Chapter 1

WHY POLLINATION IS INTERESTING

Outline

The flowering plants (**angiosperms**) account for about one in six of all described species on earth and provide the most obvious visual feature of life on this planet. In the terrestrial environment, their interactions with other living organisms are dominant factors in community structure and function; they underpin all nutrient and energy cycles by providing food for a vast range of animal herbivores, and the majority of them use animal **pollinators** to achieve reproduction. Most of the routine "work" of a plant is carried out by roots and leaves, but it is the **flowers** that take on the crucial role of reproduction.

A flower is usually **hermaphrodite**, with both male and female roles. Hence it is essentially a structure that produces and dispenses the male **gametophytes** (**pollen**), organizes the receipt of incoming pollen from another plant onto its own receptive surfaces on the **stigma**, and then appropriately guides the pollen's genetic material to the female **ovules**. The flower also protects the delicate male and female tissues (stamens and pistils) and has a role in controlling the balance between **inbreeding** and **outbreeding**, hence influencing the genetic structure and ultimately the evolutionary trajectory of the plant. But the plant itself is immobile, so that incoming pollen has to be borne on some motile carrier, sometimes wind or water but much more commonly on a visiting animal. To quote one source (Rothrock 1867), "among plants, the nuptials cannot be celebrated without the intervention of a third party to act as a marriage priest"! A pictorial overview of the stages is shown in figure 1.1, covering the processes of pollination that are the focus of this book.

A flower also serves to protect the pollen as it germinates and as the male nucleus locates the egg and then to protect the ovules as they are fertilized and begin their development into mature **seeds**. However, these later events (**germination** of the pollen and **fertilization** of the ovule) are technically not part of **pollination**, and they are covered here only as needed to understand the characteristics and effects of pollen transfer.

Since flowers bring about and control plant reproduction, they are central to much of what goes on in the terrestrial world, and pollination is a key **mutualism** between two kingdoms of organisms, perhaps the most basic type of exchange of sex for food; the plant gains reproductive success, and the animal—usually—gains a food reward as it visits the plant. But the visitor does not "want" to be a good pollinator and has to be manipulated by the plant to move on and to carry pollen to another plant. In practice, only about 1% of all pollen successfully reaches a stigma (Harder 2000).

Nevertheless, pollination by animals (**biotic pollination**) is both more common (Renner 1998) and usually more effective than alternative modes of abiotic pollen movements using wind or water, and animal pollination is usually also associated with more rapid **speciation** of plants (Dodd et al. 1999; K. Kay et al.

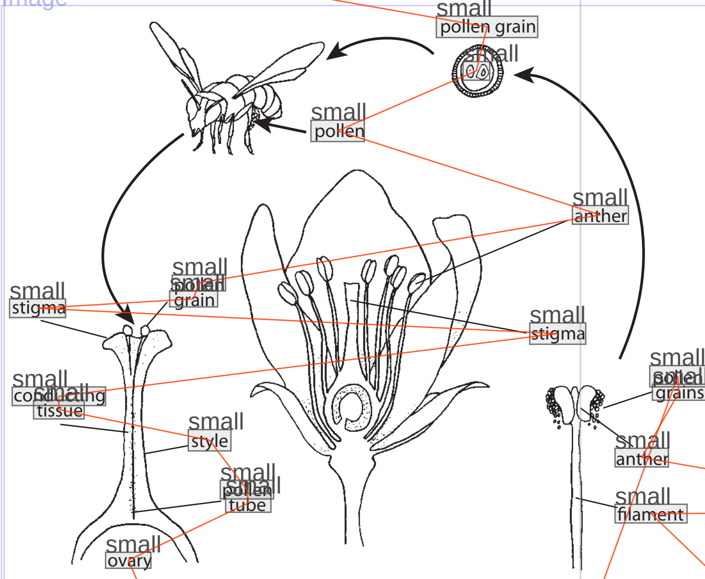

Figure 1.1 The central processes of pollination in a typical angiosperm flower, with the route taken by pollen from anther to stigma (followed by pollen tube growth into the style) in an animal-pollinated species. (Modified from Barth 1985.)

2006). Discussion of animal pollination therefore dominates this book, and around 90% of all flowering plants are animal pollinated (Linder 1998; Renner 1998). Furthermore, plants are, of course, the foundation of all food chains on the planet, and their efficient pollination *by* animals to generate further generations is vital to ensure food supplies *for* animals. Natural ecosystems therefore depend on pollinator diversity to maintain overall biodiversity. That dependence naturally extends to humans and their agricultural systems too; about one-third of all the food we eat relies directly on animal pollination of our food **crops** (and the carnivorous proportion of our diet has some further indirect dependence on animal pollination of forage crops). Pollination and factors that contribute to the maintenance of pollination services are vital components to take into account in terms of the future health of the planet and the food security and sustainability of the human populations it supports.

Beyond its practical significance, the flower-animal mutualism has been a focus of attention for naturalists and ecologists for at least two hundred years and provides almost ideal arenas for understanding some of the fundamental aspects of biology, from evolution and ecology to behavior and reproduction. It is perhaps more amenable than any other area to providing insights into the balance and interaction of ecological and evolutionary effects (Mitchell et al. 2009). Flowers are complex structures, and their complexity admirably reveals the actions, both historical and contemporary, of the selective agents (mainly, but not solely, the pollinators) that we know have shaped them. These factors make floral biology an ideal resource for understanding biological adaptation at all levels, in contrast with many other systems, where there are multiple and often uncertain selective agents.

In this first chapter, some of these central themes are introduced to set the scene for more specialist chapters; it should be apparent from the outset that while each chapter might stand alone for some purposes, it cannot be taken in isolation from this whole picture.

1. Which Animals Visit Flowers?

At least 130,000 species of animal, and probably up to 300,000, are regular flower visitors and potential pollinators (Buchmann and Nabhan 1996; Kearns et al. 1998). There are at least 25,000 species of bees in this total, all of them **obligate** flower visitors and often the most important pollinators in a given habitat.

There are currently about 260,000 species of angiosperms (P. Soltis and Soltis 2004; former higher estimates were confounded by many duplicated namings), and it has been traditional to link particular kinds of flowers to particular groups of pollinators. About 500 genera contain species that are bird pollinated, about

250 genera contain bat-pollinated species, and about 875 genera predominantly use **abiotic pollination**; the remainder contain mostly insect-pollinated species, with a very small number of oddities using other kinds of animals (Renner and Ricklefs 1995).

The patterns of animal flower visitors differ regionally. In central Europe, flower visitors over a hundred years ago were recorded as 47% **hymenopterans** (mainly bees), 26% flies, 15% beetles, and 10% butterflies and moths; only 2% were insects outside these four orders (Knuth 1898). But in tropical Central America, the frequencies would be very different, with bird and bat pollination entering the picture and fewer fly visitors, while in high-latitude habitats the vertebrate pollinators are absent and flies tend to be more dominant. Some of these patterns will be discussed in chapter 27.

2. Why Do Animals Visit Flowers?

The majority of flower visitors go there simply for food, feeding on sugary **nectar** and sometimes also on the pollen itself. Chapters 7 and 8 will therefore deal in detail with these commodities, and chapter 9 will cover a few more unusual foodstuffs and rewards that can be gathered from flowers; chapter 10 will take an economic view of all these food-related interactions, in terms of costs and benefits to each participant. Major themes in other chapters include the ways that flower feeders can improve their efficiency: learning recognition cues to select between flowers intra- and interspecifically, learning handling procedures, learning to avoid emptied flowers, and avoiding some of the hazards of competing with other visitors.

Flowers are also sometimes visited just as a convenient habitat, often simply because they offer an equable sheltered **microclimate** for a small animal to rest in, a place that is somewhat protected against bad weather, predators, or **parasitoids**. Or flowers may offer a reliable meeting site for mates or hosts or prey, or for females an **oviposition** site providing shelter for eggs and larvae. More rarely they are used as a warming-up site by insects in cold climates, usually because the flowers trap some incoming solar radiation, which enhances their own ovule development, but occasionally because a few flowers can achieve some metabolic **thermogenesis** that warms their own tissues (chapter 9 will provide more details on this topic).

3. How Do Flowers Encourage Animal Visitors?

Many plant attributes contribute to attraction of visitors: J. Thomson (1983) usefully groups these as *plant presentation*. Some of these attributes are readily apparent to visitors, and these may be features of individual flowers (e.g., color, shape, scent, reward availability, or time of flowering) or features of whole plants or groups of plants (e.g., flower density, flower number, flower height, or spatial pattern). The more readily apparent plant presentation **traits** can be divided into **attractants** (advertising signals), dealt with mainly in chapters 5 and 6, which discuss visual and olfactory signals, and **rewards** (usually foodstuffs), dealt with in chapters 7–9. Aspects of the *timing* and *spacing* of flowers, and how these might be affected by competition between different flowering plants, are given more in-depth treatments in chapters 21 and 22.

Other floral attributes are more cryptic to the visitor and may only determine the reproductive success of the plant in the longer term; these might include pollen amounts, ovule numbers, the genetic structure of the plant population, the presence and type of **incompatibility** system, etc.

It is generally in the plant's interest to support and even improve its visitors' efficiency, encouraging them to go to more flowers of the same species (so ensuring that only **conspecific** pollen is taken and received) and to go to flowers with fresh pollen available and/or with receptive stigmas for pollen to be deposited upon. Many flowers therefore add signals of status to their repertoire, via color change, odor change, or even shape change. Visitors are thereby directed away from flowers that are too young or too old or already pollinated. Instead they will tend to concentrate their efforts on those (fewer) flowers per plant that are most in need of visitation, thus also being encouraged to move around between separate plants more often and to ensure **outcrossing** rather than **selfing**. Reasons for favoring breeding by outcrossing (i.e., with other plants) are covered more fully in chapter 3.

4. What Makes a Visitor into a Good Pollinator?

In many ways this is the crucial theme running through this book. It relates to what is probably the major current debate in pollination ecology, that is, to what extent pollination it is a *generalist* process and to what extent it is a *specialist* one. Pollination has in the past nearly always been categorized in terms of *syndromes*, with particular groups of flowers recognized as having particular sets of characteristics (of color and scent, shape, timing, reward, etc.) that suit them to be visited by particular kinds of animals; and it is implicit in this approach that these suites have often been arrived at and selected for by convergent evolution in plant families that are unrelated. Thus most authors have used terms such as **ornithophily** to describe the bird **pollination syndrome**, or **psychophily** for the butterfly pollination syndrome. Flower characteristics would be listed that fit each syndrome, and an unfamiliar flower's probable pollinators could therefore be predicted. Flowers in each category were seen as having a degree of specialization that suited them to their particular visitors, with some syndromes being more specialized than others. Nearly all earlier works on pollination were organized around this theme of syndromes, and it served as a useful structure for understanding animal-flower interactions for nearly two centuries. Without knowing this background it would be nearly impossible to follow the current debates that are a major focus for pollination ecologists, and it would also be very difficult to structure the information on flower attractants and flower rewards in chapters 5–9. This book thus retains a syndrome-based approach throughout its early chapters and explicitly considers the evidence in support of a syndrome approach in chapter 11; then it unashamedly covers each of the syndromes in turn in chapters 12–19, providing all the core materials on which later criticisms might be based.

The criticisms and debates focus around the reality of syndromes and how far they have been overplayed in the previous literature, perhaps blinkering or biasing our perceptions. Many authors now regard flower pollination as a much more generalized phenomenon, where most flowers get many different kinds of visitors and have *not* been and are *not* being heavily selected to specialize for the needs of one particular "best" visitor. This approach is specifically addressed in chapter 20. It will be a major argument there that the issue has been clouded by an as yet insufficient distinction between flower visitors and pollinators. So what does make a visitor into a good pollinator?

Physical Factors

Any animal that is to be an effective pollinator must have the ability to passively pick up pollen as its body moves past the **anthers** of a flower that it visits and carry that pollen to another flower. Normally this will be aided by the animal being a good *physical fit* in terms of size and shape, so that in alighting on the flower surface, or when inserting its tongue or beak of appropriate length, some specific part of its body touches the anther. Additionally pollen pickup and carriage will be aided if the animal has appropriate *surface structures*; pollen adheres well to feathers, fur, and hairy or scaly surfaces in insects but does not get transported well on shiny or waxy surfaces (and may even be damaged by certain surface secretions). Hence a small shiny beetle taking some nectar by crawling into the lower surface of a large tubular **corolla** where the anthers are in the corolla roof may well be a regular visitor to that flower but is unlikely to be an effective mover of its pollen; in effect, it is acting as a "cheat" as far as the flower is concerned and may be termed an **illegitimate visitor.**

Behavioral Factors

Different animals land on and forage at flowers in very different fashions. There are many aspects of behavior that will affect whether a given animal is going to be a good pollinator. Pollinators will seldom have a complete perception of all the aspects of plant presentation mentioned above, but they will respond to at least some of them in ways that are useful to the plant:

1. Their choices of *places and times* to visit, and exactly which flowers to visit, will be critical. Visits occurring before **dehiscence** (the splitting of the anthers to reveal the pollen) or after pollen depletion are normally of no value to the flower in fulfilling its male role, and visits before or after the stigma is receptive to incoming pollen are of no value to the flower in its female role.
2. Their *handling* of the flowers affect their pollen pickup and deposition characteristics; ideally they should receive pollen at a specific site on their bodies, and one that is also a good site for subsequent deposition of that pollen onto a stigma.

3. Their *handling time* per flower affects how many flowers are visited in a given time.
4. Their speed and directionality of *movement between plants* affect **pollen dispersal**.
5. They should not be too efficient at ***grooming*** off the pollen, or indeed at *eating* it.
6. Their ***flower constancy***, that is, the likelihood that they will move to another flower of the same species, is perhaps most critical. If they innately or by learning prefer a particular flower **phenotype**, their high constancy will usually ensure that they move neatly and sequentially among conspecific flowers, not wasting pollen by depositing it in the wrong species. Constancy to a flower (considered in detail in chapter 11) gives economies to the visitor also; it may minimize travel distances, handling times, and learning effort and maximize pollen packing.

Behavioral factors such as these are often the key to being a good pollinator and of course are affected by the animals' abilities to learn as they become more experienced as foragers. The ability to form a **search image** or to respond consistently to other cues, associating particular signals with the presence of food, hones their foraging ability and can cement their relationships with particular flowers. Hence later chapters of this book, in considering particular groups of animals that visit flowers, include careful consideration of their sensory and learning capacities.

Physiological Factors

Animals have differing physiological strategies and constraints, and these too can affect their energetic needs and thence their flower-visiting patterns, as will be discussed in chapter 10. Most animals (including nearly all invertebrates, and therefore many of the insect flower visitors) lack elaborate internal physiological regulatory systems, and their *thermal balance* and *water balance* are strongly influenced by environmental conditions. They cannot function if they are too hot or too cold or are short of water, and must forage in times and places that provide suitable microclimates, using the sun's radiation to warm up by basking, or shady places to cool down again, and seeking (usually) sites that are relatively humid. However, birds and bats are physiologically more sophisticated and can regulate their body temperature and water balance more precisely; they generate heat internally through their own metabolism (**endothermy**) and regulate their own body fluids with efficient skin exchanges, respiratory controls, and excretory organs. They can in principle forage at almost any time and in any habitat, though they may still conserve their own energy by picking more equable sites.

The distinction does not lie exactly between the vulnerable invertebrates and the highly regulated birds and mammals, however. It is now clear that a rather small proportion of insects can also show endothermy, at least some of the time when they need to warm up in the absence of solar inputs (chapter 10); this applies especially to most bees, a few hoverflies, some large moths, and some beetles, occurring more sporadically in other groups. It is perhaps no coincidence that endothermic abilities in insects are most common in the flower-visiting groups, which have access to ready fuel supplies in the form of nectar but which may also need to compete for that nectar in the cool of early mornings or at dusk.

Given the list of factors that can turn a visitor into a good pollinator, two obvious points should emerge:

1. A great many of the animals that go to flowers for a short drink of nectar may be rather poor at pollinating that flower. Those with a poor physical fit, those that cheat, and those with little or no flower constancy are likely to be especially ineffective.

2. Of all the visitors, bees are likely to be especially good as pollinators. They rely solely on flowers for food, both as adults and as larvae, and so must visit more flowers than any other animals. Their sizes, hairy surfaces, and variably long tongues, their excellent learning abilities, communication systems and floral constancy, and their endothermic capacities all equip them to visit flowers efficiently (from their own perspective) and effectively (from the plant's point of view). Although they are sometimes described as **pollen wasters** (because they, or rather their offspring back at the nest, eat so much of the pollen that they pick up), they are by far the most important pollinators in most ecosystems, and they do achieve high pollen export from visited flowers (Harder and Wilson 1997); plants have adapted over evolutionary time to make

best use of them by providing more than enough pollen to cater for their needs *and* ensure that sufficient pollen still commonly reaches other flowers.

5. Costs, Benefits, and Conflicts in Animal Pollination

Plants with hermaphrodite flowers benefit greatly because a single animal visit can allow both pickup of pollen and its deposition on a stigma, fulfilling both the **male** and **female functions** of that flower at the same time. Animals benefit greatly by finding easily acquired foods, both sugary (nectar) and often also proteinaceous (pollen). Pollination by animals may therefore be a mutualism, of benefit to both participants, but it is *not* **altruistic**; for the animals, pollination of the flowers they forage at is almost always just an irrelevant by-product. In fact the plant and animal have a conflict of interest, often with adaptation and counteradaptation going on from both sides through evolutionary time to try and get a bigger share of the benefits. So the situations that we see now are the end products of the long and sometimes quite duplicitous associations of flowers with animals.

The plant ideally wants a visitor that is cheap to feed, alighting only briefly, moving on rapidly to another plant, and being faithful to its chosen plant species; so ideally, the forager should be chronically underfed and continuously on the move. But (again ideally) the animal would prefer to be as well fed and lazy as possible, getting as much food as it can from one flower with minimum energy expenditure, being relatively sedentary, and then moving on to any other nearby flower with copious nectar, whatever its species (although we already noted that some degree of fidelity may improve its foraging efficiency).

Hence, although there are obvious benefits to both partners, there are potentially clear costs as well. The plant has to invest in attractants (its carbon and nitrogen resources are used to make flamboyant petals, pigments, and chemical scents), as well as mere rewards. If the plant reduces its rewards too far, the animal may not get enough food and will give up on that species. The plant generally also has to compete with other plant species for pollination, to obtain a share of the "good" pollinators, so it cannot afford to skimp on its offerings too much if it is growing within a reasonably diverse plant community. Many plants also have to offset the additional costs of animal exploiters: those visitors who take rewards without pollinating (thereby **cheating**, chapter 24) and the flower eaters (florivores) or foliage herbivores also attracted by the pollination cues (chapters 25 and 26). For the animals, there may be costs linked to carrying the pollen they have inadvertently picked up (sometimes it is very unwieldy and can interfere with their wings or legs or sense organs), which may favor animals trying to cheat, and there may be costs also from the potential risks of predation or parasitism at flowers, since enemies can use them as a place to find prey or hosts reliably (chapter 24). There are also costs arising from the tendencies of the plants to cheat (chapter 23) by offering no real reward and sometimes by trapping the animal.

6. Why Is Pollination Worth Studying?

Pollination ecology can provide almost unparalleled insights into evolution, ecology, animal learning, and foraging behavior (fig. 1.2). It is perhaps the best of all areas to see and understand some basic biological processes and patterns; studies that deal exclusively with pollination biology have often had major impacts on general ecological and evolutionary theory.

Pollination interactions often show us *evolution* by natural **selection** in action almost before our eyes and provide some very clear-cut examples of **adaptive radiation** and, perhaps, of plant speciation. They are particularly useful for studying **coadaptations** (**coevolution**), because such interaction often involve relatively few organisms interacting with relatively high interdependence and incorporating the most fundamental of phenomena (reproduction for the plant, food supply for the animal). There are selection pressures on each side of the partnership, offering hopes that effects at the basic level of male and female **gene flow** can be quantified, sometimes (in crop pollination especially) on a time scale that can be detected within one scientist's period of study.

In terms of *ecology*, the study of pollination sheds light on how different organisms interact and affect each other, especially the competitive effects of plants upon each other, and on the various levels of interactions of plants with pollinators, including resource allocation, competition, exploitation, and simply cheating. In the last two decades there has been an increasing stress on community-level interactions in pollination

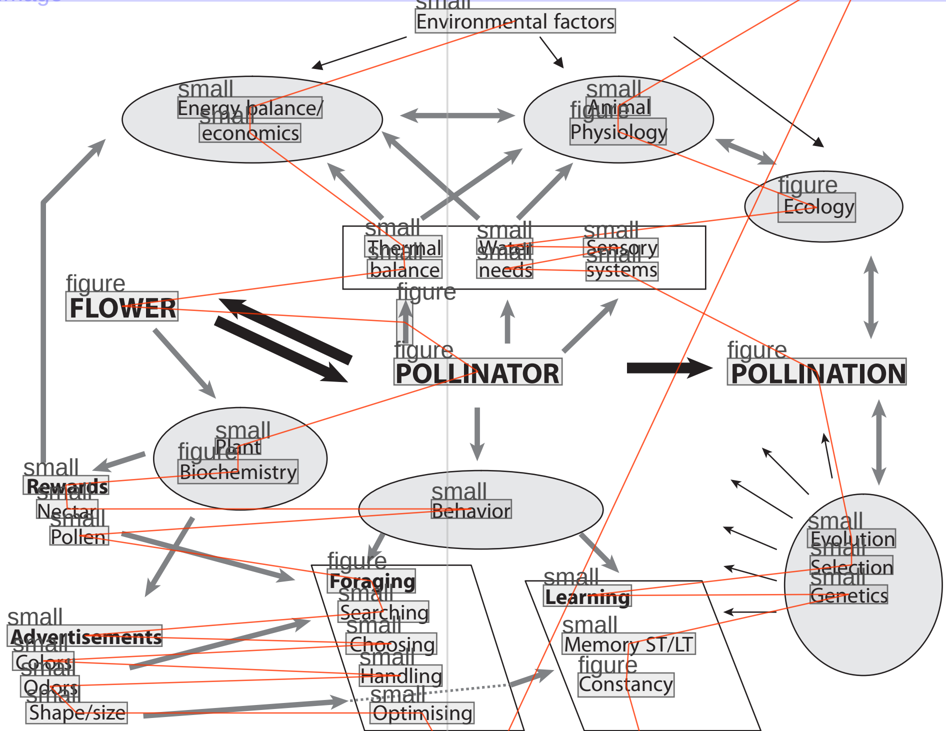

Figure 1.2 Key interactions of major biological topics and themes promoting interest in the study of pollination.

biology, now seen as an especially useful (because highly quantifiable) arena for more general work on community structures (J. Thomson 1983); so this book inevitably considers the community ecology of pollination, especially in later chapters.

Pollination biology also gives exceptional insight into the ecology of reproductive strategies and the complexities of sex and reproduction. Flowers usually are hermaphrodites, but they have many ways of organizing their sex life sequentially or spatially to maximize their reproductive output and **fitness**. This book contains rather little coverage of plant reproductive strategies beyond the basics, because the field has now become dominated by theory and modeling, and the topic has also been extensively and recently reviewed in other works (e.g., Harder and Barrett 2006).

In the realm of animal *behavior* some key influences can be especially easily measured and manipulated with flower visitors, and it is no accident that much of the key work on **visual discrimination**, learning behaviors, and above all **optimal foraging** has used pollinators, especially bees. **Optimal diet theory** can model how animals should behave in an environment offering different proportions of alternative prey as potential food items of differing value (also taking into account factors such as conspicuousness and different variances). The theory predicts that a range of outcomes from complete specialization on one kind of prey item to complete generalization on all possible items is to be expected, even from the same animal, as the prey parameters are varied. Substituting “flower” for “prey item” (and with the immense advantage of very easily quantified **caloric rewards** from nectar), it is not unexpected that pollinators similarly turn out to show almost the full range of possible foraging behaviors. Furthermore, they have proved ideal subjects with which to develop foraging models that can take into account different constraints on the foraging animals, whether from different physiological limits or from different cognitive skills. Learning ability is especially needed where resources are of intermediate predictability (Stephens 1993): that is, too unpredictable over one or a few generations for fixed behavior patterns to be favored, but not so greatly unpredictable that an individual cannot track the changes. This exactly applies to floral resources, so that we should expect flower visitors from any **taxon** to be good learners. Fortunately this is also readily tested with real or model flowers where just one trait at a time can be varied or associations of traits compared; again, social bees are ideal animals to work with, reliably emerging from their nests and traveling straight to the flowers provided, then displaying clear choices between alternative flowers.

For all these reasons, and with the added concern over human-induced effects on pollinator services in relation to biodiversity and to crops, interest in pollination ecology has burgeoned in the last ten to fifteen years, and the subject is attracting strong interest beyond the traditional academic centers of the developed world, giving us valuable insights into more varied habitats in Asia, Africa, and South America and into a greater diversity of interactions. Increasingly these systems are being modeled, and our preconceptions (of these and of other kinds of mutualisms) are being challenged. But the models are sometimes hampered by reliance on inadequate records, and understanding, of flower-visitor behaviors, and one of the most important issues for the immediate future is ensuring that the new generation of pollination ecologists understand the core subject material of floral biology and can measure and categorize *pollination* as distinct from mere *visitation* to feed into their models. We are in need of many and better quantitative studies of the *effectiveness* of visitors (for example, the average number of conspecific outcrossing **pollen grains** deposited on a stigma at an appropriate time by a given visitor in a single visit; chapter 11). Then we can properly understand plant and pollinator communities and pollination **networks**, and the effects of potential extinctions of flower visitors/pollinators on the communities of which they are a part. This book therefore hopes to provide in a single source a useful reference for all the aspects of floral biology and pollination interactions that need to be considered to give a real appreciation of these fascinating mutualisms.