FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

How long to stay on, and how often to visit a flowering plant? –
a model for foraging strategy when floral displays vary in size

Kazuharu Ohashi and Tetsukazu Yahara, Dept of Biology, Faculty of Science, Kyushu Univ., Fukuoka 812-8581 Japan (present address of KO: Biological Inst., Graduate School of Science, Tohoku Univ., Sendai 980-8578, Japan [kohashi@mail.cc.tohoku.ac.jp]).

Variation in the number of flowers open at any one time on a plant or an inflorescence, i.e. floral display size, is probably the major factor that affects pollen flow and plant fitness through behavioral responses of pollinators on plants. Many authors have reported that pollinators visit large floral displays more frequently than small ones (e.g. Heinrich 1979, Ohara and Higashi 1994), whilst also visiting more flowers on larger displays (e.g. Geber 1985, Harder and Barrett 1995). With regard to these two types of pollinator response to increased display size, it has often been explained that pollinators visit large floral displays more frequently as a consequence of the associated lower flight costs per flower (Harder and Cruzan 1990, Robertson and Maccnair 1995). However, it seems that pollinators do not always behave in a way that will minimize flight costs per flower. Rather, it has often been observed that a smaller proportion of open flowers was probed on larger displays (Pleasants and Zimmermann 1990 and references therein). This fact seems to contradict the above explanation. Why do pollinators visit a smaller fraction of open flowers during their visit to a large floral display? And if they do, then why should they visit larger displays more frequently than smaller ones?

In this article, we propose a new idea for answering these questions by exploring theoretically how foraging patterns of pollinators may depend on floral display size, from the perspective of pollinators’ optimal foraging. We then test whether observed patterns in the literature support the predictions of our model.

Predictions

The behavior of a pollinator can be described by two variables: 1) the number of flowers probed on a plant or inflorescence during one visit (‘How long should it stay?’) and 2) the frequency of visitation to a plant or inflorescence (‘How often should it visit?’). Although these variables may interact with each other through the distributions of the reward, we initially predict the optimal number of flowers for a pollinator to visit on a plant when display size is invariable, and later we expand it for those cases where display size is variable within a habitat by considering the visitation frequency per plant.

1. How long should a pollinator stay on a plant? – the number of flowers probed per plant in relation to floral display size

Firstly, we develop a simple model to predict how many flowers an optimal pollinator should visit on a plant before leaving in relation to the size of floral display. Here we use the term ‘plant’ as a general term including both individual plants and inflorescences, which would in practice be regarded by a pollinator as one unit of flower patch. The plant departure rule has been studied extensively (Pyke 1984 and references therein), but few attempts have been made previously to explain its interaction with floral display size (Pleasants and Zimmermann 1990).

We assume that nectar is a primary determinant of a pollinator’s behavior, and consider a nectar-foraging pollinator on a plant. The decision to depart from a plant may be affected by the distribution of the nectar standing crop per flower. The amount of nectar standing crop per flower is affected by two processes: depletion by a pollinator and renewal. We assume that flowers are emptied completely when visited. For simplicity, we imagine a situation where all the plants in
the habitat have the same sized floral displays and the pollinator arrival follows a Poisson distribution. Modeling with a constant rate of nectar production, independent pollinator arrivals, and complete nectar depletion on arrival at a flower, Possingham (1988) demonstrated that the probability density function of the nectar standing crop per flower would be bimodal at an equilibrium state. Here, we simply divide flowers into two categories according to their nectar standing crops: 'full' and 'empty'. Each flower is considered to have the same probability of being 'full' at any one time when pollinators' visits are random.

The rule of plant departure we consider here is a stochastic, discrete analogue of the marginal value theorem (Charnov 1976). We index the probability that a flower is 'full' by \( p \), and the probability that a pollinator having successively probed \( t \) flowers on a plant would encounter a 'full' flower at the next \( (t+1) \) probing on the same plant by \( G_{t+1} \). According to the marginal value theorem, a pollinator is predicted to leave a plant before it probes all the flowers when its instantaneous rate of energy gain on the plant has dropped to the average for the habitat. In foraging theory, foragers have sometimes been assumed to make their decisions based on the average long-term energy gain (Possingham et al. 1990). However, we adopt the short-term average energy gain (i.e. gain per flower) as the currency for our model, which is most appropriate for animals with the least memory capabilities, such as insects and birds (Real et al. 1990, Bateson and Whitehead 1996). Then, the condition for the departure from a plant is as follows:

\[
G_{t+1} < kp,
\]

where \( k \) is the mean discounting rate for visiting any flower on other plants in the habitat, i.e. \( k = \frac{((\text{flight time per flower within a plant}) + (\text{handling time per flower}))}{((\text{flight time between plants}) + (\text{handling time per flower}))} \) (0 \( \leq k \leq 1 \)).

This model depends on the assumption that \( G_{t+1} \) continually decreases while \( t \) increases on a plant (depression, Charnov et al. 1976). Without this assumption, \( G_{t+1} \) is constant and a pollinator will probe all the flowers on a plant during one visit. This prediction does not agree with the observed behavior of pollinators. We then first need to incorporate any probable depression processes into the model. A pollinator may occasionally revisit a flower on a plant that it has previously probed, which should yield little or no nectar. As the risk of revisits may increase with the duration of pollinator visits, we employ the increasing risk of revisitation as the major cause of depression for a pollinator foraging on a plant. For some plant species that produce a single unbranched inflorescence showing a regular sequence of flowering up the stem, Pyke (1978a, 1982) found a pattern of decreasing standing crop of nectar per flower proceeding from the bottom to the top. He suggested that the gain function will decelerate over time for bees working upwards on such an inflorescence. However, most plants produce more compound inflorescences composed of many branches and do not show a declining pattern of nectar production or standing crop (Corbet et al. 1981). Therefore, we do not incorporate this type of depression into the model.

Let \( F \) be the number of open flowers per plant and \( n \) be the number of 'full' flowers that the pollinator has actually encountered on the plant by the \( t \)th probing. A pollinator commits at maximum \( m \) flowers that it has previously probed on the plant to memory and avoids revisiting them. If \( t \leq m \), \( G_{t+1} = p \) (\( \geq kp \)). If \( t > m \),

\[
G_{t+1} = \frac{(Fp - n)}{(F - m)}
\]

(2)

If \( F > m \), pollinators stay on the plants until eq. 1 becomes satisfied. Thus, combining eqs 1 and 2 yields

\[
n > (1 - k)pF + mpk.
\]

(3)

When a pollinator leaves a plant with \( F > m \) flowers, the critical number of 'full' flowers it has probed on the plant \( (n_c) \) satisfies the following equation:

\[
n_c = (1 - k)pF + mpk.
\]

(4)

Since \( n_c \) varies in proportion to the critical number of flowers probed on the plant \( (t_c) \),

\[
n_c = t_c p',
\]

(5)

where \( p' \) represents the probability of probing 'full' flowers under the condition allowing a pollinator to revisit, and may be slightly smaller than \( p \). Substituting eq. 4 into eq. 5 yields,

\[
t_c = (1 - k)(p/p')F + m(p/p')k.
\]

(6)

As \( p/p' \approx 1 \) in practice, the following formula will give a good approximation to the required relationship.

\[
t_c = (1 - k)F + mk \quad (F > m),
\]

\[
t_c = F \quad (F \leq m).
\]

(7)

These relationships are shown in Fig. 1. It follows that if \( F > m \), then the number of flowers probed on a plant \( (t_c) \) increases less rapidly than the increase in the number of open flowers \( (F) \). The larger the relative cost of interplant movement \( (1 - k) \), the more rapidly the number of flowers probed per plant \( (t_c) \) increases with increasing display size \( (F) \), i.e. \( t_c \) approaches being
directly proportional to \( F \). Note that the number of flowers probed per plant \( t_c \) is affected little by the probability of being 'full' \( p \) and is determined largely by the cost of movement and the risk of revisitation.

2. How often should a pollinator visit a plant? – the visitation rate per plant in relation to floral display size

Secondly, we show how the visitation rate per plant should depend on floral display size. According to the theory of maximization of net energy gain, a single animal foraging for some patchily distributed resource should prefer the most profitable patch ('optimal patch choice', Pyke et al. 1977). If, however, several or more foragers are competing for the resources, the decisions of each animal must depend on what all the others are doing. This is the situation we have to consider in explaining the pollinator visitation rate per plant. The theoretical treatment of distribution of animals foraging under such situations has resulted in the ideal free distribution model (Fretwell and Lucas 1970). The ideal free distribution (IFD) is an outcome of the evolutionarily stable strategy (ESS) for optimal foragers on a variable resource where the individual gain rate in all local areas or patches is equalized by matching the proportion of foragers to the rate of resource production. It has previously been suggested that nectar foragers distribute themselves among flowers according to an IFD (e.g. Heinrich 1976, Dreisig 1995, Robertson and Macnair 1995, Ohashi and Yahara 1998). The IFD seems to apply well when plant populations are relatively dense and close to the pollinator's nest, i.e. net benefits (gains–flight costs) for pollinators are guaranteed to be positive. When the plant density is much lower, pollinators may concentrate on large displays rather than the expected distribution from the IFD. In nature, however, the latter case is hardly ever found probably because pollinators usually do not specialize in one species at an extremely low density.

On first sight, we consider a situation where all the plants in the habitat have the same sized floral displays. The average number of pollinator visits per flower \( (V_f) \) is the product of the average visitation rate per plant \( (V_f) \) and the average number of flowers probed per plant \( (t_c) \), divided by the number of open flowers on a plant \( (F) \). That is,

\[
V_f = V_{fr}/F.
\]  

We assume that the overall forager/flower ratio is constant. Flowers are assumed to be emptied completely when visited and the nectar content increases linearly between visits. At an equilibrium state, i.e. where the amounts of nectar produced and consumed are equal, the average nectar gain per flower \( (g) \) on a plant depends on both the average nectar production rate per flower \( (P) \) and the average visitation rate per flower \( (V_f) \) on the plant:

\[
g = P/V_f.
\]  

Next, we consider a situation where the habitat contains plants with various sizes of floral display. Even in such a situation, eq. 8 will hold within each plant. Moreover, if pollinators distribute themselves among flowers according to an IFD, the average nectar gain per flower \( (g) \) should be equalized whatever the size of floral display. Assuming simply that the average nectar production rate per flower \( (P) \) is independent of the size of floral display, then, the average visitation rate per flower \( (V_f) \) should also be independent of the size of floral display. Since the probability of a flower being 'full' \( p \) is determined by the distribution of visitation rate per flower with mean \( V_f \), this means that the probability \( p \) is the same for all sizes of floral displays. Under an IFD, therefore, the key assumption behind eq. 1 holds and the number of flowers probed per plant \( (t_c) \) will satisfy eq. 7. Substituting eq. 7 into eq. 8 yields,

\[
V_f = V_f (1 - k) F + mk \quad (F > m),
\]

\[
V_f = V_f \quad (F \leq m).
\]  

As shown in Fig. 2a, the pollinator visitation rate per plant \( (V_f) \) is now expressed as a decelerating function of the size of floral display \( (F) \) that has the asymptotic value of \( V_f(1 - k) \). The larger the relative cost of interplant movement \( (1 - k) \), the less rapidly the visitation rate per plant \( (V_f) \) increases, i.e. the visitation rate per plant approaches a constant for all sizes of display (Fig. 2b). This is an interesting result because, as we have noted previously, it has so far been believed that

Fig. 1. Correlation between critical number of flowers probed per plant \( (t_c) \) and floral display size \( (F) \). Bold line represents the required relationship. Note that as floral display size increases, the number of flowers probed on the plant before leaving increases less than proportionally if \( F > m \).
pollinators visit large floral displays more frequently in order to reduce the cost of flower-to-flower movement. If this is true, the intuitive result of increasing flight costs seems to be an increase in the degree of preference for large floral displays. Our model predicts, however, that an overall rise in the relative flight costs \((1 - k)\) leads to an equalization of the visitation rate per plant among different sizes of floral display.

**Testing the predictions**

Here we summarize previous studies on the relationship between floral display size \((F)\) and 1) the number of flowers probed per plant \((t_i)\); 2) the proportion of flowers probed on a plant \((t_i/F)\); 3) pollinator visitation rate per plant \((V_p)\); and 4) the visitation rate per flower \((V_f)\), as shown in Table 1. We then determine whether observed patterns of pollinator behavior are consistent with the following predictions of our model.

1) The number of flowers probed per plant \((t_i)\) increases with, albeit less rapidly than, display size \((F)\) if \(F > m\). Moreover, the increase is more rapid in a sparse than in a dense plant population (eq. 7). 2) The average visitation rate per plant \((V_p)\) is an increasing function of display size \((F)\) if \(F > m\). The relative preference for large displays lessens as the plant density decreases (eq. 10). 3) The visitation rate per flower \((V_f)\) is independent of the size of floral display providing that the average nectar production rate per flower does not correlate with floral display size.

For a cross comparison, the average interplant distance \((I)\) was converted into the plant density \((D)\) assuming random distributions of plants (Moore 1954):

\[
D = (N - 1)/(\pi N I^2).
\]  

where \(N\) is the number of samples used in calculating \(I\). When \(N\) is not described in the literature, we use \(1/\pi I^2\) as an estimate of \(D\).

In most of the previous studies in Table 1, the number of flowers probed per plant \((t_i)\) significantly increases with, albeit less rapidly than, floral display size \((F)\). Also, the visitation rate per plant \((V_p)\) is usually an increasing function of floral display size \((F)\). In particular, of 17 cases (populations) in Table 1, 10 demonstrated a decelerating relationship between the visitation rate per plant and floral display size. Furthermore, Klinkhamer et al. (1989) and Klinkhamer and de Jong (1990) found that more flowers tended to be probed per plant in isolated than in dense stands, while isolated plants tended to be visited evenly regardless of their display sizes. Dreisig (1995) also reported in a sparse population of *Anchusa officinalis* that the visitation rate per plant \((V_p)\) as well as the proportion of flowers probed per plant \((t_i/F)\) was independent of floral display size. The available data thus seem to provide good qualitative support for predictions 1 and 2.

Examinations of nectar production rate per flower have often yielded no significant correlation with the size of floral display (Marden 1984, Zimmerman and Pyke 1986, Harder and Cruzan 1990), although some reports have occasionally found a positive (Devlin et al. 1987) or a negative (Pleasants and Chaplin 1983) correlation. Therefore, the expected general pattern of visitation rate per flower demonstrates no correlation with display size, except for those few cases showing a positive or negative correlation. Of 16 cases, 9 (56.3\%) lack any association between display size and visitation rate per flower. The remaining four (25\%) and three (18.8\%) demonstrated negative and positive relationships, respectively. Thus, the available data are also consistent with prediction 3.

**Discussion**

Now we can give a good account of the questions that we raised in the opening paragraph of this paper: why do pollinators visit a small fraction of open flowers during their visit to a large floral display, and why should they visit larger displays more frequently than smaller ones? Firstly, the optimal number of flowers probed per plant \((t_i)\) increases with the number of open flowers \((F)\), but only slightly so if staying on a plant...
Table 1. A tabulation of reports concerning how parameters of pollinator visitation (number of flowers probed on plant, $t_c$, proportion of flowers probed per plant, $t_c/F$, visitation rate per plant, $V_p$, and visitation rate per flower, $V_f$) correlate with floral display size ($F$). The notations, $+$, $-$, and $\pm$ indicate positive, negative, and statistically non-significant relationships, respectively, found between these parameters and floral display size. Equations indicated in parentheses express the exact form of the functional relationships between the number of flowers probed per plant ($t_c$) and display size ($F$) obtained from regression analyses.

<table>
<thead>
<tr>
<th>Plant</th>
<th>$t_c - F$</th>
<th>$t_c/F - F$</th>
<th>$V_p - F$</th>
<th>$V_f - F$</th>
<th>Plant density (plants/m²)</th>
<th>Pollinator</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aconitum columbianum</td>
<td>+</td>
<td>$- +$</td>
<td>$+ 15$</td>
<td></td>
<td></td>
<td>bumblebee</td>
<td>Pleasants and Zimmerman (1990)</td>
</tr>
<tr>
<td>Anchusa officinalis</td>
<td>$(\ln t_c = -0.062 + 0.069 \ln F)$</td>
<td>$-$</td>
<td>$\pm$</td>
<td>$\pm 0.014$</td>
<td>bumblebee</td>
<td>Dreisig (1995)</td>
<td></td>
</tr>
<tr>
<td>Atractylis hirsuta</td>
<td>$+ (t_c = 0.22F)$</td>
<td>$- \pm$</td>
<td>$- \pm 0.65-0.71$</td>
<td></td>
<td>bumblebee, honey bee, etc.</td>
<td>Morse (1986)</td>
<td></td>
</tr>
<tr>
<td>Asclepias syriaca</td>
<td>$+$</td>
<td>$- \pm$</td>
<td>$\pm 0.15$</td>
<td></td>
<td>bumblebee</td>
<td>Ohashi and Yahara (1998)</td>
<td></td>
</tr>
<tr>
<td>Cirsium purpuratum</td>
<td>$(t_c = 1.117 + 0.051F)$</td>
<td>$- +$ (strong)</td>
<td>$\pm 2-20$</td>
<td></td>
<td>bumblebee</td>
<td>Klinkhamer et al. (1989)</td>
<td></td>
</tr>
<tr>
<td>Cynoglossum officinale</td>
<td>$(\log t_c = 0.48 \log F, \log t_c = -0.20 + 0.39 \log F)$</td>
<td>$- +$ (weak)</td>
<td>$\pm 0.01 &gt;$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delphinium nelsonii</td>
<td>$+$</td>
<td>$- +$</td>
<td>$\pm 0.91$</td>
<td></td>
<td>queen bumblebee</td>
<td></td>
<td>Pleasants and Zimmerman (1990)</td>
</tr>
<tr>
<td>Echium vulgare</td>
<td>$(\ln t_c = 0.57 + 0.31 \ln F)$</td>
<td>$- +$</td>
<td>$\pm 1-20$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td>Klinkhamer and de Jong (1990)</td>
</tr>
<tr>
<td>Eichhornia paniculata</td>
<td>$(\ln t_c = 0.04 + 0.6 \ln F)$</td>
<td>$- \pm$</td>
<td>$\pm 0.012$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td>Harder and Barrett (1995)</td>
</tr>
<tr>
<td>Epilobium angustifolium</td>
<td>$+$</td>
<td>$- +$</td>
<td>$\pm 3.5$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td>Schmid-Hempel and Speiser (1988)</td>
</tr>
<tr>
<td>Mercurialis alba</td>
<td>$(t_c = 3.15 + 0.145F)$</td>
<td>$- +$ (dense)</td>
<td>$\pm 1.3 &lt;$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td>Geber (1985)</td>
</tr>
<tr>
<td>Mimulus guttatus</td>
<td>$+$</td>
<td>$- +$</td>
<td>$\pm 1.2-3.3$</td>
<td></td>
<td>bumblebee, honey bee</td>
<td></td>
<td>Robertson and Macnair (1995)</td>
</tr>
<tr>
<td>Myosotis colensoi</td>
<td>$+$</td>
<td>$- +$</td>
<td>$\pm 1.2-3.3$</td>
<td></td>
<td>tachinid fly</td>
<td></td>
<td>Robertson and Macnair (1995)</td>
</tr>
<tr>
<td>Viscaria vulgaris</td>
<td>$(t_c = 0.663 + 0.33F)$</td>
<td>$- +$</td>
<td>$\pm 1.2-3.3$</td>
<td></td>
<td>bumblebee</td>
<td></td>
<td>Dreisig (1995)</td>
</tr>
</tbody>
</table>
increases the risk of revisiting flowers and if the cost of interplant movement is relatively small (Fig. 1). As a result, pollinators leave greater proportions of flowers behind on larger floral displays. Secondly, under the assumption of an IFD, pollinators are expected to equalize the visitation rate per flower. To achieve an IFD, they visit larger displays more frequently in such a way that the visitation rate per flower is similar to that with smaller ones. In other words, our model suggests that pollinators prefer large floral displays over small displays in order to efficiently utilize 'full' flowers with an even distribution over time, not in order to lessen the flight costs per flower.

The most remarkable prediction of our model is that a widening of interplant distance reduces the preference for large floral displays over small ones, as opposed to intuition. Although some authors have argued that the proportion of flowers probed on a plant increases with the mean interplant distance of the population (Heinrich 1979, Zimmerman 1981, Cibula and Zimmerman 1984, Klinkhamer and de Jong 1990, Cresswell 1997), none of them gave any thought to the effect of interplant distance on the 'attractiveness' of large floral displays over small ones. We can propose good qualitative support for this counterintuitive prediction, as shown in Table 1. At present, however, we cannot perform a more complete, quantitative test of the model because most of the previous data lack information on some of the parameters needed in this model. Constraint on pollinators' memory, which more or less reflects their habit of movement on a plant, is one critical point because it may lead to inevitable patch depression even in the absence of any spatial declines of nectar per flower. Unfortunately, the importance of this constraint has not been widely enough appreciated and no data are available on a pollinator's capacity to avoid revisitation (m). We can only inconclusively suggest that m is often smaller than the total number of flowers on the plant (F), based on Pyke's observations with hummingbirds and honeybees that the frequency of revisits increases with the number of flowers probed on a plant (Pyke 1978b, 1981). Moreover, only a few studies have measured the time spent probing a flower and traveling between flowers or plants which is required for calculating the discounting rate for visiting any flower on other plants within the habitat (k). Limited data suggest that k ≈ 0.87 for Bombus appositus foraging on Aconitum columbianum (after Pyke 1979), and k ≈ 0.65 and 0.41 for B. appositus foraging on Delphinium nelsonii (after Hodges 1981, 1985). Furthermore, no researchers so far have attempted to determine these two parameters within the same plant population. If we know these parameters in one plant-pollinator system, then we can predict t/F and compare that against the actual fraction of flowers probed on a plant. These detailed examinations await future investigation.

Note that we never expected the IFD to be taken particularly seriously, but simply assumed that any foraging behavior yielding a large variance among different-sized plants with regard to the average energy gain per flower could not be an ESS. In this sense, an equalization of the visitation rate per flower among plants assumed here is a 'quasi-IFD'. For example, if pollinators could detect and correct the subtle differences in the average traveling time per flower or the ratio of m to t, among plants, then the assumption of an equal visitation rate per flower would be violated. However, as Dreisig (1995) and other studies in Table 1 have suggested, these differences are so small that they are ignored by pollinators, or else any effect is too small to be detected at the actual level of analyses. Even if the visitation rate per flower barely depends upon floral display size, this would not reverse the main conclusion of the current study.

In our model, we ignore the effect of arrangements of flowers in inflorescences and floral designs on the parameters of pollinator behavior. For example, a pollinator's capacity to avoid revisitation (m) may be improved by a simple spiked inflorescence. Another example is the morphological aspects of flowers associated with handling time per flower. As the handling time per flower increases (with longer corolla tubes, more complex-structured flowers, etc.), the relative cost of interplant movement (1 - k) would approach zero (see definition of k). Although data are not yet available, these effects could be an important theme for future studies with a view to answering how plants can maximize pollinator visitation while minimizing within-plant movement (Iwasa et al. 1995).

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References


