6. A demonstration that this is indeed possible can be given by means of an apparatus created by C. Hutchison. This demonstration is shown on film No. 991135, entitled "Time Reversal," produced by Bell Telephone Laboratories, Murray Hill, New Jersey. It is a beautiful illustration of Gibbs' point, but its real bearing on the time-reversal question is related only to the matter of coarse-grained and fine-grained information. The irrelevance of time reversal per se has to do with the absence of any dynamics. In fact, the trick in making this demonstration work is to avoid dynamical effects by using a very viscous fluid and stirring very slowly.
7. M. T. Burgy, V. E. Krohn, T. B. Novey, G. R. Ringo, V. L. Telegdi, *Phys. Rev. Lett.* **1**, 324 (1958); B. G. Erozolimskii, L. N. Bonderenko, Y. A. Mostovoi, B. A. Obinyakov, V. P. Zakharova, V. A. Titov, *Sov. J. Nucl. Phys.* **11**, 583 (1970).
8. E. P. Wigner, *Nachr. Ges. Wiss. Göttingen* (No. 32) (1932), p. 35.
9. M. Gell-Mann and A. Pais, *Phys. Rev.* **97**, 1387 (1955).
10. This graph was kindly provided by V. Telegdi. The data points are based on the data of D. A. Jensen, S. H. Aronson, R. D. Ehrlich, D. Fryberger, C. Nissim-Sabat, V. L. Telegdi, H. Goldberg, and J. Solomon [*Phys. Rev. Lett.* **23**, 615 (1969)].
11. The most recent and highest-precision measurements of this kind are those reported in S. H. Aronson, R. D. Ehrlich, H. Hofer, D. A. Jensen, R. A. Swanson, V. L. Telegdi, H. Goldberg, J. Solomon, D. Fryberger, *ibid.* **25**, 1057 (1970); M. Cullen, P. Darriulat, J. Deutsch, H. Foeth, G. Groves, M. Holder, K. Kleinknecht, E. Rademacher, C. Rubbia, D. Shambroom, M. Scire, A. Stande, K. Tittel, *Phys. Lett. B* **32**, 523 (1970); R. K. Carnegie, R. Cester, V. L. Fitch, M. Strovink, L. R. Sulak, *Phys. Rev. D* **4**, 1 (1971).
12. V. L. Fitch, R. F. Roth, J. S. Russ, W. Vernon, *Phys. Rev. Lett.* **15**, 73 (1965).
13. This way of approaching a description of the violation of CP-invariance was first suggested to me by V. L. Telegdi, who then raised the question: Is there any corresponding way to show explicitly that the 2π mode violates T-invariance? The answer is given here.
14. S. Bennett, D. Nygren, H. Saal, J. Steinberger, J. Sunderland, *Phys. Rev. Lett.* **19**, 993 (1967); D. Dorfan, J. Enstrom, D. Raymond, M. Schwartz, S. Wojcicki, D. H. Miller, M. Paciotti, *ibid.*, p. 989; J. Marx, D. Nygren, J. Peoples, T. Kirk, J. Steinberger, *Phys. Lett. B* **32**, 219 (1970).
15. F. Coester, *Phys. Rev.* **84**, 1259 (1951).
16. R. C. Casella, *Phys. Rev. Lett.* **21**, 1128 (1968); *ibid.* **22**, 554 (1969).
17. Whenever the word deep is used in connection with physics it evokes a quotation from Neils Bohr that has been conveyed by word of mouth among physicists: "In order to define a deep statement it is first necessary to define a clear statement. A clear statement is one to which the contrary statement is either true or false. A deep statement is a statement to which the contrary is another deep statement."
18. Part of the work reported here was supported by the U.S. Atomic Energy Commission.

Energetics and Pollination Ecology

The energetics of pollinators may have wide implications in floral biology and community ecology.

Bernd Heinrich and Peter H. Raven

Color, shape, and odor are well-known characteristics of flowers which partly determine the kinds of animal pollinators that visit them (*1–4*). In turn, these characteristics are influenced, in an evolutionary sense, by the activities of the pollinators. The plants and the pollinators are part of a dynamic, coevolving system, of which the features mentioned above are only a part. Little attention has been paid to another very significant parameter of the system: the caloric reward (*5*) provided by the flowers of particular plant species. The energy budget of pollinators in relation to the food reward provided by the flowers they visit has been investigated in a few instances (for example, *6–10*), but the role that this energy budget plays in the evolution of flowering plants has not been discussed previously.

In this article we aim to provide a synthesis and point of reference for this aspect of evolution by examining floral biology and the operation of outcrossing systems in plant populations from the standpoint of the energetics of the pollinators. We attempt to point out some potentially unifying theories in this area, hoping that the recognition of these will lead the way to quantitative investigations.

Energy Balance and Cross-Pollination

That animal pollinators usually restrict their visits to the flowers of a particular plant species (*11*) is only one factor promoting outcrossing. For outcrossing to result it is also necessary that the pollinator not confine its visits to a single flower or to the flowers of a single plant. Through evolution plants could presumably reduce the frequency of such repeated visits to the same flower or plant by limiting the caloric reward that is presented at any one time. However, the meaning of a certain caloric reward can be assessed only in relation to a particular animal, because the differences between the energy requirements of different pollinators may be great. For instance, a 100-milligram bumblebee that lands on each flower may expend about 0.08 calorie per minute when walking (*12*), while 3-gram sphinx moths (*13*) and hummingbirds (*14*) expend energy while hovering at a rate of about 11 cal/min, more than a 140-fold difference. However, many other aspects of the biology of the pollinators affect net energy expenditure.

The specific amounts of nectar per flower, in terms of calories of food energy, that would promote maximum cross-pollination, are related to the characteristic rate of energy expenditure of the pollinators. For example, the flowers of saguaro cactus, *Carnegiea gigantea* (Engelm.) Britt. & Rose, which are visited by many different insects as well as by some birds and bats (*15*), produce large quantities of nectar. Some individual honeybees (*Apis mellifica* is not native to North America) tend to limit their visits on numerous foraging trips to specific flowers of the same cactus plant (*16*). Since these plants are self-incompatible, such visits do not result in seed production. Secondly, those honeybees that take the nectar from saguaro may also reduce the subsequent attractiveness of the flowers to birds and bats, which have higher rates of energy expenditure and whose visits will more often result in outcrossing.

Animals with high energy requirements may not forage at the flowers of

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some plant species which do not provide sufficient caloric reward. The nectar from flowers is often the only source of energy for the activity, maintenance metabolism, reproduction, and growth of certain pollinators, and those plant species which are pollinated regularly by animals with high energy requirements must provide large amounts of nectar. The animals of lower energy expenditure which visit such plants and which may restrict their visits to individual flowers thereby tending to reduce outcrossing should, ideally, be excluded, and flowers having ample nectar have evolved a variety of mechanisms to exclude nectar "thieves." Specialized features, such as long tubular corollas (*17*), are evidently means of restricting the visitors of these plants to those of relatively high energy requirements.

Options other than structural specializations are available to plants for the exclusion of "unwanted" foragers, and for the attraction of pollinators. In bees, for example, the relative attractiveness of the flowers to different potential pollinators can differ with respect to shape, color (*18*), scent (*19*), and perhaps also with regard to nectar concentration and type of sugar (*20*). Many flowers containing large quantities of nectar, which are pollinated by bats (*21*) or hawk moths (*22*), open and secrete nectar only briefly at night, thereby excluding many day-flying insects and birds (Fig. 1). Flowers visited by birds likewise secrete large quantities of nectar (*2–4*). These flowers, however, are scentless, often red in color, and open during the day. They are perhaps less conspicuous to insects than to birds.

Small flowers with little nectar are unattractive to large hovering animals such as hummingbirds and sphinx moths which probably cannot meet their energy requirements from them. However, insects such as bumblebees which land on inflorescences (composed of hundreds or thousands of tiny florets) of *Spiraea latifolia* L. (Rosaceae) and *Solidago canadensis* L. (Asteraceae), for example, are still able to maintain an energy balance despite the minute amounts of nectar per floret (*10*), because the energy expended in walking from one flower to another can be 100 times less than an equivalent period of flight (*23*), and because the clustered florets can be visited in rapid succession (Fig. 2).

Blooming Times

The distance between flowers is another of the factors related to the energy balance with pollinators. Although this distance is ultimately limited by population density of the plants it is altered by the time and duration of flowering. For instance, synchronous blooming of the flowers of a species in a given plant population would minimize the time and energy expenditure of the pollinators flying between plants (Fig. 3). On the other hand, brief blooms of individual plants in a given species occurring at random over an extended period would maximize the distance between flowers at any one time, and demand greater energy expenditure by the pollinators.

In any one plant species the frequency of cross-pollination would be inversely related to the number of other species in bloom at that time if the foragers visited different species of flowers indiscriminately. Cross-pollination would be more effectively accomplished, and competition by the plants for pollinators reduced, if synchronous blooms of different species were staggered so that the same pollinators could utilize the plants in succession throughout the year. Such a flowering system should be particularly advantageous when the number of species of potential pollinators is low and when the pollinators are long-lived or multivoltine—that is, having a number of generations per year. Examples of such pollinators may be the few species of bumblebees in Wisconsin (*24*), Japan (*25*), and central Maine (*26*) that visit a progression of plant species blooming at different times of the year.

Fig. 1. Flowers specializing in large foragers of high energy expenditure. The *Centropogon talamancensis* Wilbur (right) is visited primarily by the large ($\approx$ 7.5 g) hummingbird, *Eugenes fulgens spectabilis* (Lawrence), in the mountains of Costa Rica. The tubular corolla ($\simeq$ 5 cm in length) is presumably conspicuous to birds because of its bright red color; however, it excludes almost all other concomitantly occurring foragers of lower energy budget. The latter include bees as well as smaller hummingbirds. Each blossom remains in bloom throughout the year (personal communication from R. K. Coldwell). The *Datura meteloides* DC (left) being visited by the sphinx moth, *Manduca sexta* (Johan.), promotes fidelity to sphingids by flower morphology, color, and time of blooming. The large white blossoms, which open at dusk, are presumably visible to the nocturnal moths. The moths are able to reach the nectar at the base of the long ($\simeq$ 18 cm) corolla with their proboscis. There is a closed flower at left of moth. The plant remains in bloom for a month or more. Scale, 2 cm. [Photo taken near Davis, California, by H. B. Baker]

Divergence with regard to time of blooming may not always be possible. For instance, in arid regions many species of annual plants grow and flower only for short durations after rains. Bees are very richly represented in number of species (*27*), and cross-pollination would be more effectively accomplished if the flowers diverged with regard to (i) daily time of blooming, (ii) amount of caloric reward provided, (iii) type of flower product (nectar or pollen or both) provided, and (iv) structures affecting access to the nectar or pollen. These changes in turn would provide opportunities for the many concurrently active, sympatric species of bees to specialize (*27*) and diverge in relation to particular plant species, and would thereby decrease their competition for food (*28*). On the other hand, the frequency of cross-pollination could also be increased if the plants provide sufficient food reward for pollinators of a number of species; the crucial factor may be the frequency of pollinating events, and not the number of species of pollinators specializing on a given flower species.

Temperature

Ambient temperature adds another dimension to the consideration of the energetics of pollination, because many of the pollinators are limited (either directly or for energetic reasons) by temperature in their foraging activity (*25*). Some foragers regulate their body temperature, often at considerable metabolic cost. Bumblebees, which can forage at ambient temperatures of 5°C or less, do so at an energy expenditure two or three times that at 26°C (*9, 10*). In addition, heat production for temperature regulation of the nest (*10, 29*) at night may deplete most of the nectar collected during the day (*30*). In terms of energetics, heat production specifically for temperature regulation is equivalent to increasing the flight distance between flowers. Therefore, flowers which are pollinated at low temperatures (*8*) should either provide more caloric rewards than those blooming at high temperatures, or be closer together so that they can be visited in rapid succession.

The energetic interactions of insect pollinators with flowers is often more complex. For example, although bumblebees at low ambient temperatures produce endogenous heat which elevates body temperature while they are on flowers with relatively large amounts of nectar (*8, 9*), the mosquitoes *Aedes nigripes* Zett. and *A. impinger* (Walker), not only feed from, but also bask in the flowers of *Dryas integrifolia* M. Vahl (Rosaceae) at 81°N in the Arctic (*31*). These and other heliotropic flowers present their paraboloid corollas continuously to the sun, yield a direct source of food energy to the pollinators, and provide a microclimate that should reduce the energy expenditure for endogenous heat production in some of the pollinators.

Those insect-pollinated flowers of temperate regions which open in early morning and in the evening are generally large (Fig. 1). They are visited by large insects capable of temperature regulation and foraging at relatively low ambient temperatures. For example, the relatively large ephemeral blossoms of *Oenothera* (Onagraceae) are visited at night by sphinx moths (*22*) which have a high rate of energy expenditure (*13, 32*). In the plant genus *Gaura* (Onagraceae), most outcrossing species open near sunset and are pollinated by medium-sized, nonhovering moths such as noctuids. The flowers last only part of a day. In two species of *Gaura*, however, the flowers open near sunrise, when ambient temperatures are considerably lower than in the evening. These have larger flowers and greater nectar production. They are visited by bumblebees early in the morning, and by many different kinds of smaller insects later in the day when ambient temperatures are high (*33*). Similarly, those bees which forage before daylight are generally larger (and presumably have higher net rates of energy expenditure) than those which feed after the sun has risen (*34*). *Bombus edwardsii* (which weighs about 0.12 gram) has a thoracic temperature near 37°C while foraging at 2°C (*10*) from a species of manzanita *Arctostaphylos otayensis* Wies. & Schreib. (Ericaceae). This implies that these bees have a high rate of energy expenditure. Each flower of this manzanita contained an amount of sugar equivalent to 1.5 calories (*35*). The energy expenditure of maintaining a thoracic temperature of 37°C at an ambient temperature of 2°C should approximate 0.8 cal/min (*36*). Thus the bees were presumably making an energetic profit even while foraging in near frosty conditions. At noon, when the manzanita was visited by many small insects, each flower contained sugar equivalent to a mean of only 0.32 calorie. It may be energetically most profitable for the bees to forage in the early morning when there is either little competition for nectar or the rate of nectar secretion is high (*9*). However, bumblebees visited the

Fig. 2. Apportionment of food rewards on the same inflorescence via time of blooming of individual florets. The long-tongued bumblebee, *Bombus vagans* F. Smith (left), forages from the nectar-rich *Epilobium augustifolium* L. in which the blossoms on a spike mature in sequence. (Note flower buds near top of spike and seed capsules near the bottom.) *Bombus ternarius* Say, a short-tongued bee (right), forages for nectar from *Solidago canadensis* L., in which the caloric reward at any one time is sufficient for these bees if the tiny florets of the panicle bloom synchronously. Scale, 2 cm. [Photographed near Farmington, Maine]

inflorescences of goldenrod, *Solidago canadensis* (Asteraceae) (Fig. 2), which contained "minute" amounts of nectar per blossom, only at relatively high ambient temperatures (*10*).

Alternative Strategies

In situations where a high degree of phenotypic uniformity is advantageous, self-pollination may provide an alternative system to outcrossing for flowering plants (*37*). It may be the only system possible if enough food cannot be provided to flower visitors, especially if ambient temperatures are, in general, low. In the high Arctic, where many plants are autogamous (*37*), there is often competition between flowers for pollinators (*6, 8*) and most of the outcrossed plants produce relatively large amounts of nectar, especially at the more northerly portion of their range (*8*). Given similar population structure and growth limitations one may tentatively predict that plants blooming in early spring in temperate regions would have flowers with high caloric rewards or small, inconspicuous and autogamous ones without nectar. In many situations, however, the maintenance of variability may be so highly selected for that autogamy is not possible. This would result in some plant groups being prevented from fruiting in areas where their regular pollinators cannot live.

The physical nature of the environment, as well as temperature, should affect the nature and the extent of outcrossing in plants. The composites (family Asteraceae), which are best represented in deserts and semiarid regions, and the orchids (family Orchidaceae), which are most richly represented in the tropical rain forests, will now be examined in the light of the energetics of pollination relationships to illustrate two contrasting systems which both achieve out-crossing.

Most composites maintain outcrossing systems even though the caloric rewards per inflorescence are not great. In their inflorescences the individual flowers, each with very little or no nectar, open serially and the cluster as a whole remains attractive to foragers for up to several weeks. Those members of this plant family with little nectar can probably maintain outcrossing systems only if they occur in relatively dense colonies, inasmuch as pollinators of high energy expenditure cannot consistently forage from them while making long flights between individual flowers. However, rather than genetic material being transferred between widely separated plants by pollen, the influx of seeds (carried by the wind or by other means) to locally inbreeding colonies could also insure the same effect as cross-pollination—that is, genetic variability of the species population.

Orchids have their metropolis in the tropics, where they are able to maintain outcrossing systems even though the individuals are often widely separated. They do this by extreme precision in pollen transfer and reception (*4*). Pollen from a single flower becomes attached to the foraging insect in a mass, the pollinium, and then usually remains affixed to the insect until it visits another flower of the same species. Here the pollinium is retrieved by specialized floral structures. Shape and placement of the pollinia (*4*), as well as specialized floral structures for its reception, preclude loss of the pollen at other flower species. Each time a pollinium is transferred, tens or hundreds of thousands of dustlike seeds can be produced. (In contrast, each floret in Asteraceae produces a single seed.) Such orchid flowers can be cross-pollinated by an animal that has visited only two flowers widely separated in space as well as time; there is no need for the pollinator to make repeated

Fig. 3. Synchronously blooming plants with minute amounts of nectar. The fly, *Bombilius major* L. (right) is foraging from *Geranium molle* L. When these flowers occur in dense colonies they are also visited by bumblebees on warm days (near Berkeley, California). The *Stellaria* sp. and *Hieracium aurantiacum* L. (left) are not visited by large bees (near Farmington, Maine), in part because the food rewards of these flowers are insufficient for these foragers. Scale, 1 cm.

visits to the flowers of the same species. Therefore orchids need not maintain an energetic balance with their pollinators, and perhaps half of all orchid species offer no energy reward. Attraction to the flower can therefore be on other bases. Many orchids are effective mimics of other flowers that do offer rewards, or of females of the corresponding male insects which pollinate the flowers (*4*).

Community Ecology

All of the interactions considered up to this point take place within communities, and the flower-forager relationships are often not one-to-one. Cross-pollination in any species is also affected by the availability of other kinds of plants in bloom at the same time (*38*) as well as by the presence of competitors for the same flowers (*39*). Many foragers rely on the flower products from a community of plants both at any one time and also over extended periods of time. Furthermore, pollen is sometimes gathered from one species of plant and nectar from another (*10, 27, 40*).

The indirect interactions between pollinators sometimes occur in unexpected ways. For example, large numbers of nectar and pollen foragers are known to promote greater yields of seed production in red clover and other legumes (*38, 41*), and it has been repeatedly speculated that short-tongued bumblebees, which take nectar by piercing the corolla without effecting cross-pollination, reduce the amount of seed production. It was therefore proposed that seed production in red clover could be increased if the short-tongued nectar robbers were eliminated (*42*). However, it has been shown several times that an increased population of these non-pollinators significantly increased seed production in red clover (*43*). On the basis of energetics it can be postulated that (under conditions of ample nectar secretion) the "actual" pollinators (long-tongued bumblebees) visited more flowers when less nectar remained per flower after "robbing."

Certain kinds of community interactions are characteristic of particular regions of the world, and are related to the physical and biological features of these regions. The following idealized examples are chosen to represent patterns that have been observed in different environments, and these patterns are discussed in relation to energetics.

Lowland Moist Tropics

In the moist lowland tropics, competition and herbivore pressure, among other factors, have led to decreased population densities of the species of plants growing there (*44*). The warm, equitable climate allows flowering throughout the year, and a succession of species may bloom. Bees, which are as a group the most specific of flower-visiting animals, do not have nearly as many species in the moist tropics as in the arid regions of the world (*27*). Moreover, there are very few oligolectic bees—that is, bees that consistently restrict their pollen-gathering activities to one or a few related species in the presence of other pollen sources (*27, 45*). Both of these trends are contrary to the usual situation in the moist tropics, where higher numbers of species and greater specialization are characteristic of most animal groups. Most tropical bees are not oligolectic probably because they are long-lived and multivoltine, having therefore to change from one plant to another through the course of the year. This lack of specialization presumably restricts opportunities for speciation in bees.

In the tropics, and particularly in undisturbed rain forest, most plant species have small, often greenish, inconspicuous flowers (*46*). In these plants, dioecism, protandry, protogyny, and other mechanisms that promote outcrossing even if the pollinators are relatively generalized, are common (*47*). Pollination systems in which beetles, flies, and other insects visit small and relatively unspecialized flowers probably represent the systems that originated in the tropical rain forest.

Recently, Janzen (*48*) has identified two very different systems whereby tropical plants promote outcrossing even within a highly dispersed population. Some tropical plants produce great masses of flowers at certain unique times of year, especially where there is a dry season (*49*). These plants may then be visited by large numbers of insects, including some with high energy requirements. Mass flowering is mainly limited to plants growing in relatively open situations and to the forest canopy (*50*), presumably because only such plants have enough energy to divert to simultaneous bloom.

The second reproductive system outlined by Janzen (*48*) involves wide-ranging pollinators such as euglossine and other large bees, sphinx moths, hummingbirds, and bats. A few relatively large flowers are produced continuously in an inflorescence that may itself last several months or more. Each flower provides a relatively great caloric reward, which allows their visitors to fly a regular path between them, even when the distances involved are up to several hundred meters. Examples of plant families containing genera with this kind of pollination system in the lowlands of Central America are Apocynaceae, Fabaceae, Convolvulaceae, Curcurbitaceae, Solanaceae, Lecythidaceae, Clusiaceae, Heliconiaceae, Marantaceae, and Costaceae. Many of these plants grow and produce flowers under the forest canopy, and a smaller proportion of their total carbohydrate reserves is necessary for flower production than in the mass-flowering species. Even if individual inflorescences do not produce an open flower each day, the animals may continue to visit them more or less regularly (*48*), thus further tending to maximize outcrossing. Their flowers may become structurally specialized to exclude all except their particular pollinators, which, however, do not usually confine their visits to only one of the above families.

Tropical Mountains

The growing seasons are relatively long on tropical mountains, but low prevailing ambient temperatures exclude many of the smaller insect pollinators. However, the number of bird-pollinated species of plants increases markedly at higher elevations throughout the tropics (*3, 4*). Furthermore, bumblebees, which can also thermoregulate (*9, 10*), occur on the neotropical and Asian mountains (*51*). Because of the emphasis on larger pollinators having high energy requirements, the nectar provided by the flowers must be more readily available, or in larger amounts, if outcrossing is to be regularly maintained. Outcrossing is often not possible, and in many species it is not necessary. For example, a large percentage of the flora on the mountains in West Java is autogamous (*52*). The problems faced by mountain plants are similar to those of temperate plants that bloom early in the spring.

Temperate Regions

In temperate regions, plants of a given species are usually less dispersed than in the tropics. They often bloom in dense colonies, and can utilize foragers of relatively low energy expenditure, particularly if the bloom occurs during the warm part of the year.

Vertebrate pollinators with high energy requirements have a much less clearly defined role in the temperate zone than in the tropics, given the characteristic population structures and our hypothesized energy strategies of temperate plants. Flower-visiting bats and birds are basically tropical animals that seasonally invade, but only to a limited extent permanently colonize, the temperate regions.

When the plant species are few and their population density is high, then the caloric reward that must be provided to attract and maintain pollinators is minimal. This situation can be compounded by a scarcity, or unreliability of nectar gatherers (because of temperature or other factors), but some plants have evolved to bloom still more synchronously and have ultimately become wind-pollinated (*53*). Wind pollination in angiosperms is almost exclusively a phenomenon of temperate regions, where it has evolved on a number of occasions. Some genera, such as *Quercus* and *Lithocarpus* (Fagaceae), and several genera of grasses (Poaceae), which are characteristically wind-pollinated in temperate regions, are sometimes insect-pollinated in the tropical rain forest (*50*), where widely scattered plants cannot be effectively wind-pollinated.

Conclusions

The energetic aspects of the relationship between flowers and their animal pollen vectors are directly applicable to community ecology, evolution, biogeography, and physiology. We have indicated new and potentially fruitful lines of research in these areas.

We suggest that a balance must exist between the energy expended by foragers and the caloric reward of the flowers if cross-pollination is to be maximal. A flower must provide sufficient reward to attract foragers, but it must limit this reward so that the animals will go on to visit other plants of the same species.

When a plant population becomes widely dispersed, the animal pollinators require increased energy rewards per flower; this leads to relationships with larger pollinators that travel over long distances. Such a system is observed in the humid lowland tropics, where some plants produce few large flowers per day in long lasting inflorescences.

Consistently low temperatures should, on the basis of energetics, result in flowering systems similar to those found in populations in which the individuals are widely separated. Alternatively, at high plant population densities, synchronous blooms visited by foragers with low energy requirements can affect cross-pollination without having to provide high caloric rewards per flower. Furthermore, staggering of synchronous blooms of different species would allow the utilization of the same species of pollinators for many species of plants. Staggering of blooms may not be possible in the short growing season of arid regions where, for bees, specialization of the flowers has ensured that the bees continue to visit (and cross-pollinate) other flowers of the same species, rather than the many other sympatric ones. Conversely, many orchids, which occur in widely scattered populations, offer no food reward. They compensate for this by mimicry of other flowers having nectar, or of insects, and by precise methods of pollen transfer.

References and Notes

1. C. Darwin, *The Different Forms of Flowers on Plants of the Same Species* (Appleton, New York, 1898); P. Knuth and E. Loew, *Handbuch der Blütenbiologie* (Engelmann, Leipzig, 1898–1905) vols. 1–3; J. H. Lovell, *The Flower and the Bee* (Constable, London, 1918).
2. V. Grant and K. A. Grant, *Flower Pollination in the Phlox Family* (Columbia Univ. Press, New York, 1965); *Hummingbirds and their Flowers* (Columbia Univ. Press, New York, 1968).
3. K. Faegri and L. van der Pijl, *The Principles of Pollination Ecology* (Pergamon, New York, 1966).
4. L. van der Pijl and C. H. Dodson, *Orchids and their Pollinators* (Univ. of Miami Press, Miami, Florida, 1967).
5. We have largely omitted pollen (and other attractants of flowers) because it does not contribute directly to the energy budget of most pollinators, and have assumed that most pollinators rely directly or indirectly on the nectar of flowers for their energy. The indirectness of this reliance is, however, illustrated in the social bees which store food in the nest. These stores provide a source of energy for those members of the colony which can then specialize in other tasks such as nest building and upkeep, water carrying, and collection of the pollen that provides a source of protein for the larvae.
6. B. Hocking, *Trans. Roy. Entomol. Soc. London* **104**, 223 (1953).
7. O. P. Pearson, *Condor* **56**, 317 (1954).
8. B. Hocking, *Oikos* **19**, 359 (1968).
9. B. Heinrich, *Science* **175**, 185 (1972).
10. ———, *Z. Vergl. Physiol.* **77**, 49, 65 (1972).
11. V. Grant, *Evolution* **3**, 82 (1949).
12. It has been assumed, for the sake of this approximation, that the respiratory rate of the bee (which is not producing additional heat for temperature regulation) is 10 ml of oxygen per gram per hour. The utilization of 1 ml of oxygen yields about 5.0 calories during carbohydrate combustion.
13. B. Heinrich, *J. Exp. Biol.* **54**, 141, 153 (1971).
14. R. Lasiewski, *Physiol. Zool.* **36**, 122 (1963).
15. S. M. Alcorn, S. E. McGregor, G. Olin, *Science* **133**, 1594 (1961).
16. S. E. McGregor, S. M. Alcorn, E. B. Kuitz, Jr., G. D. Butler, Jr., *J. Econ. Entomol.* **52**, 1002 (1959).
17. A. Kerner, *Flowers and Their Unbidden Guests* (Paul, London, 1878).
18. A. D. Brian, *J. Anim. Ecol.* **26**, 71 (1957).
19. D. A. Levin, *Evolution* **22**, 444 (1969); C. H. Dodson, R. L. Dressler, H. G. Hills, R. M. Adams, N. H. Adams, *Science* **164**, 1243 (1969); J. B. Free, *Behaviour* **37**, 269 (1970).
20. R. Beutler and A. Schöntag, *Z. Vergl. Physiol.* **28**, 254 (1940); W. Loh and H. Heran, *ibid.* **67**, 436 (1970).
21. H. G. Baker, *Quart. Rev. Biol.* **36** (1961); ——— and B. J. Harris, *Evolution* **11**, 449 (1957).
22. D. P. Gregory, *Aliso* **5**, 357 (1963).
23. Based on a comparison of the rate of metabolism at rest and the rate of metabolism in flight, which differ by approximately 100 times; H. W. Ludwig, Sonderabdruck *Verh. Deut. Zool. Ges. Wien* **30**, 355 (1962).
24. R. E. Fye and J. T. Medlar, *Wis. Acad. Sci. Arts Lett.* **43**, 75 (1954).
25. S. Miyamoto, *Insectes Soc.* **7**, 30 (1960).
26. B. Heinrich, unpublished results.
27. E. G. Linsley, *Hilgardia* **27**, 543 (1958).
28. ——— and J. W. MacSwain, *Evolution* **12**, 219 (1958).
29. R. A. Cumber, *Trans. Roy. Entomol. Soc. London* **100**, 1 (1949).
30. A. D. Brian, *Bee World* **35**, 61 (1954).
31. B. Hocking and C. D. Sharplin, *Nature* **206**, 215 (1965).
32. J. E. Heath and P. A. Adams, *J. Exp. Biol.* **47**, 21 (1967).
33. P. H. Raven and D. P. Gregory, *Mem. Torrey Bot. Club*, in press.
34. E. G. Linsley, J. W. MacSwain, P. Raven, *Univ. Calif. Publ. Entomol.* **33**, 59 (1964); ——— and M. A. Cazier, *J. Kans. Entomol. Soc.* **43**, 251 (1970).
35. Fifty flowers of *Arctostaphylos otayensis* contained 0 to 5 μl ($\bar{x} = 2.6$ μl) of 10 to 18 percent ($\bar{x} = 15.5$ percent) nectar solution. On the basis of glucose at 3.7 cal/mg per flower, the average flower contained (3.7 cal/mg × 2.6 mg × 0.155) = 1.5 cal. These observations were made in the Botanical Garden at the University of California, Berkeley.
36. An approximation derived from the animals' cooling rates. See (*9* and *10*).
37. G. L. Stebbins, *Amer. Natur.* **91**, 337 (1957); V. Grant, *Origins of Adaptations* (Columbia Univ. Press, New York, 1963).
38. S. N. Holm, *Annu. Rev. Entomol.* **11**, 155 (1966); G. H. Vansell, *J. Econ. Entomol.* **37**, 528 (1944).
39. T. Kikuchi, *Sci. Rep. Res. Inst. Tohoku Univ. Ser. IV Biol.* **30**, 143 (1964).
40. M. Percival, *New Phytol.* **54**, 353 (1955).
41. R. J. Walstrom, *J. Econ. Entomol.* **51**, 64 (1958).
42. F. W. Swart, quoted by Holm (see *38*). See also *Herb. Abstr.* no. 1639, 30 (1960).
43. R. P. Hawkins, *Ann. Appl. Biol.* **49**, 55 (1961); L. Morrison, *N.Z. J. Agr. Res.* **4**, 560 (1961); A. Pedersen, *Årsskr. Kogl. Vet. Landbokjsk* **49** (1945).
44. D. H. Janzen, *Amer. Natur.* **104**, 501 (1970).
45. C. D. Michener, *Bull. Amer. Mus. Natur. Hist.* **104**, 1 (1954).
46. H. G. Baker, *Cold Spring Harbor Symp. Quant. Biol.* **24**, 177 (1959).
47. P. S. Ashton, *Biol. J. Linn. Soc.* **1**, 155 (1969).
48. D. H. Janzen, *Science* **171**, 203 (1971).
49. ———, *Evolution* **21**, 620 (1967).
50. P. W. Richards, *The Tropical Rain Forest* (Cambridge Univ. Press, New York, 1952); Sodestrom and Calderón, *Biotropica* **3**, 1 (1971).
51. J. B. Free and C. G. Butler, *Bumblebees* (Collins, London, 1959); see also (*29*).
52. W. M. Docters van Leeuwen, *Verh. Kon. Akad. Wetensch.* (*Amsterdam*) **31**, 1 (1933).
53. D. R. Whitehead, *Evolution* **23**, 28 (1969).

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