

Plant reproductive intervals and pollinators in the aseasonal tropics: a new model

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What factors determine reproductive intervals and modes of pollination in plants of the aseasonal tropics? To answer this general question, we present a new explanation for some community patterns of plant reproductive intervals and pollinators observed in a lowland dipterocarp forest in Sarawak, Malaysia, using a mathematical model featuring different display effects for different types of pollinators. Predictions from the model matched with the following observed patterns: (i) flowering intervals were different among forest strata (forest floor < understorey < canopy < subcanopy and emergent), and not in the exact order of stratum height; (ii) among generalist pollinators, the proportion of social foragers was maximum in intermediate forest stratum; and (iii) plants pollinated by specialist pollinators were found on the forest floor and in gaps.

Keywords: display effect; reproductive interval; pollination; mortality; productivity; forest strata

1. INTRODUCTION

In some tropical areas, including Sarawak, Malaysia, annual cycles in climate and plant phenology are not clearly discernible (Yap 1982). In tropical rainforests of such aseasonal areas, some plant species reproduce almost continuously (Corner 1952), whereas others separate reproductive events by a long interval (>10 years; Ng 1981). To explain long reproductive intervals of some tropical plants, the seed-predator satiation hypothesis (Janzen 1971a,b) has often been applied (Janzen 1974; Ashton *et al.* 1988). In a review of the adaptive significance of mast fruiting in seasonal regions, Kelly (1994) claimed that predator satiation and efficiency for wind pollination could be of adaptive significance for mast fruiting in some plants. Although this conclusion can also be applied to long reproductive intervals of plants in the aseasonal tropics, it cannot explain why some plants have long reproductive intervals and others do not in the same forest.

Here we provide another possible explanation based on 'display effect' (i.e. a large number of flowers results in large pollinator attraction per flower for some pollinators (Thomson *et al.* 1982; Sih & Baltus 1987)). Relations between pollination systems and plant habits have been discussed in the theory of energetics of pollination by Janzen (1971c) and Heinrich & Raven (1972). They report that plants in higher strata can attract a large number of generalists by massive blooming, whereas understorey plants cannot provide a large display because of low productivity. Instead, these plants attract specialized pollinators by offering rich nectar that is protected from

other visitors by morphological specialization of the flowers. We hypothesize that each plant has an optimal length of reproductive interval for pollinator attraction, which depends on the habitat condition and the mode of pollination it uses. To test this, we provide a mathematical model incorporating both merits and demerits of long reproductive intervals to predict community patterns, and the predictions from the model are compared with observed patterns in a tropical rainforest in Malaysia.

2. THE MODEL

We developed a mathematical model to investigate how the display effect of a plant may affect its reproductive success, and thus, how long an interval it should have between each reproductive event.

For simplicity, we make the following assumptions: (i) each plant has a species-specific mature (maximum) size; (ii) after reaching mature size, productive parts do not grow; (iii) the surplus of net production (mostly constant) from which body-maintenance costs (constant) are subtracted is used for reproduction; (iv) death of a plant occurs by chance, and is not affected by reproductive events, because the main mortality factor of adult forest trees is disturbance (Whitmore 1989, 1990); and (v) for opportunist insects, we deal only with attraction by olfactory substances, although display effect in visual attraction might also be important.

(a) *Display effects*

Display effect is defined as the number of attracted pollinators per flower and it is obtained from dividing total attracted pollinators by total flowers of an individual. In what follows, we assume different types of display effect for three types of pollinators: opportunist insects, social foragers and specialists.

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(i) *For opportunist insects*

Opportunist insects do not communicate with each other, and are attracted to rich flower patches. Initially, we consider the effect of floral odours in opportunist pollinator attraction. The odour density around an individual plant, g , is proportional to the number of its flowers, f , and decreases with the distance from the centre of flower patch, ρ . Provided that each flowering period is not extremely short and that the flowering odour substance diffuses with no directionality, g can be expressed with a constant B , as $g = Bf/\rho$ (see Appendix A). Opportunist insects are able to detect flowering odour that is stronger than the threshold density, G . Thus, the maximum distance, R , from the plant individual that opportunist insects can be attracted is obtained as $R = Bf/G$.

Assuming that the distribution of insects is homogeneous and a constant proportion of insects that detect odour are attracted to flowers, the number of attracted insects, n , is proportional to the volume of the sphere of radius R , and can be expressed with a constant value H as $n = HR^3$. Eliminating R from the above two equations yields $n = H(B/G)^3 f^3$. By dividing the number of attracted insects by number of flowers, we obtain the display effect, D , as

$$D = n/f = H(B/G)^3 f^2.$$

Modifying this equation, we consider more general cases in which the display effect can be expressed as

$$D(f) = Cf^s, \quad (1)$$

where s is a positive constant representing the degree of sensitivity of display effect against the number of flowers ($s=2$ and $C=H(B/G)^3$ in the above case).

(ii) *For social foragers*

Social foragers communicate with their own colony members. Each colony has scout foragers that recruit foragers (Roubik 1989). Scout foragers monitor floral resource and can evaluate the quality of visited flower patches (i.e. how much floral resources a plant individual contains). They ignore poor flower patches (i.e. plant individuals with small numbers of flowers) and continue seeking richer ones. When they find a plant individual with a larger number of flowers than a threshold, they recruit the colony members and harvest the floral resources (for discussion of mechanisms of movement among individuals, see Roubik (1989), Khoo (1992) and Roubik *et al.* (1995)). It is assumed here that the number of recruited foragers per plant is proportional to the number of flowers, because scout foragers correctly evaluate the quality of each patch. Therefore, the display effect for social foragers can be expressed as

$$D(f) = \begin{cases} 0 & \text{if } f < f_0 \\ K & \text{if } f \geq f_0 \end{cases}, \quad (2)$$

where f_0 and K are the threshold flower number for social foragers and the constant number of attracted social foragers per flower, respectively.

(iii) *For specialist pollinators*

Specialist-type flowers exclude generalists and offer reward only to their specialist pollinators (Faegri & von der Pijl 1979). Specialist insects know the amount of reward remaining in each flower, and visit flowers with rich rewards (ideal free distribution (Fretwell & Lucas 1970)). They know the essential benefit of visiting a flower and the visitation frequency is not affected by any attractive display, so that each flower should be visited evenly. Therefore, display effect for specialists is independent of the number of flowers, and it can be expressed as

$$D(f) = L \quad \text{if } f > 0, \quad (3)$$

where L is the species-specific constant.

(b) *Effect of long flowering interval*

The number of flowers, f , in each reproductive event is proportional to flowering interval x , and it can be expressed as $f = Ax$, where A is a constant coefficient representing productivity of the plant. What is the demerit of long flowering intervals? The most important risk is the decrease in reproductive chance due to the death during the intervals. The survivorship probability, l , at time t after reaching the mature size is $l(t) = e^{-mt}$, where m is the plant mortality rate. The expected number of reproductive events, E , throughout the lifetime of the plant individual can be expressed as

$$E = \sum_{i=1}^{\infty} l(ix) = \frac{e^{-mx}}{1 - e^{-mx}}. \quad (4)$$

Therefore, the total number of pollinators, y , expected to be attracted throughout the lifetime is

$$y = D(f) \times f \times E = D(Ax) \frac{Axe^{-mx}}{1 - e^{-mx}}. \quad (5)$$

Note that $D(f)$ is dependent on what type of pollinators the plant individual attracts as mentioned in §2a.

(c) *Optimum reproductive intervals*

By uniting 'display effect' and 'effect of flowering interval', we can discuss whether an optimal reproductive interval for a plant individual exists and how long it is.

(i) *For opportunist insects: social foragers and specialists absent*

The expectation of attracted insects y can be obtained from equations (1) and (5) as

$$y = \frac{A^{s+1} C x^{s+1} e^{-mx}}{1 - e^{-mx}}. \quad (6)$$

The optimum reproductive interval, x_{opt} , giving the maximum y is obtained (see Appendix B) as $x_{\text{opt}} = \alpha/m$, where α is the solution of the following equation with respect to a :

$$e^{-a} = 1 - \frac{a}{s+1}, \quad (7)$$

which cannot be solved analytically, but it is obvious that it depends only on s . Therefore, as the mortality rate m increases, the optimum reproductive interval x_{opt} decreases. In this case, plant productivity A does not affect the flowering interval that realizes the maximum lifetime pollinator attraction.

(ii) *For social foragers: opportunists and specialists absent*

From equations (2) and (5),

$$y = \begin{cases} 0 & \text{if } 0 < x < f_0/A \\ \frac{KAxe^{-mx}}{1 - e^{-mx}} & \text{if } x \geq f_0/A \end{cases}$$

As y is a decreasing function of x for the range $x > f_0/A$, y takes its maximum value at $x_{\text{opt}} = f_0/A$. Thus, the optimum flowering interval x_{opt} is affected only by the plant productivity A in this case.

(iii) *In case there exist only specialist pollinators*

Display effect is independent of the number of flowers per individual (equation (3)). From equations (3) and (5),

$$y = \frac{LAxe^{-mx}}{1 - e^{-mx}} \text{ for } x > 0.$$

As y is a decreasing function of x for the range $x > 0$, in this case, $x=0$ (i.e. continuous reproduction) results in maximum pollinator attraction. Then, the expectation of the total number of pollinators attracted throughout the lifetime y_1 is

$$y_1 = \lim_{x \rightarrow 0} y = \frac{AL}{m}. \quad (8)$$

Thus, there are three possible types of display effect and optimal flowering interval for a plant individual depending on which pollinators it uses. The type of pollinators a plant individual uses depends on what type of flowers the plant individual has. In general, flowers are divided into two types: generalist-type and specialist-type. Generalist-type flowers, which do not have any mechanisms to avoid visits by generalist pollinators, attract any generalist-type pollinators, whereas specialist-type flowers attract only the matching specialist-type pollinators. Therefore it is necessary to consider the optimal flowering interval for the case where a plant individual with generalist-type flowers attracts both opportunist insects and social foragers.

The display effect of generalist-type flowers is, therefore, the sum of the display effects for the two types of generalist pollinators and it can be expressed as

$$D(f) = \begin{cases} Cf^s & \text{if } f < f_0 \\ Cf^s + K & \text{if } f \geq f_0 \end{cases}. \quad (9)$$

Here, we assume that the number of social foragers per flower is not affected by the existence of opportunists and vice versa, because social foragers can harvest floral resources much more effectively than opportunists, whereas opportunists cannot evaluate the remaining resources before visiting flowers. From equations (5) and (9), the expected number of pollinators y is

$$y = \begin{cases} \frac{A^{s+1}x^{s+1}e^{-mx}}{1 - e^{-mx}} C = y_a & \text{if } f < f_0 \Leftrightarrow x < f_0/A \quad (10a) \\ \frac{Axe^{-mx}}{1 - e^{-mx}} (CA^s x^s + K) = y_b & \text{if } f \geq f_0 \Leftrightarrow x \geq f_0/A \quad (10b) \end{cases}$$

The maximum value of y is the larger of the maxima y_a for $x < f_0/A$ (equation (10a)) and y_b for $x \geq f_0/A$ (equation (10b)). Therefore, in generalist pollination there exist the following three phases depending on A .

Phase I. When plant productivity per capita A is small (figure 1a), both the range and the maximum value of y_b are small and hence the optimum interval x_{opt} is identical to the value of x that gives the maximum y_a (that is, $x_{\text{opt}} = \alpha/m$) and flowers are pollinated only by opportunist insects.

Phase II. When A is larger than the critical value, the maximum value of y_b exceeds the maximum y_a , and x_{opt} shifts to that value of x that gives the maximum y_b (that is, $x_{\text{opt}} = f_0/A$) (figure 1b). Flowers then become pollinated both by social foragers and opportunist insects. The proportion of social foragers to total pollinators, S_{II} , is $S_{\text{II}} = K/(K + Cf_0^s)$.

Phase III. For $A > f_0/\alpha$ (figure 1c), x_{opt} is identical to α (referred to as β), that is, the solution of $dy_b/dx = 0$. As A increases, β increases and approximates to α/m . The proportion of visits by social foragers, S_{III} , can be expressed with β as $S_{\text{III}} = K/(K + C(A\beta)^s)$. Because $\beta > f_0/A \Leftrightarrow A\beta > f_0$, $S_{\text{III}} < S_{\text{II}}$ holds, that is, the proportion of visits by social foragers is less than phase II.

3. PREDICTIONS FROM THE MODEL

In this section, we present actual predictions ($P_{\text{i-iv}}$) derived from the above model.

(a) *For generalist-type plants: optimal reproductive intervals changing along forest strata*

In general, plant productivity is positively correlated with height, as an increase in plant size usually brings better light conditions. Manokaran & Kochummen (1987) showed that plant mortality differs among species of different size groups in the following sequence in a lowland dipterocarp forest in Malaysia: emergent < main canopy < subcanopy < understorey. With regard to the relationship among plant mature size in closed (mature-phased) forests, we assume the following.

1. Productivity A is an increasing function of plant size ($A_{\text{understorey}} < A_{\text{canopy}} < A_{\text{emergent}}$).
2. Mortality m is a decreasing function of plant size ($m_{\text{understorey}} > m_{\text{canopy}} > m_{\text{emergent}}$).
3. The following two relationships are assumed: $f_0/A_{\text{emergent}} < \alpha/m_{\text{emergent}}$ and $\alpha/m_{\text{understorey}} < f_0/A_{\text{understorey}}$.

With these assumptions, we predict the following sequential changes in the expected pollinators and the optimal flowering interval for generalist-type plants along the gradient of plant mature size.

- P_{i} Plants of small mature size (i.e. understorey). First, the optimum reproductive interval (i.e. α/m) increases as plant size increases because of the decrease in mortality rate m (indicated by filled triangles and arrow (1) in figure 2). This range corresponds to phase I (see above) and figure 1a.
- P_{ii} When plant mature size exceeds the critical value, social foragers appear and the optimum reproductive interval shifts up to f_0/A (arrow (2) in figure 2).
- P_{iii} Plants of intermediate mature size. The optimum reproductive interval, f_0/A , decreases as mature size increases because of the increase in A (indicated by open circles and arrow (3) in figure 2). The ratio of

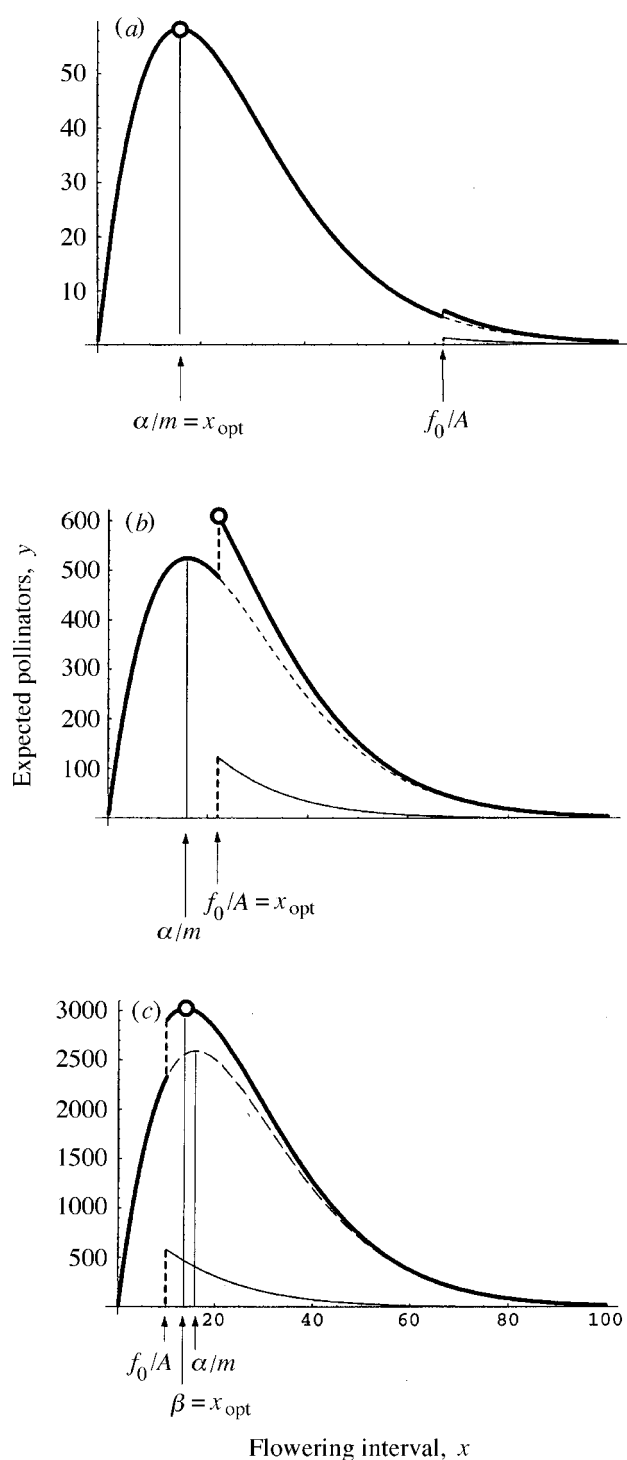


Figure 1. The relationship between the reproductive interval (x) and the number of pollinators attracted throughout the lifetime (y) of a generalist-type plant. In each panel, thin curves represent the numbers of opportunist insects (broken line) and social foragers (solid line) attracted to the plant, the thick curve represents the total numbers (i.e. y -value in equation (10)) and the open circles indicate the maximum y . (a) $A=3$. When productivity A is low (phase I), the optimum value of x is α/m , and flowers are pollinated only by opportunist. (b) $A=9$. As A becomes larger, the optimum value of x shifts to f_0/A (phase II). (c) $A=20$. When A increases further, the optimum value of x shifts to β (phase III), which is always slightly smaller than α/m , and the proportion of opportunist increases again. Other parameters: $s=2$, $K=0.2$, $f_0=200$, $m=0.1$.

social foragers to the total pollinators is highest. This range corresponds to phase II and figure 1b.

P_{IV} Plants of largest mature size ($A/m > f_0/\alpha$, i.e. emergent). The optimum reproductive interval ($\beta \simeq \alpha/m$) increases again because of the decrease in m (indicated by filled circles and arrow (4) in figure 2). This range corresponds to phase III and figure 1c.

In summary, we predict that as a tree becomes taller the optimum reproductive interval increases initially, then decreases, and finally increases again. The proportion of social foragers among the pollinators increases with tree height, reaching a maximum at intermediate heights and decreasing thereafter.

(b) Prediction for specialist plants: conditions for specialist pollination

Under what conditions should tropical plants make specialist-type flowers to attract specialists as pollinators? To answer this, we obtained the ranges of the two plant variables A and m that are necessary for specialist attraction, provided that the other parameters are given. As the number of expected opportunist insects is never larger than that of the total number of generalist pollinators (i.e. $\text{opportunist} \leq \text{opportunist} + \text{social foragers}$), the necessary condition for plants to have specialist pollination is, by definition, to have values of A and m that offer more expected specialist pollinators than opportunist insects. As shown in equation (8), the maximum number of specialist pollinators y_1 , attracted throughout the lifetime of a plant, is given by $y_1 = AL/m$, whereas the maximum number of expected opportunist, y_2 , is obtained from equation (6) as

$$y_2 = \left(\frac{\alpha A}{m}\right)^{s+1} \left(\frac{s+1-\alpha}{\alpha}\right).$$

Specialists can be chosen as pollinators only when the following condition is satisfied

$$y_1 \geq y_2 \Leftrightarrow \left(\frac{m}{A}\right)^s \geq \frac{\alpha^s}{L}(s+1-\alpha).$$

From above relationship, it is suggested that only when A (productivity) is small and/or m (mortality) is high can specialists be used as pollinators. This condition on A and m is incompatible with the condition for pollination by social foragers (i.e. sufficiently large A). This brings the following prediction.

P_V Specialist-type plants can attract more pollinators in layers of low productivity with high mortality, so that they should be observed more in the lower layers such as the forest floor.

4. TESTING THE PREDICTIONS OF THE MODEL

The predictions of the model were tested from the field data of the Canopy Biology Plot (200 m \times 400 m (8 ha), 4°2' N, 113°50' E) in Sarawak, Malaysia, collected by Momose *et al.* (1998). They collected 7240 (including 6883 generalists) individuals of flower-visiting insects. The proportion of social foragers among generalist flower visitors was maximum in intermediate (subcanopy and main canopy) forest strata (figure 3). This pattern was

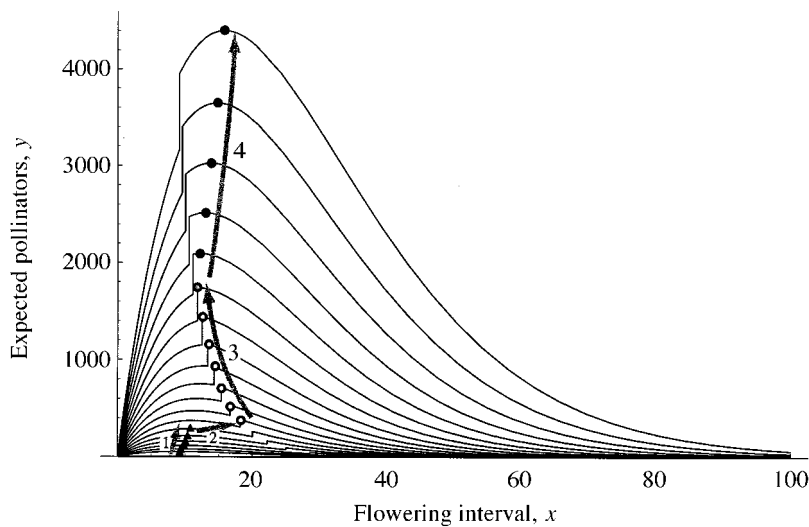


Figure 2. The change in the number of total attracted generalist pollinators together with the increase in plant productivity A and decrease in mortality m of a general-type plant is depicted. Here we assume the following negative correlation between A and m : $m = 0.2 - A/200$. The lowest curve is for $A = 5$ and $m = 0.175$; the highest is for $A = 22$ and $m = 0.09$. The interval of A is 1. The gradient of A and m in this figure corresponds to plant mature size, so that it is predicted that as plant mature size increases, the optimum reproductive interval first increases (indicated by filled triangles, arrow (1)), then jumps to a longer interval (to the lowest open circle, arrow (2)), then decreases (open circles, arrow (3)), and finally, in the largest size range, increases again (filled circles, arrow (4)). Other parameters: $s = 2$, $K = 0.2$, $f_0 = 200$.

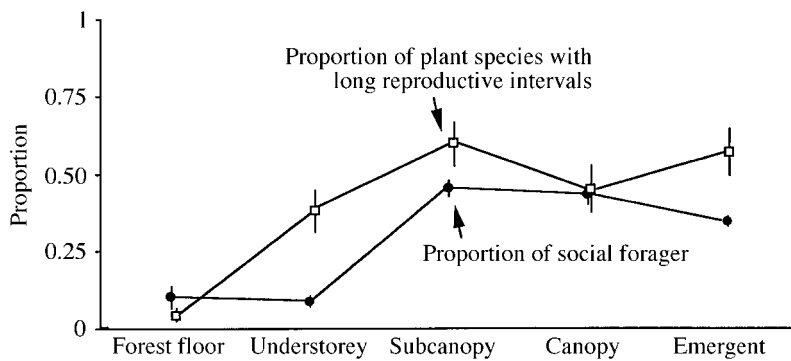


Figure 3. Frequency of social foragers on flowers and reproductive intervals of plants observed at various forest strata (based on the data in Momose *et al.* (1998)). Squares, proportion of social foragers among generalist flower visitors (6883 individuals) collected on flowers in various forest strata. Circles, proportion of plant species with long reproductive intervals (reproduced only once during the 53 months) among 212 plant species of various forest strata.

statistically significant (whole pattern, $\chi^2 = 397$, $p < 0.001$; understorey trees compared with subcanopy trees, $\chi^2 = 577$, $p < 0.001$; canopy trees compared with emergent trees, $\chi^2 = 215$, $p < 0.001$). These data match the predictions of the model (P_{i-iv}), except that a low density of social foragers was observed in lower strata (understorey and forest floor). Although Appanah & Chan (1981) reported that some dipterocarps are pollinated by thrips in Pasoh, Malaya, Sakai *et al.* (1998) showed experimentally that at our study site (Lambir, Sarawak), beetles play an important role in pollination of *Shorea parvifolia*, whereas thrips have a negligible contribution. Furthermore, in the same area, Momose *et al.* (1998) reported that beetles and bees pollinate many other dipterocarp species.

Momose *et al.* (1998) observed the reproductive events of 212 plant species over 53 months (figure 3). The proportion of the plant species with long reproductive intervals (reproduced only once during the 53 months) was the lowest in forest-floor plants and highest in the emergent strata. However, it decreased at the canopy stratum compared with the subcanopy stratum. In these strata, social foragers are dominant among generalists. As social foragers became less frequent, the proportion of the plant species with long reproductive intervals increased again (canopy to emergent strata), which supports the model's predictions (P_{i-iv}). The proportion of plant

species with long reproductive intervals is significantly higher in the subcanopy and emergent strata than in other forest strata ($\chi^2 = 9.0$, $p < 0.01$). However, no significant differences were detected in comparisons between subcanopy and canopy and between canopy and emergent strata.

Momose *et al.* (1998) identified the main pollinators of 240 species of terrestrial free-standing plants (table 1; lianas and epiphytes are excluded), and observed that plants pollinated by specialist insect pollinators were found more frequently close to the forest floors and in gaps than in other habitats ($\chi^2 = 186$, $p < 0.001$), supporting the prediction P_v .

5. DISCUSSION

Field data showed that social foragers are observed also in lower strata of the forest, although they are predicted to be seen only in higher strata. This may be because of the size variation of social bees that we ignored in the model for simplicity. The observed species were relatively small ones (*Trigona mellina*, *T. melanocephala*, *T. laeviceps* and *T. fuscobaltata*). The threshold of patch quality, f_0 , for these bees is relatively low because they have low foraging costs and a small foraging area (Roubik 1989). Larger social foragers (other species in the genera *Trigona* and *Apis*) have been observed only infrequently near the forest

Table 1. *Pollinators of plants of various habits (based on the data in Momose et al. 1998)*

(Specialist insects include trap lining bees, butterflies and moths.)

	habitat and forest strata					
	gap	forest floor	understorey	subcanopy	canopy	emergent
no. plant species	45	58	38	49	28	22
% spp. pollinated by						
vertebrate	18	0	3	22	4	0
generalist insect	47	47	95	73	96	95
specialist insect	36	53	3	4	0	5
no. spp. pollinated by						
<i>Amegilla</i>	5	12	0	0	0	0
<i>Nomia</i>	5	13	1	1	0	0
<i>Xylocopa</i>	6	0	0	1	0	0
Lepidoptera	0	6	0	0	0	1

floor (Inoue & Hamid 1994; Nagamitsu & Inoue 1997). Therefore, the qualitative prediction that they pollinate in relatively higher strata seems robust, although we cannot predict the exact threshold height of existence of social bees until we know the species-specific value f_0 of the social foragers there.

We ignored vertebrate pollinators because the display effects for vertebrates have never been observed precisely. However, we can at least predict that the display effects for them, and the costs for effective pollination by them, are different from specialist insect pollinators, because vertebrate pollination was found mainly in intermediate forest strata and not at the forest floor (table 1). To incorporate their pollination, further field observation is necessary.

Flowers in gaps and open habitats are observed to attract specialist pollinators (table 1). According to the model, specialist pollination is observed in plants with high mortality or low productivity. Productivity of gap species varies (and is related to plant size): it is generally not so high as canopy and emergent species because of smaller plant size and smaller leaf mass, but it is higher than understorey species of the same size owing to the absence of canopy shading. The mortality of gap species is much higher than plants of closed forests (Manokaran & Kochummen 1987), and the specialist pollination of gap species is explained mainly by their high mortality. However, our assumption that, once mature, plants do not grow is unrealistic, especially in gap species. The effect of growing was not considered in our model.

Pollination biology at the community level has been studied also in tropical forests in the Neotropics (Bawa *et al.* 1985; Kress & Beach 1994). In a forest in Costa Rica, medium- to large-sized bees are the main pollinators in the canopy layer, whereas hummingbirds and euglossine bees are prevalent in the forest understorey, and most plant species in any layer reproduce annually (Sanford *et al.* 1994). This forest differs in three ways from lowland dipterocarp forests in Sarawak. First, an emergent stratum is absent and so the height of the forest is lower (Lieberman & Lieberman 1994). Second, social foragers are less abundant (Kress & Beach 1994), and especially, the genus *Apis*, one of the most important components of social foragers, is absent. Third, annual-cycle seasonality

is much clearer (Sanford *et al.* 1994); that is, abiotic environmental conditions are more important factors for plant reproductive phenology than in Sarawak. For these reasons, the predictions of our model cannot be applied directly to the seasonal Neotropical forest in Costa Rica. Systematic studies in other forests in the aseasonal tropics (and also of other vegetation of Sarawak) are required for further comparison.

In the intermediate productivity range, the maximum optimum reproductive interval is predicted to match the interval that favours the highest proportion of social foragers (phase II, arrow (3) in figure 2). In our field data, this phenomenon was observed in the subcanopy stratum (figure 3). In this paper, we compared the proportion of the plant species with long reproductive intervals (those that reproduced only once during the 53 months of observation) among forest strata, but the reproductive interval of each plant species was not investigated because of the difficulty of conducting a longer census. Furthermore, phylogenetic constraints (Harvey & Pagel 1991) should be excluded by phylogenetic analysis of tropical plants in future studies.

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APPENDIX A

Provided that the density of flowering odour around a plant individual is proportional to the number of flowers f that the plant individual has, and that it diffuses from an origin (i.e. a plant individual) with no directionality, at a point ρ distant from the plant individual the odour density $g(\rho)$, which is a function of time from the start of odour production τ , can be expressed as the diffusion process (Ohkubo 1980),

$$g(\rho) = Bf \{1 - \Phi(\rho/(4C\tau)^{1/2})\}/\rho,$$

where C is a diffusion coefficient, B is a constant, and Φ is an error function. In the case when τ is not extremely small (that is, as long as the flowering period is not extremely short), the error function $\Phi(\rho/(4C\tau)^{1/2})$ is approximately equal to 0, and g can be expressed more simply as the steady state

$$g(\rho) \simeq Bf/\rho.$$

APPENDIX B

As shown in equation (6), y is a continuous and smooth function of x and takes a positive value within the range $0 < x < +\infty$ and $\lim_{x \rightarrow 0} y = \lim_{x \rightarrow \infty} y = 0$. Hence, if the equation $dy/dx=0$ has only one solution, it is the x -value that gives the maximum y . $dy/dx=0$ holds if, and only if

$$e^{-mx} = 1 - \frac{mx}{s+1}. \quad (\text{A1})$$

By substituting a for mx in equation (A1), we have equation (7) in the text. This equation has a unique solution $a=\alpha$ (>0) in the range $0 < x < +\infty$ for any positive s . Thus, the value of x that offers the maximum y is given uniquely as α/m .

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

