a pattern such that the total number of flowers in any 1 m \times 1 m square within the grid was 15; thus, reading the rows of jars successively, they contained (1, 2, 1, 2)-(4, 8, 4, 8)-(2, 1, 2, 1)-(8, 4, 8, 4) flowers each. Four observers watched the grid simultaneously for a total of 1 h, each sitting at a different corner, changing positions at 15 min intervals, and counting all insect visits within their sector of four grid squares. This was repeated four times between

11h00 and 16h00 on 9 June 1983, a warm sunny day with plentiful insect activity; the flowers were changed for each of these sessions. During this time over 3000 insect visits were recorded, and the way in which they were distributed between the jars is given in table 12. The distribution is highly non-random, but the only large contribution to χ^2 is made by an excess of visits to jars containing solitary flowers. The hypothesis that high local densities result in a greater rate of visits per flower is therefore falsified in this case.

TABLE 12. NUMBER OF VISITS AS A FUNCTION OF LOCAL FLOWER DENSITY IN *FRAGARIA* (EXPERIMENT 8)

flowers per jar	visits in session				total visits	exp. visits	$(O-E)^2/E$	visits per flower
	1	2	3	4				
1	37	78	84	59	258	204.1	14.23	258.0
2	80	109	128	94	411	408.1	0.02	205.5
4	166	229	202	182	779	816.3	1.70	194.8
8	279	422	505	407	1613	1632.5	0.23	204.1
total	562	838	919	742	3061	3061.0	16.18	204.1

Expected values in seventh column are calculated from the hypothesis that the number of visits per flowers is independent of the number of flowers per jar. The overall χ^2 of 16.2 is highly significant ($p < 0.001$), but the table shows that this effect is wholly due to an excess of visits to solitary flowers. Note that the overall mean number of visits per flowers per 2 min of observation is $3061/7200 = 0.424$, which is very similar to that experienced in obs. 1 (see table 11).

Exp. 9: Impatiens

In 1981 two similar experiments were performed with *Impatiens*. In the first experiment (exp. 9a), plants were carefully uprooted and placed immediately in 500 ml plastic beakers filled with water. They were then placed within a 6 m × 6 m square gridded at 1 m intervals, in groups of one, two, three or four plants so that each 2 m × 2 m square within the grid contained a total of ten plants. Observations were made by three people simultaneously, each of whom watched a plant or group of plants within the grid for 30 s before changing position, so that after 18 min the entire grid had been surveyed by each of the three observers. This was repeated five times. The second experiment (exp. 9b) was identical in design, except that the numbers of plants in each grid position were one, four, nine or 16, laid out so that each 2 m × 2 m square within the grid contained 30 plants. After each set of observations was completed, the flowers on each plant were counted.

The results of these two experiments, analysed according to the number of plants, are given in table 13. They are strikingly similar to the *Fragaria* results: the distribution of visits is again non-random, with the only large contribution to χ^2 being made by an excess of visits to flowers on solitary plants. Since the number of flowers varied between plants, the data were re-analysed according to the actual number of flowers at each grid position. This gave, for each experiment, a regression of visits per flower on the number of flowers, with 36 observations; it

TABLE 13. NUMBER OF VISITS AS A FUNCTION OF LOCAL PLANT AND FLOWER DENSITY IN *IMPATIENS* (EXPERIMENT 9)

plants per cup	sample size	total flowers	total visits	exp. visits	$(O-E)^2/E$	visits per flower
			exp. 9a			
1	9	101	68	48.5	7.84	0.673
2	9	213	99	102.3	0.11	0.465
3	9	325	155	156.1	0.01	0.477
4	9	300	129	144.1	1.58	0.430
total	36	939	451	451.0	9.54	9.480
			exp. 9b			
1	9	51	50	27.3	18.88	0.980
4	9	312	183	166.7	1.59	0.587
9	9	679	283	362.9	17.59	0.417
16	9	1048	601	560.1	2.99	0.534
total	36	2090	1117	1117.0	41.05	0.534

Compare table 12.

was necessary to remove the maximum and minimum values of y (visits per flower) to stabilize the variance satisfactorily. These regressions are:

$$\text{exp. 9a: } \lg y = -0.15 - 0.17 \lg x \quad (r^2 = 0.025, p > 0.10);$$

$$\text{exp. 9b: } \lg y = -0.04 - 0.17 \lg x \quad (r^2 = 0.113, p \approx 0.05).$$

The two experiments thus gave very similar results, and showed that if there is any trend in the data it is towards a lower rate of visits per flower at higher local flower densities.

6. THE SEX AND SIZE OF FLOWERS

Male flowers are larger than female flowers. This generalization was known to Knuth (1906), whose data are abstracted in table 14. More quantitative observations are very scarce. In a few cases Knuth gives rough linear dimensions for male and female flowers, and I have summarized these measurements in figure 9. To complement Knuth's survey I have given some original dry mass measurements in figure 10. These are especially interesting because they show that male flowers are nearly twice as large as female flowers in insect-pollinated plants, while there is no difference in wind-pollinated species; *Acer pennsylvanicum*, which is pollinated both by insects and by the wind, occupies an intermediate position.

More complete information for a single gynodioecious species, *Fragaria virginianicum*, is given in figure 11. The frequency distributions of petal mass for the female and the perfect flowers are clearly separate, the females being only half as large as the perfect flowers, positively skewed and highly leptokurtic. It might be argued that the perfect flowers are larger only because they have to accommodate both sets of sexual organs, the petal mass per unit reproductive structure remaining constant. Figure 12 shows that this is not the case. Larger female flowers do indeed bear more stigmata, but stamen number and petal mass vary independently in the perfect flowers. Larger perfect flowers are therefore investing relatively as well as absolutely more material in attractive tissue.

TABLE 14. SEXUAL DIMORPHISM IN FLOWER SIZE IN THE EUROPEAN FLORA

comparison	breeding system	number of species		<i>p</i>
		<i>M</i> > <i>F</i>	<i>F</i> > <i>M</i>	
1. <i>F</i> with <i>H</i>	gynomonoecy	3	0	> 0.10
	gynomonoecy and gynodioecy	21	1	< 0.001
	gynodioecy	28	0	< 0.001
	total	62	1	< 0.001
2. <i>M</i> with <i>H</i>	andromonoecy	0	1	> 0.10
	andromonoecy and androdioecy	0	2	> 0.10
	total	0	3	> 0.10
3. <i>M</i> with <i>F</i>	monoecy	5	0	0.03
	dioecy	11	1	0.003
	total	16	1	< 0.001
4. <i>M</i> with <i>H</i> or with <i>F</i>	various mixed systems	6	0	0.016
	grand total	74	5	< 0.001

The third column records the number of species in which the male-biased morph (a male or an hermaphrodite, according to the breeding system) has larger flowers than the female-biased morph; the fourth column records the number of species in which the reverse is true. The probabilities cited in the final column refer to χ^2 or exact tests of the null hypothesis that males will exceed females in one half of all cases. Source is Knuth (1906); cf. Baker (1948). Omitted from the table are the generally gynodioecious *Dianthus caesius* and *Cerastium semidecandrum* (Caryophyllaceae), in which male and female flowers are about equal in size.

In plants whose flowers are grouped into inflorescences, the male inflorescence generally bears more flowers than the female. Again, quantitative data are difficult to find, but figure 13*b*, presents some estimates for New Zealand herbs from Lloyd & Webb (1977). The frequency distributions of male and female inflorescence masses in sumac (*Rhus typhina*) are shown in figure 14. They are strikingly similar to the strawberry data of figure 11, with flower or inflorescence mass recorded irrespective of sex being strongly skewed towards low values, while sorting the data by sex shows two distributions, the males exceeding the females by a factor of about two. A similar histogram is given by Barrett & Helenurm (1981, figure 1) for *Aralia nudicaulis*, whose female inflorescences bear about 75 flowers while the males bear about 125 flowers. Male plants also seem generally to bear more inflorescences than do female plants, though this is not invariably the case (figure 13*a*). Finally, male plants usually flower more frequently than female plants (Lloyd & Webb 1977); in a recent study, Meagher & Antonovics (1982) found that male plants of the dioecious lily *Chamaelirium luteum* flowered about three times as frequently as females.

The total quantity of structural material allocated to flowers by a plant will be the product of flower mass, the number of flowers per inflorescence and the number of inflorescences per plant. A rough estimate of the difference between male and female plants can therefore be obtained by summing the intercepts of the logarithmic regressions of figures 10, 13*a*, *b*, since they all have slopes close to unity. This yields $(0.25 + 0.50 + 0.11) = 0.86$, suggesting that male plants allocate 7.2

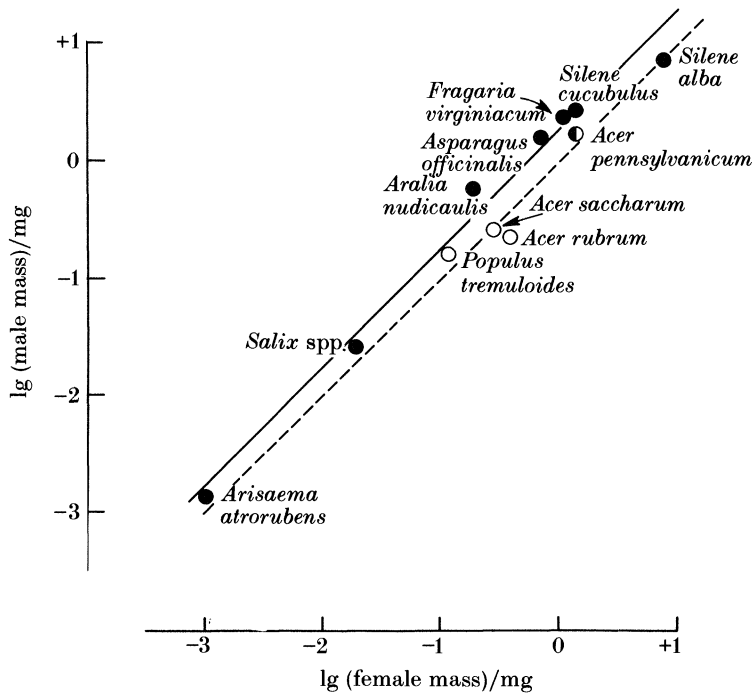


FIGURE 10. Dry masses of the secondary structures of male and female flowers in some temperate herbs and trees. ●, Insect-pollinated plants; ○, wind-pollinated trees; *Acer pennsylvanicum* (◐) is partly insect-pollinated and partly wind-pollinated. Both axes are logarithmic, and units of dry mass are milligrams. Solid line is regression of data for insect-pollinated species; regression equation is

$$y = 0.25 + 1.01x \quad (r^2 = 0.98, p < 0.001).$$

There are too few wind-pollinated species to analyse separately, but they appear to fall along the line of equality; two wind-pollinated plants (*Myrica gale* and *Thalictrum dioicum*) have essentially no secondary structures in either sex and do not appear in the figure. The elevation of the insect-pollinated data is probably biased downwards because of the inclusion of *Silene alba*, the only known temperate dioecious herb in which the female flowers exceed the male (see table 14). The value of secondary allocation per flower for *Arisaema atrorubens* was obtained by dividing the dry mass of the spathe by the number of flowers borne by the spadix. Original data, collected at Mont St Hilaire; this includes all the dimorphic species from a much larger data set on floral allocation that will be published separately.

times as much material to flowers as do females. Another way of expressing this statistic is to say that in a sexually dimorphic population with an equal sex ratio the male plants contribute about 88% of flower production.

It seems likely that the disparity in flower size established for dimorphic plants applies also to monoecious species (see table 14), and it is natural to ask whether the argument can be extended further to material allocation within perfect flowers. Table 15 summarizes allocation data for nine hermaphroditic herbs from papers by Lovett Doust (Lovett Doust & Harper 1980; Lovett Doust & Cavers 1982). The allocation ratio (as male:total) is about 50% if it is calculated for primary structures alone, or if secondary structures are shared equally between male and

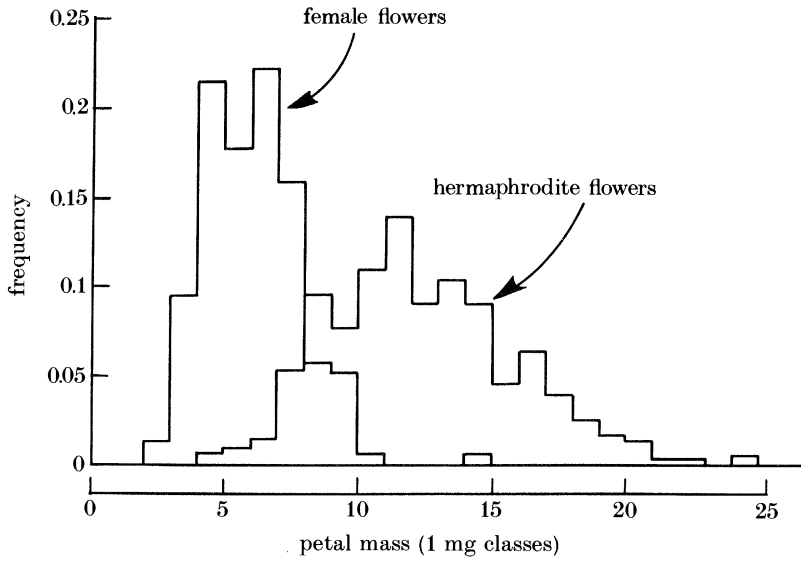


FIGURE 11. Frequency distributions of wet mass of petals in female and perfect flowers of *Fragaria virginiana*. These flowers are the same as those analysed for the rate of insect visits in figure 2. Moments of the distributions are as follows.

	female	hermaphrodite
mean	6.06	12.45
s.d.	1.80	3.49
skewness	0.81	0.50
kurtosis	4.92	3.16
<i>N</i>	158	357

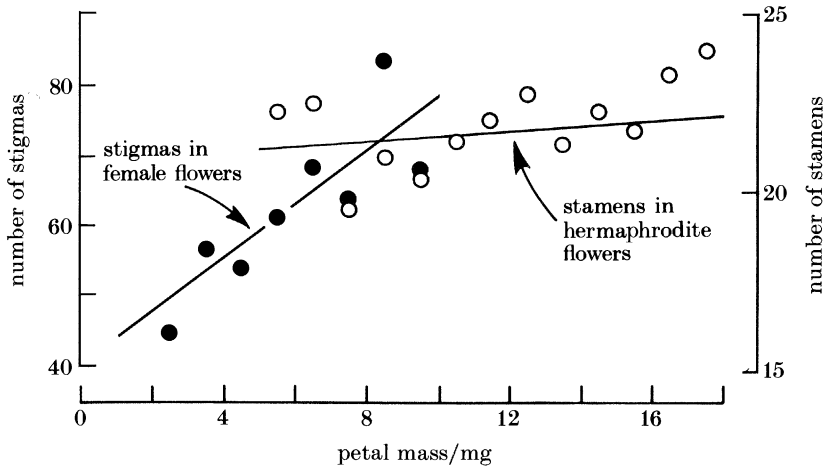


FIGURE 12. Allometry of reproductive structures in *Fragaria*. Plotted points are means at 1 mg intervals of petal mass; these are purely for illustration, the regressions being calculated from individual values. Regression equations are: (i) number of stigmas in female flowers: $y = 40.2 + 3.82x$, $N = 87$, $r^2 = 0.228$ ($p < 0.001$). (ii) number of stamens in hermaphrodite flowers: $y = 20.8 + 0.08x$, $N = 84$, $r^2 = 0.011$ ($p > 0.10$).

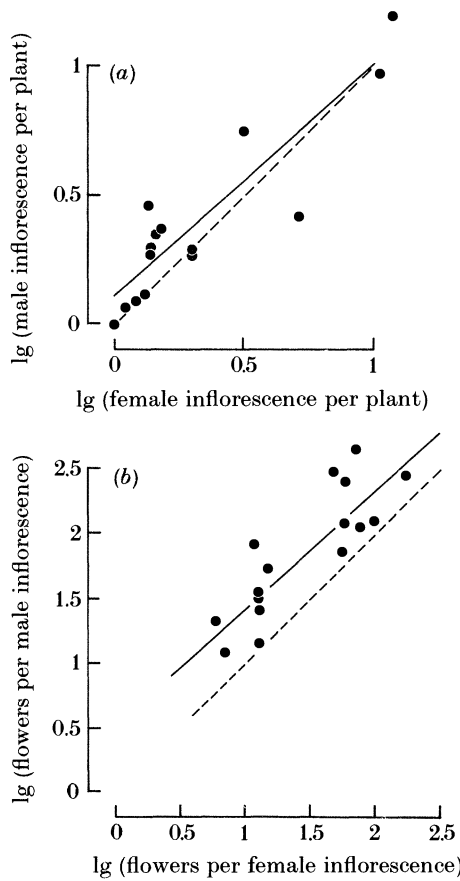


FIGURE 13. Inflorescences of dimorphic Umbelliferae. (a) inflorescences per plant; (b) flowers per inflorescence. Regression equations are:

$$(a) y = 0.11 + 0.88x \quad (r^2 = 0.80)$$

$$(b) y = 0.50 + 0.92x \quad (r^2 = 0.76).$$

For (b) a regression on arithmetic axes gives a slightly better fit ($r^2 = 0.87$). At mean x for the two data sets, male plants bear 2.42 times as many flowers per inflorescence and 1.18 times as many inflorescences per plant. Source: Lloyd & Webb (1977; table IV).

female function. However, it is over 80% if the secondary structures are assumed to be purely male in function. While they cannot be conclusive, these data suggest that the interpretation of the secondary structures of perfect flowers as being primarily male is quantitatively consistent with the greater investment in flowers made by male individuals of dimorphic species.

The greater floral investment made by males is functionally intelligible only if it procures more insect visits. Unfortunately, information about rates of visit is even scarcer than allocation data. Knuth reports that the larger male flowers are visited earlier than the smaller female flowers of *Bryonia dioica*, *Sicyos angulata*, *Valeriana dioica*, *Ribes alpinum*, *Asparagus officinalis*, *Salix* spp., and perhaps also *Mentha arvensis*, with no cases being given to the contrary. He also makes the

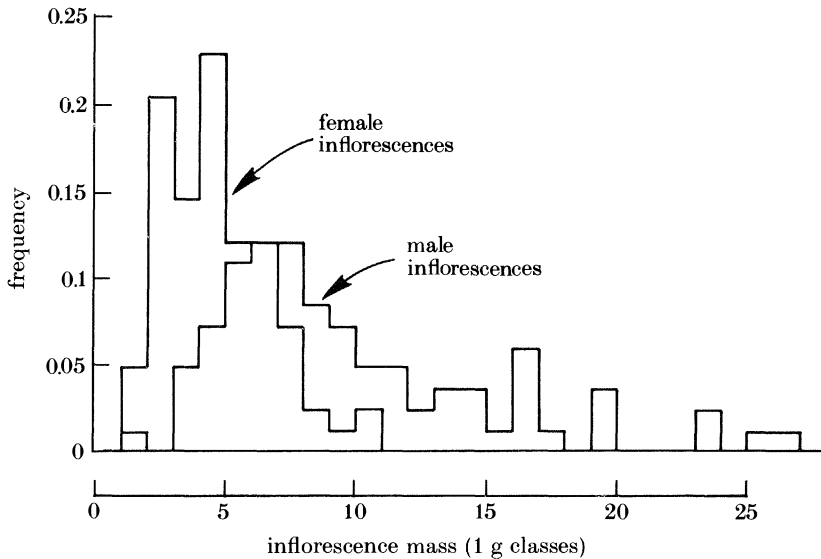


FIGURE 14. Frequency distribution of wet mass of flowers borne on male and female inflorescences of sumac, *Rhus typhina*. Original data, collected at Mont St Hilaire. Measurements were paired, with one inflorescence being taken at random and the nearest inflorescence of opposite sex then being collected. An attempt was made to sample any plant (clone) once only. The regression of the paired data, with x as female mass and y as male mass, is

$$y = 9.65 + 0.06x \quad (r^2 = 0.001),$$

showing that males were substantially larger, with no correlation between inflorescence size and location. Moments of the distributions are as follows.

	male	female
mean	9.90 g	4.68 g
s.d.	5.35	2.04
skewness	1.16	0.70
kurtosis	3.92	3.16
N	83	83

interesting observation that male and female flowers may be visited, not only by different numbers, but also by different types of pollinators. In the gynomonocious *Nepeta glaucoma* the female flowers are visited by short-tongued bees such as *Apis* and *Nomada* while the hermaphroditic flowers are visited by the longer-tongued *Bombus*; honeybees visit only the male stocks of *Viscum album*, while flies visit both male and female stocks.

In *Fragaria virginiana*, my observation (obs. 1) show that female flowers received on average 0.272 visits per 2 min of observation (43 visits to 158 flowers), while the corresponding rate for perfect flowers was 0.426 (152 visits to 357 flowers); these data have $\chi_1^2 = 6.58$, $p < 0.01$.

The most remarkable instance of a discrimination by insects between male and female flowers is that described by Bell *et al.* (1985) for *Impatiens capensis*. Since the flowers borne by *Impatiens*, though protandrous, are perfect, the material allocation to male and female corollas is necessarily the same, since they are

TABLE 15. ESTIMATES OF SEX ALLOCATION IN PERFECT FLOWERS

	allocation per flower			est. male allocation			
	<i>M</i> (male structures)	<i>F</i> (female structures)	<i>A</i> (attracting structures)	(i)	(ii)	(iii)	
1. <i>Lilium superbum</i>	0.373	0.062	0.543	0.857	0.645	0.916	
2. <i>Lilium candidum</i>	0.214	0.068	0.626	0.759	0.527	0.840	
3. <i>Trillium grandiflorum</i>	0.242	0.104	0.655	0.699	0.570	0.895	
4. <i>Erythronium albidum</i>	0.375	0.187	0.438	0.667	0.594	0.813	
5. <i>Podophyllum peltatum</i>	0.302	0.204	0.467	0.597	0.536	0.769	
6. <i>Hibiscus trionum</i>	0.105	0.159	0.574	0.398	0.392	0.679	
7. <i>Amaryllis</i> spp.	0.115	0.172	0.713	0.401	0.472	0.828	
8. <i>Nicotiana rustica</i>	0.118	0.289	0.554	0.290	0.395	0.672	
9. <i>Smyrniium olusatrum</i>	P	0.427	0.114	0.459	0.789	0.657	0.886
	N	0.423	0.104	0.473	0.803	0.660	0.896
	K	0.389	0.065	0.546	0.857	0.662	0.935
	C	0.279	0.180	0.545	0.608	0.552	0.824
mean	0.380	0.116	0.506	0.764	0.633	0.885	
grand means	0.247	0.151	0.564	0.603	0.529	0.811	
± s.d.	±0.116	±0.072	±0.089	±0.197	±0.094	±0.089	

Main source is Lovett Doust & Cavers (1982; table 2), and entries in first three columns are proportion of dry matter allocated to male, female and attractive structures. Data for *Smyrniium olusatrum* is from Lovett Doust & Harper (1980; table 2) (control series) and refers to allocation per plant, the plants being andromonoecious; it is included to show that the currency of material allocation has little effect on the conclusions. Attractive structures for this species include stylopodia. The male allocation estimates are: (i) for gametes and immediate investments, $M/(M+F)$; (ii) including attracting structures, assuming them to be equally male and female in function, $M+A/2$; (iii) including attracting structures, assuming them to be wholly male in function, $M+A$.

the same structure at different ages. Male flowers, however, contain on average about 50% more nectar than female flowers. Since the male phase lasts about four times as long as the female phase, the quantity of nectar allocated to the male phase exceeds that allocated to the female phase by a factor of about six. Bumble bees, honeybees and wasps all responded to the difference in nectar standing crop by visiting male flowers more frequently than female flowers; the bumble bees, which are the specialist pollinator of *Impatiens* in Canada, showed the strongest preference for male flowers, visiting them disproportionately often in all 22 sites at which observations were made. On average, flowers received only one or two visits during their female phase but eight or nine during their male phase.

The purpose of this brief comparative sketch is to emphasize the generality of the conclusions to be drawn from the experimental work. A more extensive

discussion has been rendered unnecessary by the recent review of sexual dimorphism in plants by Lloyd & Webb (1977), who also describe general tendencies for male plants to flower earlier in life and more frequently thereafter. I hope I have said enough to establish the general rule that the predominantly male function of secondary organs in perfect flowers is reflected by the greater size and production of flowers by male individuals in dimorphic species.

This general rule, to which there are no doubt many individual exceptions, is based on observations of temperate flowers, and it may not be valid for tropical and subtropical floras. According to Bawa & Opler (1980) male flowers are smaller than female flowers in 14 out of 20 dioecious tropical trees, and male flowers had lower rates of nectar production in 5 out of 6 of these species. (Insect visits did not correspond to nectar production: 233 out of 369 visits recorded were to male flowers.) In subtropical areas of North America, Cruden *et al.* (1983) measured nectar in nine dichogamous herbs and found more sugar in the male flowers of three species and in the female flowers of four species, with the remaining two species having about the same quantity in male and female flowers. Even in temperate areas, it is far from clear that the male flowers of dichogamous herbs generally secrete more nectar than the females; certainly the reverse is true in *Digitalis*, where the younger flowers are female, are located at the base of a crowded inflorescence, secrete more nectar than the older male flowers, and are visited first and more frequently by insects (Best & Bierzychudek 1982). The interpretation of these facts is unclear; it is certainly not the case, as suggested by Bawa & Opler (1980), that the tendency for male flowers to be larger in temperate regions is because they belong to wind-pollinated species, since the comparative data given above refers to insect-pollinated species. I would suggest instead that the rule for flowers breaks down in both temperate and tropical regions when the inflorescence, rather than the solitary flower, becomes the primary unit of attraction for insects. Rules at the level of the inflorescence should continue to hold, and indeed Bawa & Opler state that male inflorescences bear more flowers than female inflorescences in dioecious tropical trees, just as they do in dimorphic temperate herbs.

7. THE FLOWER AS A MALE ORGAN

The hypothesis around which this paper is organized states that the hermaphroditic flower is predominantly male in function. Female function (fertilization of ovules) is almost completely satisfied by a single insect visit, or a very few visits, which will be made even to very small flowers, while successful male function (dispersal of pollen) requires repeated visits, which can be procured only by substantial investment in attractive structures. Any increment in secondary allocation beyond a certain minimal value increases the fraction of pollen that is dispersed but has little or no effect on the fraction of ovules that are fertilized. The evidence bearing on this hypothesis is as follows:

(i) Larger flowers attract more insects per unit time. This was demonstrated in *Fragaria* (obs. 1) and confirmed experimentally in *Impatiens* (exp. 1). In other work with *Chrysanthemum* and *Impatiens* (obs. 2 and obs. 3) the effect was weak, and could only just be detected with the sample sizes used.

(ii) Larger flowers or inflorescences set more fruit but do not set more seeds per fruit. Thus, no effect of floral mutilation on seed set could be demonstrated in *Impatiens* (exp. 5), which has several-seeded capsules; in *Asclepias* (exp. 3 and exp. 4) a weak effect was observed but could be attributed entirely to an increased production of fruits per inflorescence and not at all to a greater number of seeds in each fruit; and, finally, a rather strong effect in *Viburnum* (exp. 6) was necessarily caused entirely by an effect on fruit set per inflorescence, since each drupe contains only a single seed. These results are entirely consistent with the hypothesis that a single insect visit suffices to fertilize all or almost all the ovules per ovary in these plants, while further visits are virtually without effect.

(iii) Larger flowers or inflorescences disperse more pollen and disperse a greater fraction of their pollen. These effects were observed both in *Impatiens* (obs. 4) and in *Asclepias* (exp. 7). In the latter, large inflorescences set 50% more seed than small inflorescences but dispersed about 50 times as much pollen. In both cases, however, the effect of flower (or inflorescence) size on the fraction of pollen dispersed was only a very weak one.

(iv) In dimorphic species, male flowers are larger than female flowers, male inflorescences contain more flowers than female inflorescences, and male plants bear more inflorescences than female plants. These generalizations conform with the proposed predominance of male function in perfect flowers, which would otherwise be difficult to interpret consistently.

The failure to demonstrate a strong effect of flower size on the fraction of pollen exported prevents me from asserting that the hypothesis is firmly established by these results. Pollen export, however, is technically difficult to measure, and the negative outcome of experiments designed to detect a more easily measurable effect of flower size on ovule fertilization must be given great weight. Since an increase in flower size procures more visits but fails to raise the fraction of ovules fertilized, expenditure on attractive structures is functionally incomprehensible unless it enhances pollen dispersal.

I conclude that the hypothesis represents the best quantitative description of floral function. The direct implication of my analysis is that flower production should be counted as male and fruit production as female function in outcrossed plants; the ratio of the two then supplies a good estimate of plant gender. More precisely, if the following dry masses are measured:

K_1 , total flower; K_2 , total fruit; P , pistils in flower;

and the abortion rate (fraction of flowers which fail to develop into fruit) is A , then plant gender is estimated by

$$(K_1 - P) / [K_1 + (1 - A)K_2].$$

This is readily measured by successive censuses in the field; if only spot measurements (or even dried herbarium material) are available then A will be unknown, but $K_1 / (K_1 + K_2)$ can still be used as a crude estimate of plant gender. In this way, the interpretation of the flower as a male organ both avoids the paradox introduced by treating it as equally male and female and provides a foundation for the quantitative testing of theories about gender in flowering plants.

What success this work enjoyed is in large part due to the spirited and skilful assistance of Daniella Denti and Cremilda Dias, who were responsible for scoring all or part of observations 1, 2 and 4 and experiments 2, 4, 6 and 7. I am very grateful to the students of the 1981 and 1982 McGill Ecology Field Courses and to several graduate students and colleagues for helping with observations 3 and 4 and experiments 1, 3, 5, 8 and 9. Without the enthusiastic cooperation of many people this work could not have been done. Martin Lechowicz, Marcia Waterway and Dan Schoen patiently explained the necessary rudiments of botany to an ignorant zoologist. Finally, I wish to thank the Board of Directors of the Gault Estate for permission to work at Mont St Hilaire. This research was supported by an Operating Grant from the Natural Science and Engineering Research Council of Canada.

REFERENCES

- Aker, C. L. 1982 Regulation of flower, fruit and seed production by a monocarpic perennial, *Yucca whipplei*. *J. Ecol.* **70**, 357–372.
- Baker, H. G. 1948 Corolla size in gynodioecious and gynomonocious species of flowering plants. *Proc. Leeds Phil. Soc.* **5**, 136–139.
- Barrett, S. C. H. & Helenurm, K. 1981 Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). *Evolution* **35**, 752–762.
- Bawa, K. S. & Opler, P. A. 1975 Dioecism in tropical forest trees. *Evolution* **29**, 167–179.
- Bell, G. 1982 *The masterpiece of Nature*. London: Croom Helm.
- Bell, G., Lefebvre, L., Giraldeau, L.-A. & Weary, D. 1985 Partial preference by insects for the male flowers of an annual herb. *Oecologia*. (In the press.)
- Best, L. S. & Bierzychudek, P. 1982 Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. *Evolution* **36**, 70–79.
- Charnov, E. L. 1980 Sex allocation and local mate competition in barnacles. *Mar. Biol. Lett.* **1**, 269–272.
- Charnov, E. L. 1982 *The theory of sex allocation*. Princeton, New Jersey: Princeton University Press.
- Cruden, R. W., Hermann, S. M. & Peterson, S. 1983 Patterns of nectar production and plant–pollinator coevolution. In *The biology of nectaries* (ed. B. Bently & T. Elias), pp. 80–126. New York: Columbia Univ. Press.
- Darwin, C. R. 1876 *Different forms of flowers on the same plant*. London: John Murray.
- Knoll, F. 1922 Insekten und Blumen. Experimentelle Arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Pflanzen und Tieren. III. Lichtsinn und Blumenbesuch des Falters von *Macroglossum stellatarum*. *Abh. Zool.-Bot. Ges. Wien* **12**, 123–377.
- Knuth, P. 1906 *Handbook of flower pollination*, 3 vols, transl. from German. Oxford: Clarendon Press.
- Kugler, H. 1943 Hummeln als Blumenbesucher. Ein Beitrag zur experimentellen Blütenökologie. *Ergebn. Biol.* **19**, 143–323.
- Lloyd, D. G. & Webb, C. J. 1977 Secondary sex characters in plants. *Bot. Rev.* **43**, 177–216.
- Lovett Doust, J. & Cavers, P. B. 1982 Biomass allocation in hermaphroditic flowers. *Can. J. Bot.* **60**, 2530–2534.
- Lovett Doust, J. & Harper, J. L. 1980 The resource costs of gender and maternal support in an andromonoecious umbellifer, *Smyrniolum olusatrum* L. *New Phytol.* **85**, 251–264.
- Maycock, P. F. 1961 Botanical studies on Mont St-Hilaire, Rouville Co. Quebec. I. General description of the area and a floristic survey. *Can. J. Bot.* **39**, 1293–1325.
- Meagher, T. R. & Antonovics, J. J. 1982 Life history variation in dioecious plant populations: a case study of *Chamaelirium lutea*. In *Evolution and genetics of life histories* (ed. H. Dingle & J. P. Hegmann), pp. 139–154. New York: Springer-Verlag.
- Mulligan, G. A. & Kevan, P. G. 1973 Color, brightness and other floral characteristics attracting insects to the blossoms of some Canadian weeds. *Can. J. Bot.* **51**, 1939–1952.

- Plateau, F. 1896 Comment les fleurs attirent les insectes – Recherches expérimentales. *Bull. Acad. R. Belg.* **32**, 505–534.
- Salisbury, E. J. 1942 *The reproductive capacity of plants*. London: Bell.
- Schaffer, W. M. & Schaffer, M. V. 1977 The adaptive significance of variation in reproductive habit in the Agavaceae. In *Evolutionary ecology* (ed. B. Stonehouse & C. Perrins), pp. 261–276. College Park, Maryland: University Park Press.
- Werren, J. H. 1980 Sex ratio adaptations to local mate competition in a parasitic wasp. *Science, Wash.* **208**, 1157–1159.
- Willson, M. F. & Burley, N. 1983 *Mate choice in plants*. Princeton, New Jersey: Princeton University Press.
- Willson, M. F. & Price, P. W. 1977 The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* **31**, 495–511.
- Willson, M. F. & Rathke, B. J. 1974 Adaptive design of the floral display in *Asclepias syriaca* L. *Am. Midl. Nat.* **92**, 47–57.

PROCEEDINGS OF
THE ROYAL SOCIETY
OF LONDON

B. BIOLOGICAL SCIENCES

ISSN 0080-4649

Volume 224 Pages 131–265 Number 1235

22 April 1985

PUBLISHED BY THE ROYAL SOCIETY
6 CARLTON HOUSE TERRACE LONDON SW1Y 5AG

PROCEEDINGS AND PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY

Notice to contributors

The Royal Society welcomes suitable communications for publication in its scientific journals: papers estimated to occupy up to 24 printed pages are considered for the *Proceedings* and longer papers and those with numerous or large illustrations for the *Philosophical Transactions*.

Detailed advice on the preparation of papers to be submitted to the Society is given in a leaflet available from the Executive Secretary, The Royal Society, 6 Carlton House Terrace, London SW1Y 5AG. The 'Instructions to authors' are also printed in every fifth volume of the *Proceedings* A and B (volume numbers ending in 0 or 5). The basic requirements are: a paper should be as concise as its scientific content allows and grammatically correct; standard nomenclature, units and symbols should be used; the text (including the abstract, the list of references and figure descriptions) should be in double spaced typing on one side of the paper. A leaflet giving detailed advice on the preparation of illustrations is available from the Executive Secretary; diagrams should be expertly drawn at about twice the proposed final size, preferably with lettering in the correct style but if this is not possible the lettering should be inserted not on the original drawings but on a set of copies; where photographs are essential the layout should be designed to give the most effective presentation.

The initial submission of a paper must be through a Fellow or Foreign Member of the Society, but subsequent correspondence will be conducted direct with the author. The latest lists of Fellows and Foreign Members are to be found in the current edition of the *Year Book of the Royal Society*. A copy of 'Notes for the guidance of Fellows communicating papers' is available from the Executive Secretary. In the event of any difficulty, an author is invited to seek the assistance of the Executive Secretary.

No page charge is levied, and the first 50 offprints of a paper are supplied to the author gratis.

The Editors particularly welcome short communications to *Proceedings*; as far as possible they will be given expeditious treatment both in consideration and in printing, and this will be facilitated if a paper is submitted with a firm recommendation by a Fellow.

Associate Editors: series B, Biological Sciences

(For Standing Orders see current Year Book.)

Professor P. Allen	Sir Cyril Clarke	Professor D. Noble
Dr W. F. Bodmer	Professor J. P. Cooper	Professor J. G. Phillips
Dr Q. Bone	Dr K. Dalziel	Professor D. J. Weatherall
Professor F. W. Campbell	Dr L. L. Iversen	

Copyright

© 1985 The Royal Society and the authors of individual papers.

It is the policy of the Royal Society not to charge any royalty for the production of a single copy of any one article made for private study or research. Requests for the copying or reprinting of any article for any other purpose should be sent to the Royal Society.

Notes and Records

This journal was first published in 1938 as a house journal for Fellows of The Royal Society. It has since developed into one of the foremost journals of the history of science, containing articles by distinguished contributors from the United Kingdom, the U.S.A. and many other countries. The high standard of presentation, with plates and diagrams where these would be of value to the reader, and quality of the articles leave it unsurpassed in the field of history of science journals.

One volume is published annually in two parts and may be obtained through any bookseller or direct from The Royal Society at £15.75 (U.K. addresses) £16.50 (overseas). Separate parts are available at £9.50 (U.K. addresses) and £10.00 (overseas).

A cumulative author and title index to volumes 1 to 20 (1938–1965), containing approximately 1500 entries, undoubtedly enhances the value of *Notes and Records* to historians of science, and is available at £3.00 (U.K. addresses) and £3.20 (overseas).

The contents of the latest issue (Vol. 39 No. 1) are:

	PAGE
Early printers to the Royal Society 1663–1708	1
By CHARLES A. RIVINGTON	
Fresh light on John Dalton	29
By DONALD CARDWELL and JOAN MOTTRAM	
Georg Christoph Lichtenberg, F.R.S.	41
By LINDE KATRITZKY	
Sir William Brooke O'Shaughnessy, F.R.S. (1809–1889), Anglo-Indian forensic chemist	51
By MEL GORMAN	
Of 'Medals and muddles' The context of the discovery of thallium: William Crookes's early spectro-chemical work	65
By FRANK A.J.L. JAMES	
Sherrington and industrial fatigue	91
By H.M. SINCLAIR	
Some comments on the development of free radical chemistry	105
By W.A. WATERS, F.R.S.	
Note on A.G. Cock's paper 'Chauvinism in science': The International Research Council, 1919–1926	125
By Dame MARY CARTWRIGHT, F.R.S.	

PROCEEDINGS OF THE ROYAL SOCIETY, SERIES B

Number 1235 22 April 1985 Volume 224

CONTENTS

CLARE, A. S., WALKER, G., HOLLAND, D. L. & CRISP, D. J. The hatching substance of the barnacle, <i>Balanus balanoides</i> (L.)	pages 131-147
CHAMBERLAIN, A. C. Prediction of response of blood lead to airborne and dietary lead from volunteer experiments with lead isotopes	149-182
ADAMS, D. J. & BEVAN, S. Some properties of acetylcholine receptors in human cultured myotubes. [Plates 1-2]	183-196
MONTGOMERY, J. C. & SAUNDERS, A. J. Functional morphology of the piper <i>Hyporhamphus ihi</i> with reference to the role of the lateral line in feeding. [Plates 1-2]	197-208
SAUNDERS, A. J. & MONTGOMERY, J. C. Field and laboratory studies of the feeding behaviour of the piper <i>Hyporhamphus ihi</i> with reference to the role of the lateral line in feeding	209-221
BELL, G. On the function of flowers	223-265

Published by the Royal Society, 6 Carlton House Terrace, London SW1Y 5AG

*Printed in Great Britain
for the Royal Society at the University Press, Cambridge*

LINKED CITATIONS

- Page 1 of 1 -



You have printed the following article:

On the Function of Flowers

G. Bell

Proceedings of the Royal Society of London. Series B, Biological Sciences, Vol. 224, No. 1235. (Apr. 22, 1985), pp. 223-265.

Stable URL:

<http://links.jstor.org/sici?sici=0080-4649%2819850422%29224%3A1235%3C223%3AOTFOF%3E2.0.CO%3B2-Z>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

References

Regulation of Flower, Fruit and Seed Production by a Monocarpic Perennial, *Yucca whipplei*

Charles L. Aker

The Journal of Ecology, Vol. 70, No. 1. (Mar., 1982), pp. 357-372.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198203%2970%3A1%3C357%3AROFFAS%3E2.0.CO%3B2-8>

Floral Sex Ratios and Life History in *Aralia nudicaulis* (Araliaceae)

Spencer C. H. Barrett; Kaius Helenurm

Evolution, Vol. 35, No. 4. (Jul., 1981), pp. 752-762.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198107%2935%3A4%3C752%3AFSRALH%3E2.0.CO%3B2-X>

Dioecism in Tropical Forest Trees

K. S. Bawa; P. A. Opler

Evolution, Vol. 29, No. 1. (Mar., 1975), pp. 167-179.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28197503%2929%3A1%3C167%3ADITFT%3E2.0.CO%3B2-A>