Evolution of style-length variability in figs and optimization of ovipositor length in their pollinator wasps: a coevolutionary model

K. N. GANESHAIAH, PRARTHANA KATHURIA,
R. UMA SHAANKER* and R. VASUDEVA

Department of Genetics and Plant Breeding, *Department of Crop Physiology, University of Agricultural Sciences, Gandhi Krishi Vignana Kendra, Bangalore 560 065, India

Abstract. Monoecious figs reward their pollinators—agaonid wasps—by allocating a proportion of the flowers for egg laying, and retain the rest for seed production. It has been suggested that these proportions could be regulated by producing short-styled and long-styled flowers such that pollinator wasps could only use the former as their ovipositor does not reach the ovules of the latter. Thus the wasps can lay eggs only in the short-styled flowers and raise their offspring, and the ovules of uninfested, long-styled flowers can develop into seeds. This implied that figs bear dimorphic female flowers, with a bimodal distribution of style length. However, recent studies have shown that style length is distributed normally, with no evidence of bimodality. Therefore the regulation of allocation of flowers to the wasps does not seem to be through the production of two distinct kinds of female flowers. In this article we suggest that two factors govern the proportion of flowers rewarded to the wasps: (i) passive regulation, which is a consequence of the optimization of wasp ovipositor length, and (ii) active regulation, where figs are selected to enhance the variance of style length. We show that these arguments lead to certain predictions about the optimum ovipositor length, the proportion of the flowers available to the wasps, and the coefficient of variation of style length. We also show that data for 18 fig–wasp associations conform well with these predictions. We finally suggest that the regulatory process outlined here can be extended to evolution of style length in dioecious fig species also.

Keywords. *Ficus*; Agaonidae; pollinators; wasps; ovipositors; style length; coevolution.

1. Introduction

Figs (*Ficus* spp.) and their pollinating agaonid wasps are regarded as probably the most faithful partners of any known plant–pollinator mutualistic relations (Galil and Eisikowitch 1968a; Janzen 1979a; Wiebes 1979; Kjellberg *et al.* 1987; Patel *et al.* 1993; Moore 1994). Typically in any fig–pollinator-wasp association, the wasp carries pollen grains from the male flowers and helps in pollination and fertilization of the female flowers; in turn, the host plant offers to the wasps some female flowers in whose ovules they can lay eggs and rear offspring (Galil and Eisikowitch 1968a,b,c; Ramirez 1969, 1978; Janzen 1979a; Newton and Lomo 1979; Wiebes 1984; Corner 1985; Bronstein 1988). Thus the fig plants and the pollinating wasps reward each other. To achieve this they have evolved certain features (see next section) that distinguish them from other plant–pollinator systems (Ramirez 1974; Janzen 1979a).

One such feature the fig plant is thought to have adopted is the production of two distinct types of female flowers—short-styled and long-styled flowers (Ramirez 1974). It has been suggested that the wasp can lay its eggs in the ovules of the short-styled flowers, but not in the long-styled flowers as its ovipositor does not reach their ovules (Galil and Eisikowitch 1968a, 1971, 1974; Ramirez 1974; Janzen 1979a). Such a strategy implies that style-length distribution has two modes corresponding to the short and long styles.

For nearly three decades it was believed that by this strategy fig plants can regulate the proportions of the flowers allocated to the wasps and for seed production (Janzen 1979b; Murray 1985; Moore 1994). The argument was so strongly appealing that there were few rigorous attempts to verify the details (but see Johri and Konar 1956; Galil and Eisikowitch 1968a; Newton and Lomo 1979; Bronstein 1988; Nefdt 1989; Kjellberg *et al.* 1994; Kathuria *et al.* 1995). All the 21 monoecious species studied so far have shown a normal distribution of style length with no indication of bimodality. Thus fig plants do not seem to employ dimorphism in style length as a strategy to regulate the extent of depredation by wasps.

In this paper we suggest that optimization of ovipositor length in the wasp is one of two routes by which the proportions of flowers available to the wasp and used by the fig plant for seed production may be regulated. On the basis of our proposal we predict (i) the proportions of flowers available to the wasp and used by the fig plant for seed production and (ii) the optimum ovipositor length, and show that these predictions are corroborated by the available data. We also discuss our argument in the context of the coefficient of variation of style length and predict that the coefficient of variation is about 30 per cent. We show that the existing data support this prediction as well.

2. Biology of the fig–pollinator-wasp association

Monoecious figs bear unisexual flowers on the inner side of the closed spherical inflorescence, the syconium, in two temporal phases—the female phase and the male phase, in that order (figure 1). Mated females of the pollinating wasps emerge from the male phase of the syconium carrying pollen grains on their body or in thoracic pockets evolved exclusively for this purpose, and search for a syconium in the female phase (Chopra and Kaur 1969; Ramirez 1969; Galil and Eisikowitch 1973). Once they locate such a syconium, which almost always will be on another tree, they enter it through the ostiole, a special opening with unidirectionally oriented scales that offer only one-way entry to wasps into the syconium. In the process of entering through the ostiole, the wasps lose their wings and hence get trapped in the syconium, where they unload their pollen grains onto the stigmas of the female flowers and lay an egg each in the ovules of those female flowers whose style lengths are equal to or shorter than their own ovipositors. It has been suggested that the number of eggs in the wasp is not a limiting factor (Grandi 1920; Pemberton 1921). Adult wasps (of both sexes) emerge in due course, coinciding with the maturation of seeds and with the opening of the male flowers. The male wasps mate with the females and also make exit holes in the syconium with their well-developed mandibles. The female wasps, after having mated with their brothers, collect the pollen grains, exit the syconium via the holes made by the males, and go in search of other syconia in the female phase, starting another cycle (figure 1).
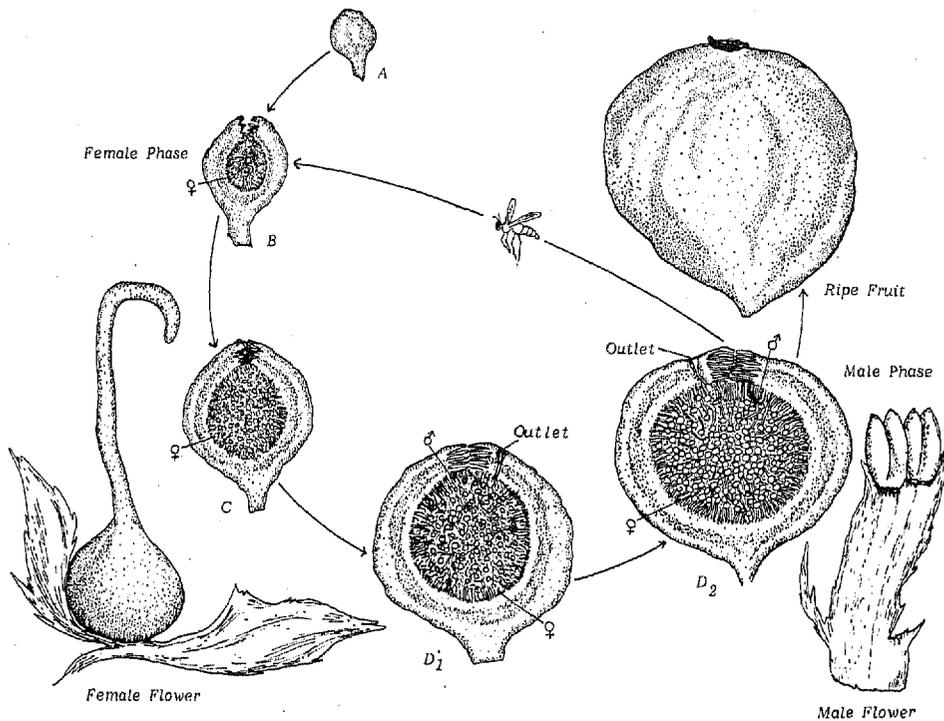
Figure 1. Sequence of events in the wasp-mediated pollination of figs and the development of fig fruits.

Thus style length determines whether a particular flower will produce seed or allow a wasp to develop. But the evolutionary forces that shape the distribution pattern of style length and thence regulate the proportions of flowers available to the wasp and for seed production are not clearly understood. We propose that these proportions in a syconium are regulated in two ways: (i) passively, by optimization of ovipositor length and (ii) actively, by increase of variance of style length.

3. Optimization of ovipositor length—passive regulation

The ovipositor of the pollinating wasps is very long, generally measuring more than half the length of their body. It is invariably covered by a pair of protecting sheaths whose length is almost equal to that of the ovipositor (Kjellberg *et al.* 1987). Together they constitute an important component of the reproductive resource of the wasp. For instance, in *Eupristina masoni*, the pollinating wasp of *Ficus benghalensis*, these organs together weighed about $0.17\,\mu g$, constituting 4–5 per cent of the body weight (personal observations). Obviously it is costly for the wasp to produce them and selection does not favour an indiscriminate increase in ovipositor length. Further, longer and heavier ovipositors may also hinder flight and may also get mutilated during the constrained entry of the wasp into the syconium (Bronstein 1992). We have in fact recovered wasps in the syconium that had broken their

ovipositors while entering through the ostiole. However, it is not clear if the probability of such damage to the ovipositor is related to its length.

At the same time, since the wasps can potentially oviposit in all the flowers with a style shorter than their ovipositor, the proportion of flowers a wasp can usurp increases with the length of its ovipositor organ. Therefore selection can be expected to optimize the length of the ovipositor such that wasps maximize the fitness gained with respect to the investment in the ovipositor.

3.1 *Benefit and cost of increasing ovipositor length*

The direct and immediate benefit of having a longer ovipositor is an increased proportion of flowers that becomes available to the wasp to oviposit in. Several independent studies have shown that style length shows a normal distribution with a single mode. Nefdt (1989) studied 11 species and observed that all exhibited a single mode. A study at our centre of ten tropical species also revealed a single mode (Kathuria 1995 and Kathuria *et al.* 1995); the distribution of style length did not deviate significantly from normal distribution. Others (Johri and Konar 1956; Galil and Eisikowitch 1968a; Newton and Lomo 1979; Bronstein 1988; Compton and Nefdt 1990) also have reported normal distribution of style length.

Given that style length is normally distributed, the benefit to the wasp with ovipositor length of x units $[B(x)]$ would be the proportion of flowers whose style lengths are equal to or less than x units, and is given by

$$B(x) = \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{x} \exp\left\{-1/2\left[(x-\mu)/\sigma\right]^2\right\},\tag{1}$$

where μ is the mean style length and σ the standard deviation.

As shown in figure 2, this benefit, which in essence is the number of eggs (offspring) the wasp can lay (raise), increases in a sigmoidal pattern with ovipositor length. This can be considered as the fitness gained by the wasp in return for investing in producing the corresponding length of ovipositor.

The cost of the ovipositor can be considered to be a linear function of its length and hence is given by

$$C(x) = xc,\tag{2}$$

where c is the cost of producing each unit of ovipositor.

An increase in investment in the ovipositor results in a cost to the wasp and its fitness can be expected to decrease as an inverse function of the length of the ovipositor. Thus the eventual fitness to the wasp due to investment in the ovipositor is given by

$$F = \frac{B(x)}{C(x)} = \frac{\frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{x} \exp\left\{-1/2\left[(x-\mu)/\sigma\right]^2\right\}}{xc}.\tag{3}$$

The optimum ovipositor length, x, that maximizes this fitness can be estimated by differentiating equation (3) with respect to the length x and equating to zero

and then solving. To maximize $B(x)/C(x)$, we need $\delta/\delta x\,[B(x)/C(x)] = 0$. Denoting $\delta/\delta x\,[B(x)] = B'(x)$ and $\delta/\delta x\,[C(x)] = C'(x)$,

$$\delta/\delta x\,[B(x)/C(x)] = \frac{C(x)\,B'(x) - B(x)\,C'(x)}{[C(x)]^2} = 0. \tag{4}$$

Therefore

$$C(x)\,B'(x) = B(x)\,C'(x). \tag{5}$$

Since $C(x) = cx$ and $C'(x) = c$, substituting for them in equation (5) we get

$$B'(x) = B(x)/x.$$

This relation is satisfied at that value of x where a line from the origin is tangent to $B(x)$ because $B'(x)$ is the slope of the tangent to $B(x)$, and the slope of the line is $B(x)/x$. This is graphically represented in figure 2. The style length on the x-axis can be considered to directly represent the length of the ovipositor and hence the cost. The optimum ovipositor length corresponds to that value on the x-axis (represented as X_{opt}) at which the tangent drawn from the origin (shown by the dotted line) meets the benefit curve.

Note that X_{opt} also defines the proportion of flowers that can be usurped by the wasp (β^*). Accordingly, a certain proportion of the flowers ($\alpha = 1 - \beta$) is still
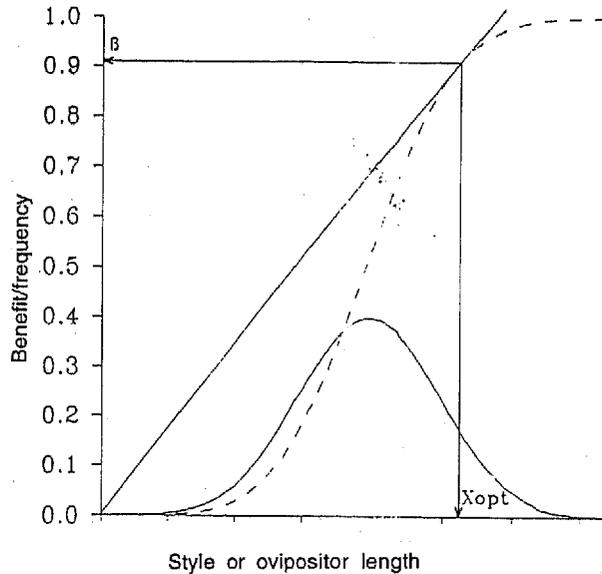
Figure 2. Optimization of ovipositor length. The solid curve represents the distribution pattern of style length. The dotted line represents the cumulative distribution of style length smaller than ovipositor length with increase in ovipositor length, and hence the benefit to the wasp of increasing its ovipositor length. The vertical line drawn to x-axis from the point where a tangent drawn from the origin meets the benefit line gives X_{opt}, the optimum ovipositor length. The proportion of the flowers available to the wasp, β, is given by the cumulative frequency of flowers corresponding to X_{opt}. The rest $(1 - \beta)$ are available to the plant for seed production.

unavailable to the wasp. In other words, if selection optimizes ovipositor length, as a default or spin-off of such a process a certain proportion of flowers (α) would be left with the plant for seed production. Thus β/α would be the reward the plant has to pay to produce every seed; to borrow the phrase by Janzen (1979b), figs have to pay β/α babies to produce one baby. In such a process, however, the plant may not have a direct control over the magnitude of α; nevertheless, as we discuss below, the plant can also use this opportunity to minimize β^* and hence β/α, though marginally.

3.2 *Test of the predictions of the proposal*

On the basis of the above argument it is possible to predict the proportion of flowers that would be usurped by the wasps (β) and the optimum ovipositor length X_{opt}. We examined data for 18 species of figs and the corresponding species of wasps. The species differed in their mean and variance for style·length (table 1), so we expected that β and X_{opt} for the species pairs could be different. We therefore estimated B/C for each species pair separately using equation (3). β and X_{opt} corresponding to the highest B/C was determined for each species pair and these are given in table 1.

3.2a *Optimum ovipositor length:*

The estimated ovipositor lengths for the wasp species were in agreement with the observed lengths (table 1). As shown in figure 3, the expected and observed ovipositor lengths were highly correlated ($r = 0.92$; $p < 0.01$; $Y = 0.29 + 0.79X$; $n = 18$). Nefdt (1989) showed correlation between ovipositor and style lengths and argued that it reflected a coevolution between the fig and the pollinating wasp such that wasps that pollinate figs with long styles should possess long ovipositors. This argument does not identify cause and consequence in the coevolution of style and ovipositor lengths and hence does not predict the strength of this relation. In fact such coevolution may not lead to a strong correlation between the two traits unless the proportion of flowers usurped by the wasps is constant across species, and there was no a priori reason to believe that this was so. On the other hand our argument indeed provides a reasonable basis to expect such constancy in the proportion of flowers available to the wasps across species (especially because, as we argue later, style length is selected to exhibit a coefficient of variation of 30 per cent). Our argument predicts a regression coefficient of 1·00 between style and ovipositor lengths. The observed coefficient of regression was indeed equal to 1 (figure 4; $b = 1·01$; SE $= 0·11$; $n = 18$). In other words, the correlations of observed ovipositor length with X_{opt} and with style length seem to emerge specifically as an outcome of the optimization of ovipositor length.

3.2b *Proportion of flowers available to the wasp:*

The proportion of flowers potentially available to the wasp has been determined for several species by a few workers by determining the proportion of flowers with style length less than the length of the ovipositor of the respective pollinating

Table 1. Observed and estimated (β) percentages of flowers of fig species potentially available to their pollinating wasps, and observed ovipositor lengths and estimated optimum ovipositor lengths X_{opt} for the respective wasps.

Fig species (Wasp species)	Per cent flowers		Ovipositor length (mm)		Style length (mm)	
	Observed	Estimated	Observed	Estimated	Mean	SD
1. *Ficus benghalensis* (*Eupristina masoni*)	81·23	90·33	1·366	1·500	1·027	0·358
2. *F. mollis* (*E.* sp.)	57·58	90·33	0·415	0·625	0·441	0·140
3. *F. drupaceae* (*E. belgaumensis*)	99·19	91·15	0·553	0·360	0·249	0·084
4. *F. racemosa* (*Ceratosolen fusiceps*)	48·33	89·44	0·988	1·300	1·023	0·222
5. *F. religiosa* (*Platyscapa quadraticeps*)	99·08	93·00	1·047	0·700	0·458	0·182
6. *F. talboti* (*Eupristina (Parapristina) keralensis*)	100·00	89·44	0·753	0·520	0·394	0·102
7. *F. amplissima* (*Maniella delhiensis*)	100·00	90·33	0·989	0·676	0·501	0·132
8. *F.* sp. (*P.* sp)	93·00	91·15	1·172	1·160	0·723	0·313
9. *F. salicifolia* (*P. awekei* Wiebes)	99·00	91·15	1·170	0·820	0·640	0·130
10. *F. burtt-davyi* (*Elisabethiella baijnathi* Wiebes)	83·00	88·00	1·400	1·100	0·800	0·230
11. *F. verriculosa* (*P. binghami* Wiebes)	60·00	89·44	0·880	1·120	0·810	0·240
12. *F. lutea* (*Allotriozoon heterandromorphum* Grandi)	93.00	91.15	1·570	1·470	1·090	0·300
13. *F. thonningii* (*Elisabethiella stuckenbergi* Grandi)	95·00	91·15	1·710	1·590	1·100	0·360
14. *F. sycomorus* (*C. arabicus* Mayr.)	98·00	88·49	1·950	1·690	1·330	0·300
15. *F. abutilifolia* (*Elisabethiella comptoni* Wiebes)	79·.00	91·15	1·710	2·020	1·360	0·490
16. *F. ottonifolia* (*Courtella camarunensis* Wiebes)	76·00	90·33	1·670	1·820	1·400	0·320
17. *F. sur* (*Ceratosolen capensis* Grandi)	55·00	88·49	1·840	2·280	1·790	0·400
18. *F. sansibarica* (*Courtella armata* Wiebes)	91·00	90·33	2·690	2·700	2·130	0·440
Mean	83·19	90·17	1·326	1·303	0·959	
SD	18·51	1·26	0·558	0·643	0·506	

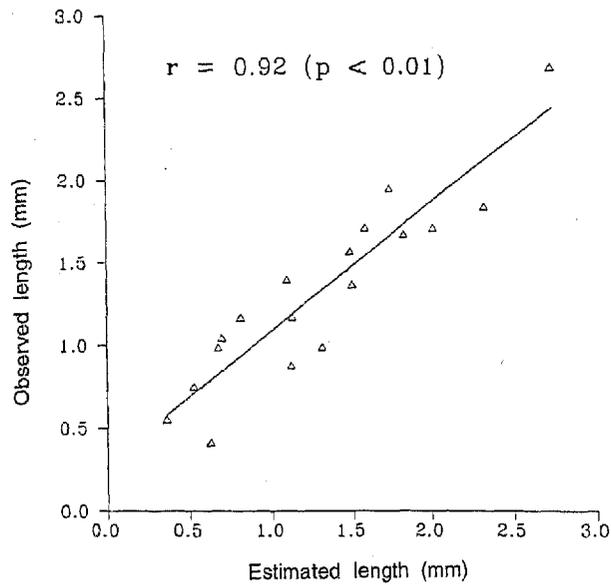Data on species numbered 1 to 8 are from Kathuria (1995), 9 to 18 from Nefdt (1989).

Figure 3. Relation between the estimated (optimum, X_{opt}) and observed ovipositor lengths of 18 species of wasps (see table 1 for the list of species).
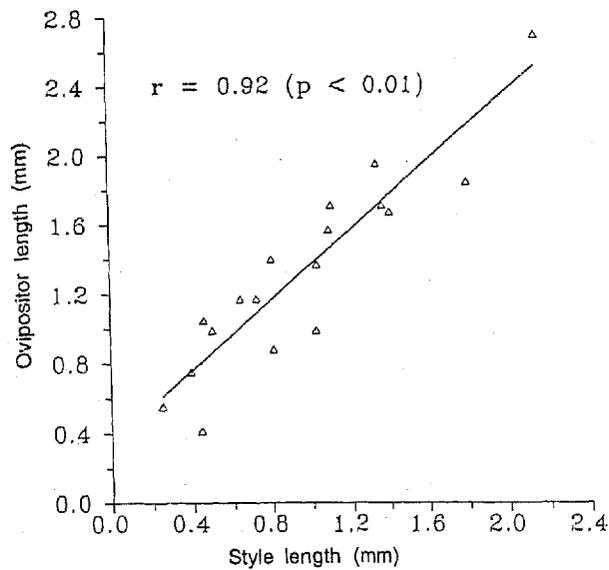

Figure 4. Relation between style and ovipositor lengths in 18 pairs of figs and their pollinating wasps (see table 1 for the list of species).

wasp (table 1). Note also that the expected proportion of flowers available to the wasp on the basis of our argument ('Estimated' in table 1) ranged from 88 to 93 per cent, with a mean of 90·17 per cent.

Several workers have suggested that the figs would allocate about equal proportions of flowers to the pollinating wasps and for seed production (Janzen 1979b; Murray 1985). These suggestions have been made either on the basis of preliminary observations or on the assumption that style length exhibits a perfect bimodal distribution. But the proportion of flowers the plant has to pay to the wasp as a reward (or cost) for receiving pollen grains predicted on the basis of our argument is clearly far above what has generally been suggested by others. The available data seem to support our prediction (table 1). For 12 of the 18 species the proportion was within the confidence interval of 81 to 100 per cent. On the contrary, in only four of the 18 species was the proportion comparable to that suggested by earlier workers (species 2, 4, 11 and 17 in table 1; range 48–60%). The estimated and the observed values showed a correlation coefficient of 0·42 ($p < 0·10$). Though the association is not statistically significant, we consider this to be suggestive of the predictive potential of our argument, though weakly, given the disparate sources of data for this analysis.

4. Spreading style length distribution—active regulation

Given that optimization of ovipositor length determines, as a spin-off, the proportion of flowers available for seed production, figs could regulate this proportion towards their advantage, though marginally. We show in figures 5 and 6 that increasing the variance of normally distributed style length leads to two consequences (see
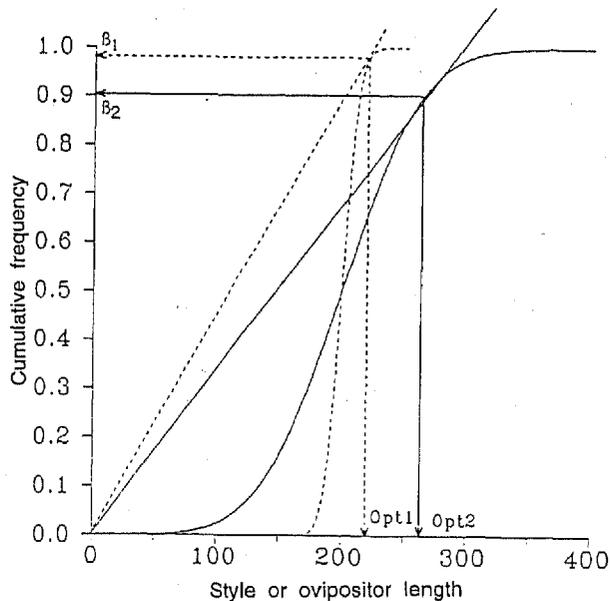
Figure 5. Effect of increasing the variance of style length on X_{opt} and β. With 200 units as mean style length two values of standard deviation (SD) were considered, viz. 10 (dotted sigmoid curve) and 50 (solid sigmoid curve) units. The cumulative frequency of benefit for each of these two standard deviations was computed using equation (1) and the optimum ovipositor lengths were estimated (given as Opt1 and Opt2 for SD = 10 and SD = 50 respectively). The corresponding $\beta1^*$ and $\beta2^*$ are also shown. Note that $\beta2^*$ is less than $\beta1^*$.
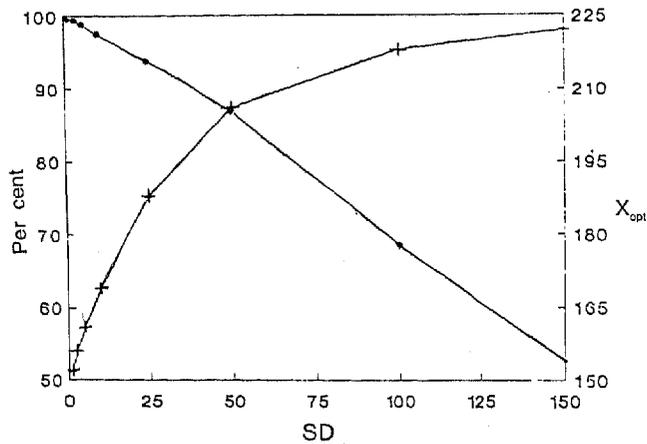
Figure 6. Effect of increasing the variance of style length on X_{opt} and β. These values were derived for the same set of conditions as in figure 5 but for a range of standard deviation (SD) values. The β and X_{opt} values corresponding to different SD values for a mean of 200 units are plotted ($-\bullet-$, β; $-+-$, X_{opt}).

figure legends for details): (i) X_{opt} increases, putting a stress on the wasp's resources, and (ii) β^* decreases, though marginally. In other words, by merely increasing the variance of style length but maintaining the normal distribution (see a later section for a discussion on why it is advantageous to maintain the normal distribution), the plant can reduce the reward to be paid to the wasp and can accordingly increase the proportion of flowers available for seed production. Therefore we predict that figs would be selected to increase the variance of style length in order to reduce the number of flowers accessible to the wasps and thence to save more of their flowers for seed production.

4.1 Limits to increasing style-length variance

Increase of variance can be attained without additional cost to the plant by merely spreading the range of style lengths but maintaining the shape of the distribution. By reducing the style length of flowers on the left side of the mean and adding to it for flowers on the right side of the mean the plant can increase the range and hence the variance without altering the total energy spent for the production of the styles. But this *per se* brings a limit on the extent to which style length can be spread and hence on the variance.

Note that style length cannot be reduced below zero on the left side, which means that the maximum reduction in style length, on an average, is the mean style length (μ). If this length is added, on an average, to flowers on the right side of the mean, the style length would increase on the right side to 2μ. In other words, while maintaining the normal distribution, the plant can increase the variance only within certain limits such that the cost of producing the styles is unaltered. One such limit that might constrain an increase in the variance seems to be that the range of style length should lie between 0 and 2μ.

A normal distribution has 99·5 per cent of its population within a range of three

standard deviations (SD) on either side. Therefore if the range of style length is limited to 0 to 2μ, all the population in this range would be covered if the SD is 33 per cent of the mean. For example, for a population with mean 100, the cost of producing styles constrains the range to between 0 and 200. For such a population, 99·5 per cent of the population would lie within this range if the SD is 33 (i.e. 33 per cent of the mean). For SD values lower than this, though most of the population would lie very much within the range, the variance would be less; for higher SD values, though the variance would be high, the population would extend beyond the range permitted given the cost of production of styles. In other words, this argument predicts that figs would be selected to produce female flowers with a 30 per cent coefficient of variation for style length.

4.2 *Test of the predictions*

The above argument predicts (i) that figs show higher variance for style length than other systems where the style length is not subjected to such selection by pollinators, and (ii) that the coefficient of variation (CV) of style length is about 30 per cent. It is rather difficult to evaluate the first prediction as it is subjective. However, we provide three kinds of evidence in support of our proposal that there is specific selection for increase of variance of style length.

(i) It might be helpful to compare the spread of style length with the spread of the length of the ovipositor of the corresponding pollinator wasp since both are biological systems and both organs are shaped in an evolutionary conflict over usurpation of the flowers by the wasps. Further, there is no a priori reason to expect that the coefficients of variation in the two cases differ except that one is a plant system and the other an insect. However, while the variation in ovipositor length of the wasps represents both the genetic variability among individuals and environmental variation, variation in style length of the flowers represents only environmental variation since all the flowers are genetically identical. Therefore in the absence of other factors, ovipositor length can in fact be expected to have higher variance than style length. But as shown in table 2, for all the 18 species pairs for which data are available, the variance of style length was always higher than that of ovipositor length of the respective pollinator. The ratio of variance of style length to that of ovipositor length ranged from 3 to 6 in ten of the 18 species pairs. This supports our prediction that figs are selected to increase the variation of style length in order to reduce the proportion of flowers usurped by the wasps.
(ii) Table 2 also provides data on CV of ovary length for eight species of figs. Clearly, the variation of ovary length is much lower than that of style length; the CV of style length was 1·5–4-fold higher than that of ovary length. In other words there appears to be a selection for higher variance of style length.
(iii) In the dioecious figs, where style length has no role in regulation of the quantum of the reward offered to the wasps, CV of style length is much lower than that in any of the monoecious species. For instance, CV of style length in the dioecious *F. caprifolia* was 11·11 in 'male' plants (see next section) and 14·88 in 'female' plants (Nefdt 1989); in *F. hispida*, another dioecious species (Kathuria 1995), these values were 19·79 (male plants) and 22·32 (female plants). Clearly, variance of style length in these species is generally less than that in the monoecious

Table 2. Coefficient of variation of style length, ovary length and wasp ovipositor length and their ratios for fig–wasp associations.

Fig species (Wasp species)	CV style length	CV ovipositor length	Ratio CV style/CV ovipositor	CV ovary length	Ratio CV style/CV ovary
1. *Ficus benghalensis* (*E. masoni*)	34·85	11·27	3·09	8·63	4·04
2. *F. mollis* (*E.* sp.)	31·74	7·71	4·12	19·90	1·59
3. *F. drupaceae* (*E. belgaumensis*)	33·73	9·94	3·39	11·35	2·97
4. *F. racemosa* (*C. fusiceps*)	21·70	5·36	4·05	8·45	2·56
5. *F. religiosa* (*P. quadraticeps*)	39·74	4·58	8·67	10·79	3·68
6. *F. talboti* (*E. keralensis*)	25·89	7·52	3·44	6·27	4·13
7. *F. amplissima* (*M. delhiensis*)	6·30	6·67	3·90	7·27	3·61
8. *F.* sp. (*P.* sp.)	43·29	3·58	12·09	12·02	3·58
9. *F. salicifolia* (*P. awekei* Wiebes)	20·30	3·20	6·66		
10. *F. burtt-davyi* (*Elisabethiella baijnathi* Wiebes)	28·75	16·42	1·75		
11. *F. verriculosa* (*P. binghami* Wiebes)	29·62	3·06	9·67		
12. *F. lutea* (*Allotriozoon heterandromorphum* Grandi)	27·52	3·12	8·82		
13. *F. thonningii* (*Elisabethiella stuckenbergi* Grandi)	32·72	6·32	5·17		
14. *F. sycomorus* (*C. arabicus* Mayr.)	22·55	6·25	3·61		
15. *F. abutilifolia* (*Elisabethiella comptoni* Wiebes)	36·02	6·43	5·6		
16. *F. ottonifolia* (*Courtella camarunensis* Wiebes)	22·85	3·59	6·36		
17. *F. sur* (*Ceratosolen capensis* Grandi)	22·35	3·36	6·65		
18. *F. sansibarica* (*Courtella armata* Wiebes)	20·65	1·48	13·94		
19. *F. pertusa* (*Pegoscapus silvestri* Grandi)	56·00	15·00	3·70		
Mean	30·34	6·57	6·03		
SD	9·07	4·07	3·27.		

Data on species numbered 1–18 are from sources given in footnote to table 1, on 19 from Bronstein (1988).

species. In other words, there appears to be a selection for higher variance of style length in monoecious figs.

The mean CV of style length was around 30 per cent ($x = 30.34 \pm 9.07$; $t = 0.16$ for the null hypothesis that $x = 30$; $p > 0.50$; $n = 19$). In other words, as predicted the variance of style length seems to have spread to the limits permissible by the cost of production. However, two species had a higher value of CV (species 8 and 19, with 43.9 and 56 per cent respectively, table 2). It is important to note that these limits may also be influenced by other morphological and biological constraints. For instance, both maximum and average style length may also be constrained by the size of the fruit and the thickness of the rind; if the rind is very thick, for a given fruit size there is less space in the flower for the style to extend. However, despite these factors the variance of style length is in the range predicted by the argument.

5. Conclusions and implications

We have argued that in figs apportionment of flowers to the pollinating wasp and for seed production occurs passively as a consequence of optimization of ovipositor length in the wasp and actively by the figs by increase of the variance of style length. Our argument offers certain predictions with respect to ovipositor length, proportion of flowers that can potentially be usurped by the wasp, and the variation of style length; these predictions are strongly supported by available data on figs and their pollinator wasps.

Our model does not address the consequences of presenting style length in a uniform, or trough-like, or a highly skewed distribution without altering the cost of producing the styles. A uniform distribution will result in a linear increase in the benefit, which means that the selected optimum ovipositor would be equal to the longest style; this would not leave any flowers for seed production and hence either the mutualistic relation collapses or plants with such style distribution are not selected. Note that there are a few species with more than 95 per cent of female flowers with styles shorter than the ovipositor of the corresponding pollinator wasp. But the distribution pattern of style length in these cases is not uniform; rather they exhibit a normal distribution.

The consequences of the trough-like distribution (which in essence is bimodal) would be similar to those of the normal as long as the amplitude of the first mode (corresponding to the short styles) is equal to or smaller than that of the second mode (corresponding to the long styles), because then the process of optimization would favour an ovipositor that allows the usurpation of all, of the flowers in the first mode and a certain proportion of the flowers in the second mode.

The regulatory mechanisms suggested here may be operating in dioecious figs also. In these species there are different types of trees, viz. 'males' which bear syconia with relatively short-styled female flowers and male flowers, and 'females' which bear syconia with only long-styled female flowers (Janzen 1979a). It is observed that wasps can lay eggs and raise their offspring only in the female flowers of the 'male' trees; wasps entering syconia of the 'female' trees do not seem capable of laying eggs in their flowers (Patel *et al.* 1993).

Our argument also suggests that though style lengths in the 'female'-tree syconia

are slightly longer, the wasps can be expected to optimize their ovipositor to these flowers also such that a certain proportion of the female flowers in 'female'-tree syconia can also be usurped by them. However, 'male' trees (with relatively shorter-styled female flowers) are known to bloom more frequently, and hence in effect their population is higher than that of the 'female' trees (i.e. long-styled flowers). Consequently, wasps encounter short-styled female flowers at a higher frequency than they do long-styled female flowers. The optimization of ovipositor length can hence be expected to occur for the whole of the mixed population of short-styled and long-styled flowers and not separately for 'male' and 'female' trees. For this reason, the optimized ovipositor length in wasps that pollinate dioecious species may be expected to render almost all of the female flowers in male syconia (as they have short styles) and only a few or none in female syconia (as they have longer styles) available for oviposition. Clearly the extent to which the flowers in female syconia escape depredation by wasps depends upon the relative values of the means of the style lengths, the nature of the distribution patterns, and the relative flowering rates of the two types of trees in the population. It is likely that when there is greater amount of overlap in these parameters between the two groups, a proportion of flowers in the female trees may also be usurped by the wasps. This prediction can be tested by determining the extent of overlap in the style lengths of the female flowers of 'male' and 'female' trees.

Finally the optimization process proposed here may not be restricted to figs alone. For instance, speed of predators may be optimized on the basis of the distribution of the speed of the prey; proboscis length in nectar-foraging moths and butterflies may be optimized on the basis of the distribution of the length of the corolla tube or nectar tube of the host plant. There are a number of situations where such predatory organs of the consumer may be optimized on the basis of the normal distribution of the features of the prey or of the producer on which the consumer survives.

References

Bronstein J. L. 1988 Mutualism, antagonism, and the fig–pollinator interaction. *Ecology* 69: 1298–1302

Bronstein J. L. 1992 Seed predators as mutualists: ecology and evolution of the fig–pollinator interaction. *Insect–Plant Interactions* IV: 2–43

Chopra R. N. and Kaur H. 1969 Pollination and fertilization in some *Ficus* species. *Beitr. Biol. Pflanz.* 45: 441–446

Compton S. G. and Nefdt R. J. C. 1990 The figs and fig-wasps of *Ficus burtt-davyii. Mitt. Inst. Allg. Bot. Hamburg* 23a: 441–450

Condit I. J. 1947 *The Fig. Chronica Botanica* (Waltham, MA, USA:)

Corner E. J. H. 1985 *Ficus* (Moraceae) and Hymenoptera (Chalcidoidea): figs and pollinators. *Biol. J. Linn. Soc.* 25: 187–195

Galil J. 1977 Fig biology. *Endeavour* 1: 52–56

Galil J. and Eisikowitch D. 1968a Flowering cycles and fruit types in *Ficus sycomorus* in Israel. *New Phytol.* 67: 745–758

Galil J. and Eisikowitch D. 1968b On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49: 259–269

Galil J. and Eisikowitch D. 1968c On the pollination ecology of *Ficus religiosa* in Israel. *Phyto-morphology* 18: 356–363

Galil J. and Eisikowitch D. 1971 Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol.* 70: 773–787

Galil J. and Eisikowitch D. 1973 Topocentric and ethodynamic pollination. in *Pollination and dispersal*

(eds.) N. B. M. Brantjes and H. F. Linskens (Nijmegen: Department of Botany, University of Nijmegen). pp. 85–100

Galil J. and Eisikowitch D. 1974 Further studies on the pollination ecology of *Ficus sycomorus*. II. Pollen filling and emptying by *Ceratosolen arabicus* Mayr. *New Phytol.* 73: 551–528

Grandi G. 1920 Studio morfologico e biologico della *Blastophaga psenes* (L.). *Ball. Lab. Zool. Partice* 14: 63–204

Janzen D. H. 1979a How to be a fig? *Annu. Rev. Ecol. Syst.* 10: 13–51

Janzen D. H. 1979b How many babies do figs pay for more babies? *Biotropica* 11: 48–50

Johri B. M. and Konar R. N. 1956 The floral morphology and embryology of *Ficus religiosa* Linn. *Phytomorphology* 6: 97–111

Kathuria P. 1995 Reproductive strategies of common figs: Fig–fig-wasp interactions. M.Sc. (Agri.) thesis, University of Agricultural Sciences, Bangalore

Kathuria P., Ganeshaiah K. N., Uma Shaanker R. and Vasudeva R. 1995 Is there dimorphism for style lengths in monoecious figs? *Curr. Sci.* 68: 1047–1049

Kjellberg F., Anstett M.-C. and Herre E. A. 1994 Yucca sex. *Nature* 370: 604

Kjellberg F., Michaloud G. and Valdeyron G. 1987 The *Ficus–Ficus* pollinator mutualism: how can it be evolutionarily stable? in *Insects–Plants* (eds.) V. Labeyrie, G. Fabres and D. Lachaise (Dordrecht: W. Junk) pp. 335–340

Moore P. D. 1994 The Yucca expediency. *Nature* 368: 588–589

Murray M. G. 1985 Figs (*Ficus* spp.) and wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol. J. Linn. Soc.* 26: 69–81

Nefdt R. J. C. 1989 Interactions between fig wasps and their host figs. M.S. thesis submitted to Rhodes University, South Africa

Newton L. E. and Lomo A. 1979 The pollination of *Ficus vogelii* in Ghana. *Bot. J. Linn. Soc.* 78: 21–30

Patel A., Hossaert-McKey M. and McKey D. 1993 Ficus–pollinator research in India: Past, present and future. *Curr. Sci.* 65: 243–253

Pemberton C. E. 1921 The fig wasp in relation to the development of fertile seeds in the Moreton Bay fig. *The Hawaiian Planters' Record* 24: 297–319

Ramirez B. W. 1969 Fig wasps: mechanism of pollen transfer. *Science* 163: 580–581

Ramirez B. W. 1974 Coevolution of *Ficus* and Agaonidae. *Ann. Miss. Bot. Gard.* 61: 770–780

Ramirez B. W. 1978 Evolution of mechanisms to carry pollen in Agaonidae (Hymenoptera, Chalcidoidea). *Tijdschr. Entomol.* 121: 279–293

Wiebes J. T. 1979 Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10: 1–12

Wiebes J. T. 1984 Fig wasp–fig co-evolution. *Antenna* 8: 122–127