Empty flowers

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Abstract. Bell (1986) predicted that plants should be able to grow a proportion of their flowers that do not produce any nectar, which thus escape the costs of nectar production, while gaining the benefits of insect pollination because most insect visitors either cannot discriminate, or would lose too much time attempting to do so. He worked out an ESS model predicting the proportion of 'cheating' flowers and discriminating insects: the proportion of cheaters should be D/H, where D is the discrimination time, and H the handling time of the insect visitors. We have tested Bell's hypothesis using the flowers of *Cerinthe major* L. (Boraginaceae) visited by *Anthophora plumipes* (Pallas) (Hymenoptera, Anthophoridae). From measurements of D and H, we predicted that 73% of flowers should be cheaters. Inspection of the ranked nectar production of individual flowers on individual days shows that between 75 and 85% are relatively low nectar producers. Reasons for this pattern are explored; in particular, the way in which nectar production varies with flower age may constitute a mechanism by which plants can play a mixed strategy.

Key-words: Evolutionary stable strategy, foraging, nectar

Introduction

Most flowers are structures designed to attract insects that transfer pollen grains (see Bell, 1985). The cost of gaining this pollination service is the reward that must be provided for the insect: nectar, pollen, oil, water, etc. (Vogel, 1983; Willmer, 1986). Several authors (see Dafni, 1984) including Bell (1986) suggested that some individual plants would attempt to cheat on their conspecifics, obtaining the benefits of import and export of pollen, without paying the costs of nectar production. Bell formalized this idea into a model, which resulted in an unrealistic game, with the frequency of cheating plants being cyclical. Bell's further ESS analysis suggests that if plants can play a mixed strategy and vary the proportion of cheating flowers they make, and if some insects can learn to discriminate between cheaters and non-cheaters, then the ESS prediction is that the proportion of cheaters should equal D/H, where D is the time required to discriminate between a cheating and a non-cheating flower, and H is the handling time on non-cheating flowers.

There are two main elements to this hypothesis: the first concerns differences in nectar production between individual flowers on a plant, and between individual plants; and the second, the ability of insect visitors to discriminate nectar-rich from nectar-poor flowers.

Not a great deal is known about patterns of nectar secretion between individual flowers on single plants, or between individual plants. Gross differences between plants have often been demonstrated (Feinsinger, 1978; Zimmerman, 1981a,b; Brink, 1982; Pleasants & Chaplin, 1983; Pleasants & Zimmerman, 1983; Cruden, Hermanutz & Shuttleworth, 1984; Zimmerman & Pyke, 1986; Burquez, 1988; Real & Rathcke, 1988), but there are no detectable between-plant differences in some species (e.g. in *Impatiens capensis* [Marden, 1984b]).

Similarly, very little is known about whether insect visitors can discriminate between flowers with and without nectar. In an elegant study, Marden (1984a) showed that the flowers of *Apocynum* and *Trifolium* visited by bumblebees contain more nectar than rejected flowers, but that bumblebees could not discriminate on *Aconitum* or *Epilobium*. Wetherwax (1986) discovered that honeybees could discriminate between nectar-rich and nectar-poor flowers of *Lotus*. Corbet *et al.* (1984) and Kato (1988) found that bumblebees avoid visiting recently visited flowers, and suggested that they were not sensing remotely the levels of nectar, but perceived an evanescent chemical mark left by a previous visitor. Bees are easily able to discriminate flowers on odour alone (Dobson, 1987); even very slight odour cues are enough (Marden, 1984a). Recently, Schmitt & Bertsch (1990) have confirmed experimentally that bumblebees do mark flowers with scents.

The work presented here is a test of Bell's hypothesis. We calculated the mean discrimination time and handling times for a particular
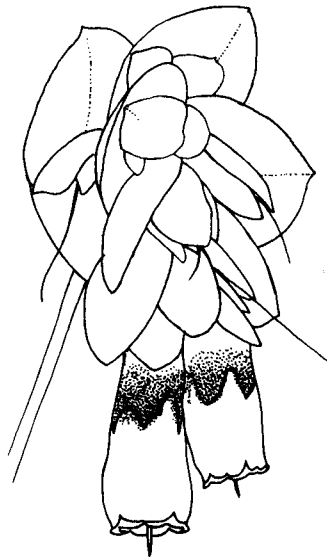
Fig. 1. The inflorescence of *Cerinthe major*.

forager, and from this predicted the proportion of empty flowers. We then measured the nectar productivity of individual flowers in a patch to test our prediction. We chose a large flower with a deep corolla, precisely the situation where Bell predicts a high proportion of cheaters to occur. The chosen flower was *Cerinthe major* L. (Boraginaceae), a plant of stony ground in mediterranean Europe with a large (2–3 × 0·7 cm) cream and blackish/purple corolla (Fig. 1).

Materials and methods

The study was conducted between 4 and 18 April 1989 at the Quinta da São Paulo Field Station, Sobreda di Caparica, near Lisbon, Portugal. This period covered most of the flowering period of *Cerinthe* at the study site: the visitors that we recorded at flowers probably represent most of the visitors to the flowers, and therefore probably the pollinators too (currently under study). Fifty-six individual plants and individual flowers on plants were marked, bagged with muslin, and some or all used in most of the nectar experiments. We assume that bagging does not affect the conclusions drawn from our results. Nectar was withdrawn from flowers by gently inserting 1-µl microcapillary tubes (Camlab, Cambridge, UK) into the corolla and down past the bases of the stamens into the protected chamber where nectar is secreted: capillary action draws up the nectar into the tube. Nectar volumes were measured by recording the length of the column; where volumes permitted, nectar was transferred to a pocket refractometer modified for small volumes (Bellingham & Stanley, Tunbridge Wells, Kent, UK) to determine its concentration in g solute per 100 g solution (Bolten *et al.*, 1979). No nectar concentrations are used here, since virtually all concentrations fell between 18 and 25% sucrose equivalents; only nine of more than 200 readings were lower than this, almost certainly due to the addition of dew or rain. Only three readings were higher (27, 30 and 36%). Thus we feel justified in using nectar volume as an accurate index of the rewards in each flower.

In our study of diel patterns of secretion, the first sample was the overnight accumulation, since flowers were bagged the previous evening. All times are quoted in British Summer Time (BST). We use non-parametric tests where possible since nectar production is not a normally distributed variable; the specific tests described in Meddis (1984) were particularly useful. Since all our hypotheses were tested *a priori*, we used one-tailed tests where appropriate.

Visitors to *Cerinthe* were almost exclusively males and females of the solitary bee *Anthophora plumipes* (Pallas). Two males patrolled around the patch of *Cerinthe*, rarely visiting the flowers themselves but allowing females (and one female in particular) but not other species to forage. Females approached flowers and hovered at the entrance before either flying to another flower or landing and probing for nectar. The time spent in stationary hovering (as judged by the observer) in front of the flower was defined as the discrimination time, D, while the time spent actually landed on the flower was defined as the handling time, H (both recorded using hand-held digital stop-watch). In all cases except one (discussed below), we believe that the recorded handling time reflected the time spent ingesting nectar.

Males rarely interfered with the foraging of females, and we never saw an attempted mating. Individual flowers were visited infrequently: the probability of being visited, and the consequences of a visit are under study.

Results

C. major is an annual that flowers in a very distinctive manner (Fig. 1). Each inflorescence grows continually at the tip, producing flowers sequentially as it recurves. A new flower opens on average every 2–4 days (F. Gilbert, N. Haines & K. Dickson, unpublished observations), but the older ones die off very quickly. Thus the inflorescence
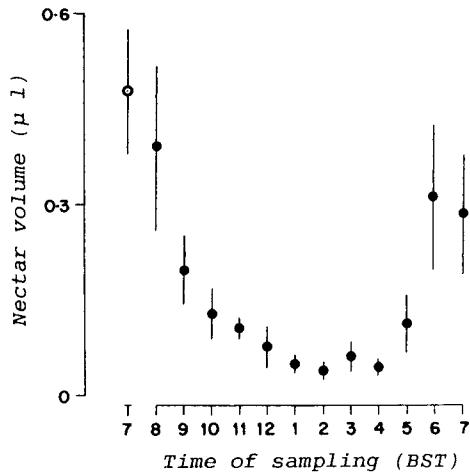
Fig. 2. Mean volumes of nectar secreted during 1 day. The concentration of the nectar was 18–25% sucrose equivalent. The first reading represents the overnight accumulation of nectar. SE bars are plotted.

has only two flowers at any one time, the older one behind the younger. Preliminary studies indicated that the older flower contains very little nectar compared to the younger (see below), and was never visited by *Anthophora*: therefore the patterns reported here are for the younger flowers only, and Bell's hypothesis is tested just for this subset of the flowers.

1 *The diel pattern of nectar secretion*

Twenty flowers on separate plants were bagged overnight and repeatedly sampled hourly from 07.00 to 19.00 h BST. The first sample represents the overnight accumulation of secreted nectar, whereas subsequent samples are the volumes secreted per hour. On average there was a morning and an evening peak of secretion (Fig. 2). However, this masks substantial interplant variation: classifying flowers by eye from graphical plots, some individual flowers accumulated a great deal by 07.00 h but secreted very little during the day (Fig. 3a); others secreted mostly in the evening (Fig. 3b); yet others had a larger morning peak of secretion (Fig. 3c); lastly, some plants produced only small amounts overall, doing so mainly between 09.00 and 15.00 BST (Fig. 3d). The initial rate of secretion, between 07.00 and 08.00 h, was very highly correlated with total daily production (Fig. 4).

There were substantial differences between plants in their total daily production of nectar. The highest producer secreted more than 6 μl of about 22% sucrose equivalents (1·44 mg sugar, 8·13 mJ)

in a single flower, whereas the lowest producer only secreted 0·03 μl.

Were these differences between flowers within plants, or true differences between plants that were constant over time? We tested two *a priori* predictions. If all the flowers of some plants always secrete large amounts of nectar, and those of others small amounts, then: (a) there should be a significantly large ratio of the between-plants to between-flowers-within-plants variance in nectar production; and (b) if flowers from the same plants are resampled 4 days later, there should be a positive correlation between amounts secreted on day 1 and day 4, i.e. plants that were relatively high producers on day 1 should remain relatively high producers on day 4.

To test whether variation existed between plants over and above the variation between individual flowers, we performed a one-way analysis of variance on data from the flowers of 12 plants. Significant differences between plants as compared to the variation between flowers within plants would be indicated by a significant F-ratio. On this basis there were significant differences between plants ($F_{11,16} = 9.65$, $P \ll 0.001$) all accounted for by the high productivity of flowers of one plants (when deleted, $F_{10,15} = 1.14$, NS): a non-parametric one-way analysis also gave the same pattern. Because we could not make replicate measurements of the nectar secretion of individual flowers (since age confounds the measurement — see below), we could not estimate the variance components of between-plants, between-flowers-within-plants, and within-flower ('error') variation (even assuming that the rate of nectar secretion is a normally distributed variable).

To test the second prediction, we measured nectar productivity in a similar way (but sampling only three times during the day, at 11.00, 15.00 and 18.30 h) 4 days later, using flowers from the same plants. Several flowers were sampled on each plant, and the average total day's production compared with the previous estimates: we used this procedure rather than sampling from the actual flowers used on day 1 because of age effects (see below) on individual flowers, and because we found significant interplant differences. We predicted a positive slope to the correlation between production on days 1 and 4. There was one extreme outlier, a plant that was one of the lowest producers on day 1 and by far the highest on day 4 (twice as productive as the second highest). We have no explanation for this anomaly, but suspect slight damage to the flower from a micropipette (it was the first to be sampled on day 1). Without
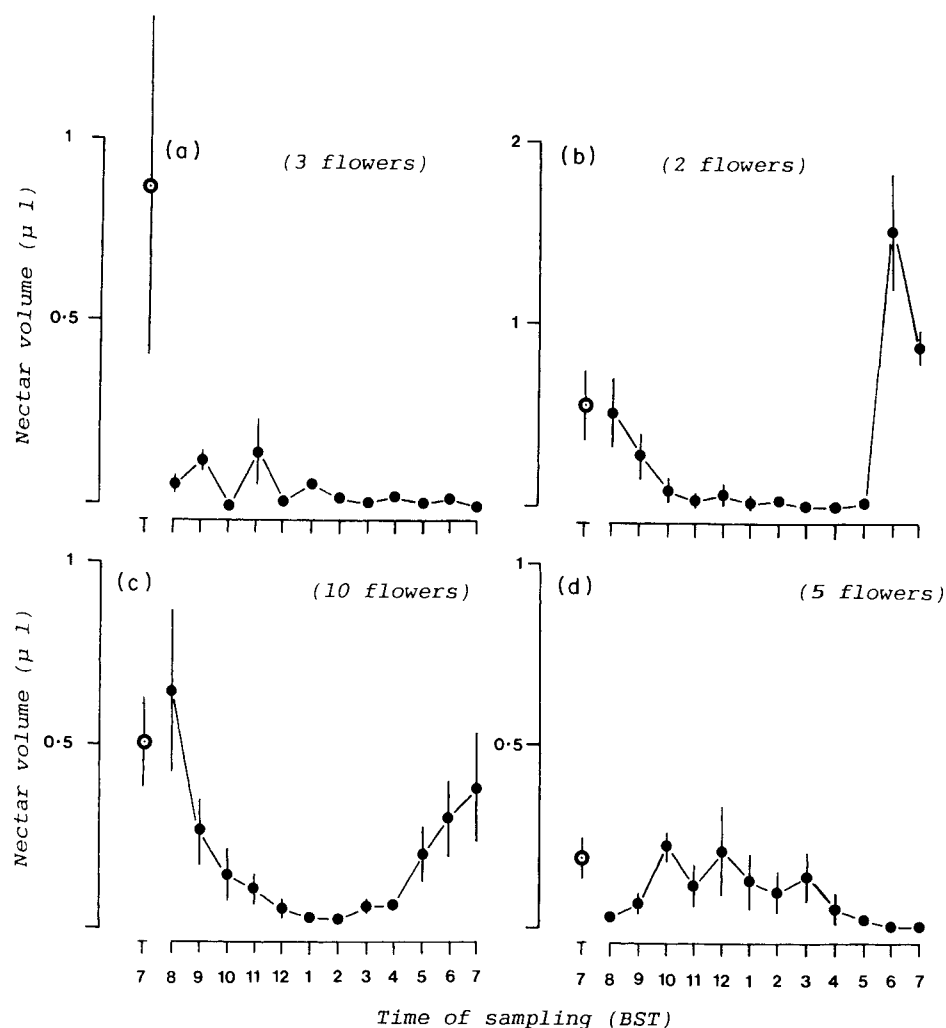
Fig. 3. Mean volumes of nectar secreted during 1 day by subsets of the flowers. Each subset has a similar rhythm of nectar secretion. Means ± SE are plotted.

exclusion, there was no significant correlation ($r = 0.11$, $n = 20$, NS); excluding the point leads to a significant positive correlation (Fig. 5a).

The fact that only one of 12 plants showed elevated rates of secretion is entirely consistent with the low proportion of highly productive plants found below (section 6). Although we can say nothing about the variance among flowers, the fact that all the flowers of the one highly productive plant among the 12 plants sampled show elevated secretion rates indicates that plants may well differ in nectar-secretion strategy.

We conclude therefore that there were significant differences in secretion rates between individual plants: for most plants there were no differences between plants as opposed to between flowers within plants, but at least a few plants had elevated rates of secretion in most or all of their

flowers. Bearing in mind the problems of excluding supposed outliers, we suspect that these differences between plants persist through time.

2 The effect of plant age

The two flowers of single inflorescences on 20 plants were sampled by bagging overnight, removing all accumulated nectar at 08.00 h, and resampled again at 11.00 h. Nectar productivity was always very low in the older of the two flowers (Fig. 5b).

These data and suggestions from the literature led to an *a priori* prediction that nectar production should decrease throughout the life of the flower, and therefore we emptied flowers at 08.00 h and resampled them at 09.00 h, for flowers between 1
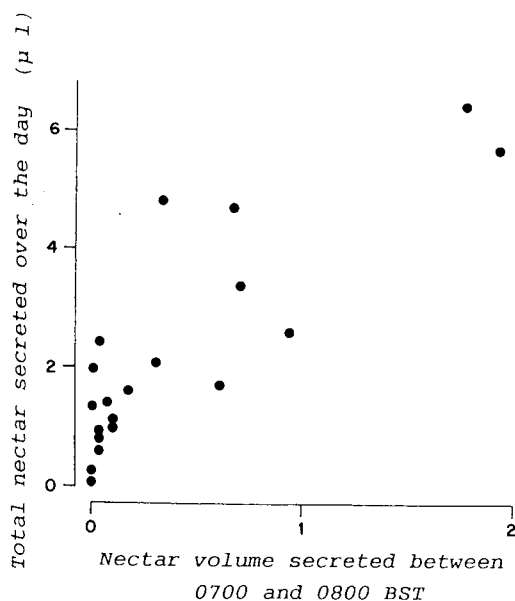
Fig. 4. Plot of nectar productivity during the first hour, 07.00–8.00 h BST, against the total production over the day. The two measures are highly correlated ($r_s = 0.79$, $P < 0.001$).

and 6 days old (Fig. 5c). A one-way specific rank test supported the prediction ($Z = 2.37$, $P < 0.01$) although not enough flowers 2–3 days old were sampled to substantiate it adequately. From the plot, it is conceivable that secretion was bimodal with age, but further data would be required to test this suggestion.

3 *The effect of the number of flowers per plant*

If nectar production is a significant drain on photosynthetic production, then there should be fewer resources available per flower when plants have many flowers. We addressed this question experimentally, by measuring nectar production on 1 day in a single experimental flower from each of six plants with several inflorescences, then removing all inflorescences except the experimental one on each plant, and remeasuring nectar production the following day. We predicted that nectar production after treatment should exceed that of the same individual before treatment; this occurred in five out of the six plants (sign test, $P = 0.11$). This test is of course confounded by flower age, but is conservative. If we assume that nectar production should drop by about 40% between days 1 and 2 (Fig. 5c), then all six plants increased production over expectation ($P = 0.016$).

4 *The effect of nectar removal*

In some flowers, the act of removing nectar is said to stimulate further nectar production (e.g. Gill, 1988a), whereas in others it is said to inhibit production (e.g. Zimmerman & Pyke, 1986). The phenomenon of nectar resorption (Corbet, 1978; Corbet *et al.*, 1979; Corbet & Delfosse, 1984; Burquez, 1988) makes it likely that nectar removal generally increases net secretion by reducing resorption. We tested this by choosing 12 plants and randomly allocating to each one of four treatments. All flowers were bagged overnight, and the accumulated nectar removed at 09.00 h next morning. Subsequently the different treatments were: removal only once at 18.00 h; removal twice (13.00, 18.00 h); removal four times; and removal every 30 min. Since plants differ in total productivity, data were transformed to $\log_e$ (total diel production) − $\log_e$ (overnight accumulation). A one-way rank analysis tested the *a priori* specific hypothesis that the rank order of nectar production increases with increasing frequency of removal. This was supported (Fig. 5d, $Z = 1.86$, $P < 0.05$), although inspection of the mean values of Fig. 5d suggests that probably only very frequent removal has any real effect on the availability of nectar.

5 *Visits by* Anthophora

We expected that handling time should increase (and discrimination time decrease) as nectar secretion rates increase. We marked and bagged 56 plants, removed the overnight accumulation of nectar, and measured the nectar production between 08.00 and 09.00 h: we have already shown that this is highly correlated with total daily production (see above). This measurement was used to characterize the expected reward from each plant. We then measured the discrimination and handling times for foraging *Anthophora* bees. Nearly all data probably come from a single female that foraged extensively in the patch; nearly all measured discrimination times were followed by a visit to the flower.

One extreme outlier had a measured time on the flower more than three times the next highest value; we suspect that this measurement contained much more than the time spent handling nectar found in the flower, and we therefore omitted it from the analysis. With this caveat, there is indeed a significant positive slope to the regression line predicting handling time from nectar productivity (Fig. 6a) for the 42 visited flowers.
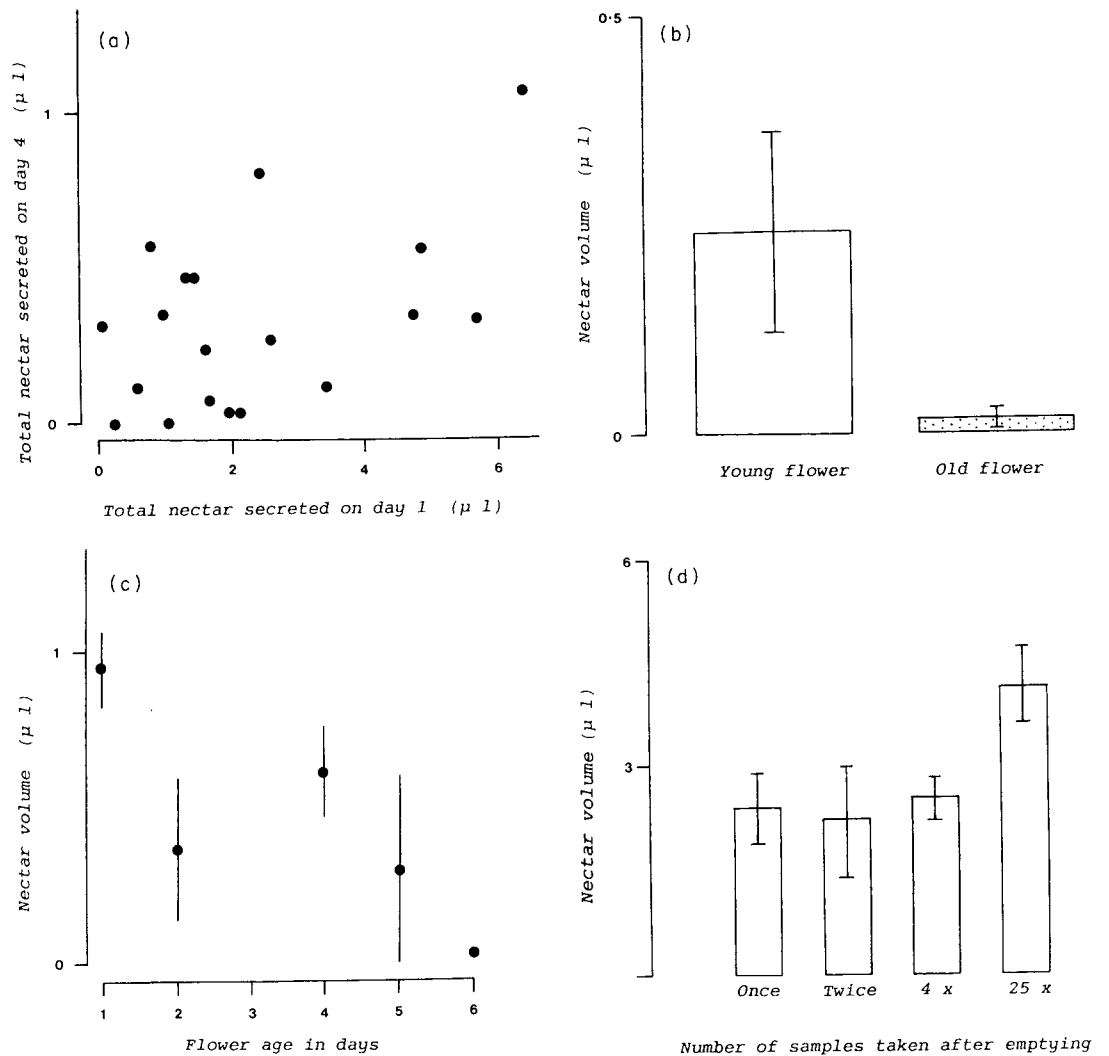
Fig. 5. (a) Plot of the nectar production of 1 day against the mean nectar production of the same inflorescences 4 days later. One extreme outlier has been omitted (see text). Productivity on the 2 days is correlated ($r = 0.49$, $n = 19$, $P \approx 0.02$, one-tailed). The differences in the scales of the axes arise because of sampling differences (see text). (b) Nectar productivity of the two flowers on the same inflorescence. There is a highly significant difference between the two (Wilcoxon signed rank test, $t = 0$, $n = 17$, $P \ll 0.001$). (c) Nectar production *vs* flower age in days. (d) Cumulative nectar production between 09.00 and 18.00 *vs* number of times sampled during the day.

Also as predicted, there is a significant negative relationship between discrimination time and nectar productivity (Fig. 6b) for the 47 flowers approached by *Anthophora*.

6 Testing Bell's prediction

During any particular hour, the ratio between the greatest observed secretion rate and mean secretion rates of flowers never fell below 3·5, and reached more than 7 in the early afternoon and again in late afternoon. Thus assuming that these differences in secretion rates also reflect differ-

ences in nectar standing crop (see below), there is a huge advantage in being able to pick out flowers that contain large amounts of nectar.

The mean discrimination time was 2.08 ± 0.12 s ($n = 247$), and the mean handling times was 2.83 ± 0.17 s ($n = 210$). Thus Bell's (1986) prediction is that 73% of the flowers on a plant should be cheaters. Since we picked single inflorescences on each plant at random, each with one productive flower (see above), this should also be the proportion of cheating flowers in our sample. Fig. 7a shows the 20 plants sampled most intensively for total production over the day, ranked according to
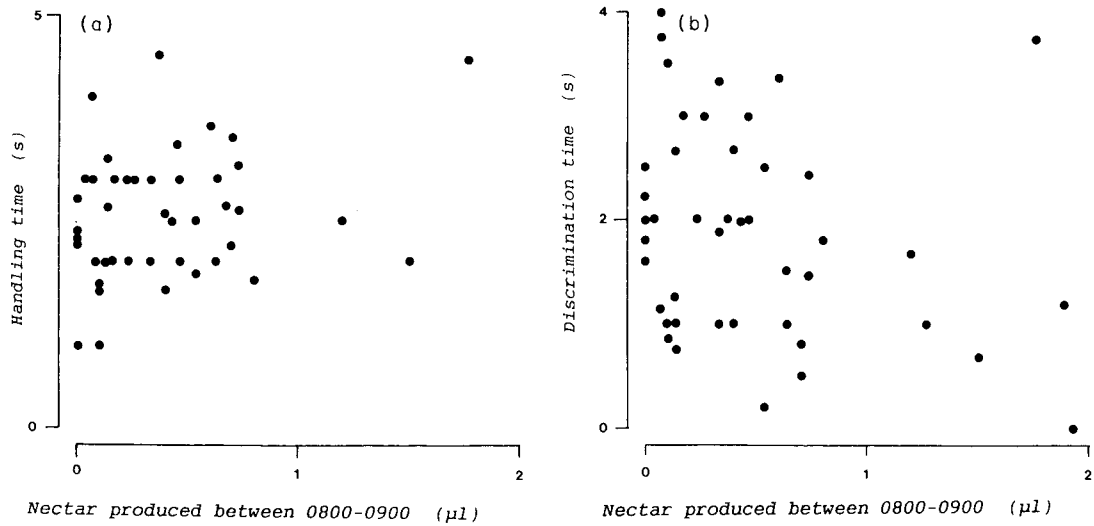
Fig. 6. (a) Handling time by *Anthophora* against the nectar production of the same flowers during 08.00–09.00 h BST. One extreme outlier has been omitted, where it is obvious that most of the time spent on the flower was not connected with obtaining nectar. There is a significant correlation between the two measures ($r = 0.39$, $n = 45$, $P < 0.01$, one-tailed). (b) Discrimination time by *Anthophora* against the nectar production of the same flowers during 08.00–09.00 h BST. There is a signfiicant correlation between the two measures ($r = -0.25$, $n = 47$, $P < 0.05$, one-tailed).

productivity. All flowers produced some nectar. However, there is a distinct change of slope at rank 6, separating a large number (75%) of relatively low producers from a small number of high producers. Fig. 7b shows a similar plot of ranked productivity for the less complete data of the volume secreted during the first hour after removal of the overnight accumulation (08.00–09.00 h) for

47 flowers. Again there is a sharp discontinuity between the mass of low producers (85%) and a few highly productive flowers. We take the change of slope to indicate a real split between secretors and cheaters: no valid statistical test is known to us that will *a posteriori* separate data into two significantly different groups, and therefore we rely on judgement. In neither case is the observed
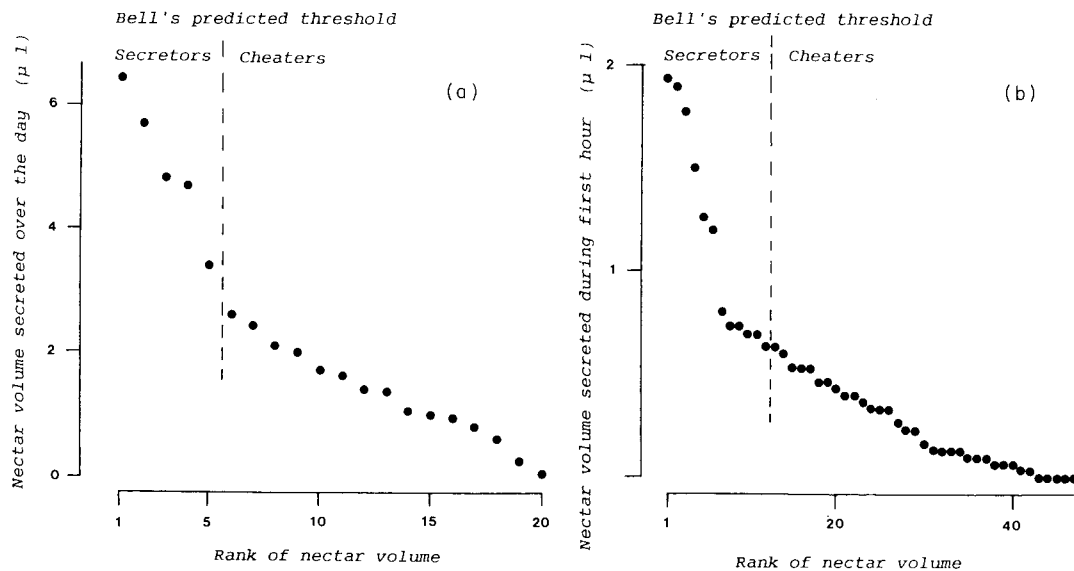

Fig. 7. Ranked nectar production for (a) the 20 flowers sampled intensively throughout the day, and (b) 47 flowers sampled only once, an hour after removal of the overnight accumulation. The dotted line shows Bell's predicted threshold between secretors and cheaters. Notice the distinct change in slope separating relatively low producers from highly productive flowers. There are no significant differences in either case between the observed and predicted numbers ($\chi_1^2 = 0.04$ and 3.51, NS).

numbers of cheaters and secretors significantly different from Bell's prediction (see legend to Fig. 7).

Discussion

Many discussions about plant–pollinator interactions are contingent upon nectar production being costly (Heinrich, 1975; Charlesworth & Charlesworth, 1987). Few studies of reproductive allocation include estimates of the allocation to nectar, so we know very little about whether this is true. The only estimates are high (Schemske, 1978; Pleasants & Chaplin, 1983; Southwick, 1984), and these disregard resorption (Corbet, 1978; Corbet & Delfosse, 1984; Burquez, 1988). All measurements of nectar production should be regarded as indicating the balance between secretion, resorption and removal (Corbet, 1978).

Recent experiments have measured the extent to which photosynthesis by floral structures alleviates the drain on total plant resources; even omitting nectar costs, floral photosynthesis is inadequate to provide carbon for reproductive demands (Williams, Koch & Mooney, 1985). While nectar production represents a high carbon demand, it appears to be buffered against short-term fluctuations in photosynthetic rate (Zimmerman & Pyke, 1988). When we reduced the number of flowers on plants to a single inflorescence, nectar production increased over expectation, supporting the idea that nectar production is a significant drain upon resources in *Cerinthe*.

We assume that selection will favour plants that optimize the balance between the costs and benefits of nectar production, an assumption of Bell's hypothesis of cheating flowers. Experimental addition of nectar to flowers led to greater pollen deposition in *Epilobium* (Galen & Plowright, 1985), and increased fruit set during part but not all of the flowering season, but had no effect on pollen removal in *Blandfordia* (Pyke, Day & Wale, 1988). These studies provide at least some support for the assumption that nectar productivity is a trait under selection.

What is the distribution of nectar productivity among individual flowers, or between plants? It is common to find female flowers in monoecious or dioecious species with a lower nectar production than males (e.g. *Rubus*: Ågren, Elmqvist & Tunlid, 1986; see review by Dafni, 1984). Little information exists in the literature about hermaphrodite flowers, but this encourages the belief that empty or low-producing flowers are common (e.g. Corbet & Willmer, 1981), although there are some excep-

tions (e.g. Southwick, 1983). Two papers show approximately normally distributed productivity among individual flowers (Bertsch, 1983; Pleasants & Chaplin, 1983), but most show very left-skewed distributions (Gill & Wolf, 1977; Feinsinger, 1978; Brink & De Wet, 1980; one of four *Heliconia* spp. in Dobkin, 1984; Marden, 1984b; Zimmerman & Pyke, 1986).

The most comprehensive dataset is from *Impatiens capensis*, but Marden (1984b) used the measured secretion rates for each hour, pooling across individuals, so that his plot cannot be used to identify cheating flowers (since individual flowers may have had widely varying secretion rates between hours). Nevertheless his data fit a negative exponential, as do ours: most data sets on nectar standing crop show a similar distribution between individual flowers (Brink, 1982; Pleasants & Zimmerman, 1983; Cruden et al., 1984; Zimmerman, 1988). Marden (1984b) was unable to find significant between-plant as compared to within-plant differences, a failure expected if plants do indeed play a mixed strategy as Bell envisages. However, as here, many studies do find substantial differences in nectar productivity between plants.

When there are large differences in nectar production between individual flowers, the important confounding influence is flower age and/or flower gender (which are often linked); observed differences may be 'merely' a reflection of the age/gender structure of the population of flowers. In the literature there are interesting differences in findings about the effects of flower age on nectar production; rather less is known about the effect of gender independent of age.

Several studies found no age effects (Bertsch, 1983; Pleasants, 1983; Marden, 1984b; Zimmerman & Pyke, 1986), but not all involved measuring individuals through time (e.g. Marden's failure to document age effects in *I. capensis* did not involve following individuals through time; his study can be compared with that of Bell *et al.* [1984] who did find an effect of flower gender [linked to age] in the same species).

Several studies found nectar production either declining (Voss *et al.*, 1980) or reaching peak very quickly and then declining throughout the life of the flower (Carpenter, 1976; Bond & Brown, 1979; Frost & Frost, 1981; Bertin, 1982; Pleasants & Chaplin, 1983; Southwick, 1983; Southwick & Southwick, 1983; Cruzan, Neal & Willson, 1988). Some plants actually signal when they have been pollinated or are old, advertising these reduced rewards (Gori, 1983, 1989; Delph & Lively, 1989).

Other studies found nectar secretion increasing with flower age (Pyke, 1978; Brink & de Wet, 1980; Corbet & Willmer, 1980; Best & Bierzychudek, 1982; Robertson & Wyatt, 1990).

The major difference between these two lists of plants is that most of the latter groups have a dense linear flowering spike, where flower position determines its age, and Pleasants (1983) put this forward as a possible explanation for the difference. However, *Cerinthe* does not fit into this pattern, in that it does not have a large inflorescence, and yet age effects occur on nectar production. Similarly, *Passiflora* does not fit, for the same reason (Corbet & Willmer, 1980). *Polemonium* also does not fit (Zimmerman & Pyke, 1986) since it has a large inflorescence, yet no age effects were found. S.A. Corbet (personal communication) suggests that the differences in findings may reflect the degree to which the experimenters have considered the entire life of the flower. We do not consider that this can be the whole story. We predict that differences between species in the effects of age and probably gender on nectar production will be found to be real, with an evolutionary explanation.

We suggest that it is possible plants can create a patchwork of flowers with different nectar production characteristics through the effect of age and/or gender on nectar production. G. Bell (personal communication) suggests that there may be an ESS for nectar production, varying with age and gender, because of the different benefits of insect visits to old *vs* young and male *vs* female flowers.

Thus in *Cerinthe* the few high producers of Fig. 7 may be freshly opened flowers, and the rest older: however, the proportions of each group indicate flowers being replaced every 4–6 days, but actually they are replaced every 2–4 days (F. Gilbert, N. Haines & K. Dickson, unpublished observations). Because of this difference, we believe that age structure is not the complete explanation, and that substantial differences in nectar productivity between individual plants and individual flowers either partly or wholly explain these patterns, with flower age perhaps contributing. However, from the point of view of a forager, and for testing Bell's hypothesis, we believe that it does not matter how the pattern comes about: the result is clear.

Our data indicate that the female *Anthophora* in our flower patches could discriminate between flowers on a basis related to rates of secretion. This could be, for example, on the basis of flower age: the female was never seen to visit the older of the two flowers. This implies that some proximal signals, detectable age- or gender-related changes

such as position, colour, or perhaps short-term differences in nectar standing crop, are correlated with longer-term differences in nectar productivity. Our positive correlation between handling time and nectar productivity supports the idea that nectar production rate and standing crop are correlated. On the other hand, Zimmerman (1988) only found a low correlation between nectar production and standing crop. This study found significant correlations between hourly rates of secretion and overall productivity, but we did not measure standing crop in the experimental flowers. Differences in standing crop are expected to reflect nectar productivity when the rate of removal or the inter-visit interval is independent of either (S.A. Corbet, personal communication). Visitation rates to individual flowers were low in this study, and are under further investigation. Perhaps of use would be a model of the way in which the mean and variation in rewards change during exploitation: Possingham (1988) predicted the way in which foraging changes the distribution of nectar in flowers, and it remains to be seen whether his model can be used in the context of bee foraging.

Previous suggestions that foragers discriminate between individual flowers on a basis related to reward have been reviewed by Corbet *et al.* (1984), and good experimental evidence is provided by Corbet *et al.* (1984) for a traplining bumblebee, and by Marden (1984a), Wetherwax (1986) and Kato (1988). Trapline foraging seems the antithesis of our interpretation of the behaviour of the *Anthophora* female we were watching, since systematic visiting suggests much less flexibility. Bumblebees (Manning, 1956; Thomson, Maddison & Plowright, 1982; Thomson, Peterson & Harder, 1987) and hummingbirds (Gill, 1988b) are known to trapline, presumably by memorizing the spatial position of highly rewarding flowers. Since the female *Anthophora* was effectively the only forager in the patch, with the male preventing access by others, she could have memorized the positions of highly rewarding flowers early in the day, and concentrated her visits on them. However, the negative relationship between discrimination time and nectar productivity implies a decision-making process at each flower.

In conclusion, most plants of *Cerinthe* produce relatively small amounts of nectar, but others are highly productive; there may well be differences between the rates of secretion of flowers on a single plant, but our data suggest that there are differences between plants over and above these between-flower differences. At least at the low

visitation rates of this study, the standing crop appears to reflect rates of secretion. It is possible that these patterns are the product of the age structure of flowers together with the way in which nectar production varies with age. In some species of plant rates of nectar production decrease with age, whereas in others they increase: there are possible evolutionary explanations for these differences.

At least one forager to *Cerinthe* appears to discriminate between flowers on a basis related to their probable nectar content. The ratio of the discrimination time to the handling time does appear to coincide with the proportion of low-producing flowers. Therefore these data appear to support Bell's idea of an ESS between plants and their insect visitors. Clearly the idea that the discrimination by insect visitors and floral nectar productivity has reached an ESS needs pursuing further in other types of flower. We suggest that the relationship between nectar production and flower ageing might be one mechanism by which flowers play a mixed strategy.

Acknowledgments

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