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The evolution of hermaphroditism

An experimental test of the resource model

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Summary. Most plants are hermaphrodite (cosexual). Charnov et al. (1976) advanced the hypothesis that cosexuality is favoured in plants because a convex fitness set is generated by a non-additive relationship between male and female resource costs. In the first experimental test of this hypothesis, reproductive costs were measured in a male × female factorial design using male, female, cosexual, and neuter cucumber plants. Costs were measured by plant's vegetative growth response to treatments. The results show that male costs in the system used have negligible effect upon plant growth and female function, and imply a convex fitness set, in accordance with Charnov et al.'s model. Female function (fruit set) has an inhibitory effect upon vegetative growth and male flower production, favouring protandry.

Key words: Hermaphrodite – Cosexuality – Reproductive costs – Growth

After the evolution of sex itself, the evolution of hermaphroditism (cosexuality) versus dioecy (unisexuality) represents a major challenge to evolutionary theory (Maynard Smith 1978; Charnov 1982). Most models incorporate four basic variables: resource costs of reproduction, trade-offs between fitness gained from allocation to male versus allocation to female function (the "fitness set"), selfing rate and inbreeding depression (Lloyd 1982). Charnov et al. (1976) proposed that the shape of the fitness set could be decisive in determining the advantage of cosexuality over unisexuality. They suggested that a convex fitness set (Fig. 1), which favours cosexuality, might be common in angiosperms because (1) plants can easily combine male and female functions in a single flower, and (2) pollen production usually preceeds seed production, allowing a temporal separation of the resource costs of each sexual function. Both (1) and (2) give cosexual individuals a higher fitness than unisexual ones for the same resource costs. A test of the resource hypothesis requires that costs of male and female function be measured in unisexual and cosexual plants in a factorial experiment which allows both the magnitude and the interaction of male and female costs to be measured. I report the results of the first such experiment here.

Methods

Eighty monoecious gherkin cucumber plants (*Cucumis sativus* cv Venlo) were grown in an unheated greenhouse in individual 1.3 litre pots of "Levington's" soilless compost. Vines were trained up a trellis and lateral branch initials were removed to produce a monopodial growth form. Plants were regularly watered to pot capacity, but no supplementary nutrients were administered during the experiment. Twenty plants were assigned at random to each of three treatments and a control. Functionally unisexual (two treatments) and functionally neuter plants (one treatment) were created by surgical removal of male and/or female flower buds as soon as they appeared.

The number of nodes and the number and position of every new flower and fruit on each plant were recorded at three-day intervals. Female flowers on cosexual and female plants were cross-pollinated by hand. Each plant produced only a single mature fruit. When the intact, control plants (cosexuals) had ceased growth, all plants were harvested and separate measurements were made of the dry weight of above ground vegetative parts and of fruit.

Results

Male plants and neuter plants responded to treatment by additional vegetative growth compared to intact controls (Table 1). The additional growth, measured either in units of dry weight or number of nodes, is a measure of the resource costs of the missing sexual function(s) that circumvents the problems of currency which beset the usual methods of measuring reproductive allocation (see Discussion).

Judged by either node number or dry weight, female function had a highly significant effect upon vegetative

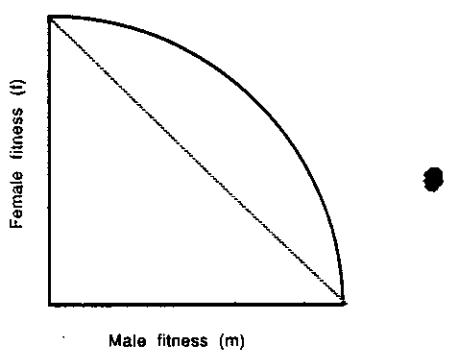

Fig. 1. The hypothetical trade-off between fitness gained through allocation to male function and fitness gained through allocation to female function. The *curve* illustrates a convex fitness set. The *diagonal broken line* illustrates the situation where there is a linear trade-off in fitness between male and female function so that m + f = 1 (after Charnov 1982)

Table 1. Vegetative growth, fruit weight and date of female anthesis of functionally cosexual, male, female and neuter cucumbers

Functional gender	Growth measured in		Mean weight of fruit (g)	Mean date of F anthesis
	g dry wt	nodes		
M+F	18.06 (3.3)	24.85 (3.48)	12.95 (3.1)	23.90 (7.2)
M	39.01 (4.2)	33.89 (2.35)	–	–
F	19.85 (4.6)	24.65 (3.5)	12.34 (3.4)	23.10 (5.2)
O	40.70 (5.2)	35.33 (2.7)	–	–

Values are means of 20 (M+F & M) or 18 (F & O) replicates per treatment with standard deviations shown in parenthesis

Table 2. Analysis of variance of plant size at the end of the experiment based upon (**a**) plant dry weight and (**b**) number of nodes

(a) Source	Sum-of-squares	df	*F*-ratio	*P*
Male	7.336	1	0.78	0.380
Female	1842.471	1	195.99	<0.001
Male* Female	12.809	1	1.36	0.247
Error	676.879	72		

(b) Source	Sum-of-squares	df	*F*-ratio	*P*
Male	57.164	1	3.02	0.086
Female	8278.820	1	437.899	<0.001
Male* Female	0.044	1	0.002	0.962
Error	1361.215	72		

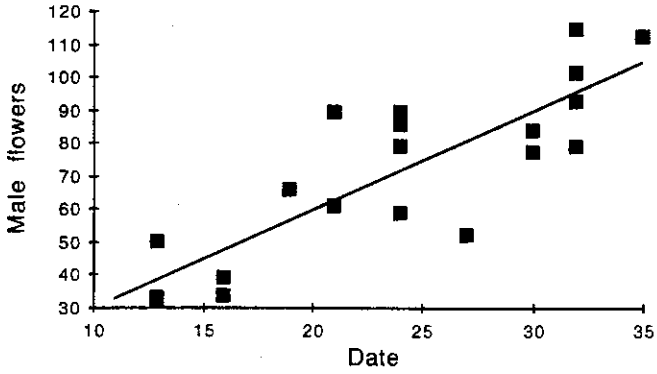

Fig. 2. The relationship between total number of male flowers produced per plant and date of anthesis of the first female flower to produce a fruit. The regression equation is MALE FLOWERS = $-0.48+3.016$ DATE, $r^2=0.71$, $F_{1,18}=43.28$, $P<0.001$

growth, but male function had none and there was no significant male × female interaction (Table 2). There was considerable variation in the date of first female anthesis within female and cosexual treatments but neither this nor fruit dry weight varied significantly between the treatments ($t=0.42$, $P=0.69$; $t=0.571$, $P=0.571$ respectively).

Cosexual plants in the experiment produced a mean of 72 male flowers compared to a mean of 134 for males. The date of anthesis of the first female flower to produce a fruit strongly influenced the final size of plants, and consequently the number of male flowers produced in the cosexual controls. Individuals in which female anthesis occurred early set fruit early, ceased male flower production earlier and produced fewer male flowers in total than individuals with later anthesis (Fig. 2).

Discussion

Measurement of reproductive costs

It is traditional to measure reproductive costs in plants in terms of an instantaneous measure such as dry weight, or (more rarely) mineral allocation to reproductive organs (Willson 1983). Three problems with the usual methods of measuring plant reproductive allocation necessitated the use of the alternative, experimental approach employed in this study. The first problem is to identify the correct currency of reproductive cost. Quite aside from this, a second problem arises because the traditional method assumes that it is possible to separate the plant into organs solely concerned with reproduction and those solely concerned with growth. There are several demonstrations that green fruit and accessory reproductive structures contribute carbohydrate to their own formation (e.g. Bazzaz and Carlson 1979; Bazzaz et al. 1979). These studies make a nonsense of the notion, central to traditional measures of allocation, that functions are discretely divided among a plant's parts.

A third problem is that the physiological costs of reproduction, measured in whatever units are appropriate, are likely to be time-specific (e.g., Lovett-Doust and Eaton 1982). A single fruit may incur a heavier cost in terms of subsequent vegetative growth for a young plant than for an older one, as was observed in the present study (Fig. 2).

Taking an instantaneous harvest and using this to measure reproductive allocation ignores the fact that allocation behaviour is temporally patterned, that reproductive costs are time-specific, and that in perennial plants trade-offs may occur with periods outside the procrustean framework imposed by the investigator.

In plants with indeterminate growth, such as cucumbers, the usual allocation between reproduction and growth can be altered by excision of flower buds. If this procedure is continued as more buds are produced, there is generally a significant increase in vegetative growth compared to intact controls (Leonard 1962). In effect, these experiments force plants to divert resources normally allocated to reproduction into vegetative growth. These experiments offer the investigator a measure of reproductive allocation calculated in units of vegetative growth. In principle, excision experiments and other experimetal methods of altering reproductive allocation (Antonovics 1980) offer a solution to the three main obstacles of the conventional methodology. (1) The currency in which reproductive costs are levied becomes irrelevant because the plant itself performs the conversion between reproduction and growth when buds are removed. (2) The contribution a plant's reproductive organs make to net photosynthesis (either directly or by increasing photosynthetic rate in other parts) is automatically removed with the organs themselves so that the reproductive cost measured by the increase in vegetative growth in excised plants is only that borne by the rest of the plant when reproduction does occur. (3) Variation in costs per flower through the season is adjusted automatically because the

conversion of reproductive resources into vegetative ones is a physiological one performed by the plant itself.

Relative costs of male and female function

These results suggest a negligible cost of male function in the experimental system studied. This is also implied by comparisons between cosexual and female cucumber genotypes which show no difference in fruit yield or plant weight due to the lack of male flowers in intact females (Denna 1973; Wehner and Miller 1985). The present results are therefore not likely to be an artifact of surgery. Though male function has no cost in terms of female function, there is a strong negative effect of female function on the number of male flowers produced (Fig. 2).

Wild (and cultivated) cucumbers are strongly protandrous (Silvertown 1985) and thus effectively achieve the temporal separation of resource allocation to male and female function necessary to generate a convex fitness set. A convex fitness set arises with protandry because male function has no measurable cost in terms of female function and vice versa when male flowers are produced before fruit set. Consequently, a protandrous hermaphrodite acquires the same fitness as a female, plus an additional amount from male function. The precise shape of the function which relates male flower numbers to their contribution to fitness cannot be determined in this study. Without this it isn't possible to draw an actual fitness set from the experimental data. However, unless male flower number is actually *inversely* related to plant fitness, which is very unlikely, a zero cost to male flowers must generate a fitness set of convex shape.

The corrollas of female flowers are similar in size to those of males and therefore presumably contribute little to the cost of female function. The high cost of female function in cucumbers is correlated with fruit set (McCollum 1934) and must have been exaggerated in this cultivar by artificial selection for fruit size. However, the negligible cost of male flowers, and the high cost which female function levies on male function, clearly demonstrate that relative resource costs favour the evolution of cosexuality when this is combined with protandry. Protandry is common in cosexual plants (Faegri and van der Pijl 1979).

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