

Seed and pollen dispersal by animals: convergence in the ecology of contamination and sloppy harvest

D. H. JANZEN

*Department of Biology, University of Pennsylvania,
Philadelphia, Pennsylvania 19104, U.S.A.*

Seed dispersal and pollen movement by animals have very much in common, though we know so little of either that it is hard to be specific. The focus has been on animals at the fruit crop rather than the seed shadows that they generate (and the fate of those seeds), and on the animals that arrive at flowers rather than where they take the pollen obtained or whence came the pollen they are carrying. 'Seed dispersal' is a word that does not imply the fate of the seed; 'pollination' relates to the fate of the pollen grain, and therefore the two words are not of parallel meaning. In like manner, seeds (the zygote contained within) are different individuals from the parents while pollen is much more like the parent. The following areas are discussed with respect to how seed and pollen movement compare: ability of parent plant to assess success; gene flow; dependency of animals on seeds, pollen and bait; disruption by animal loss; secondary movements; fate of most seeds and pollen; syndromes; selection for maximization of movement; exclusion of 'unwanted' animals; adjustments to the needs of the animals; seeds and pollen as contaminants; necessity of dispersal and outcrossing. We need much more knowledge of what actually is happening in nature with seed and pollen shadows, and improved ability to think like a plant.

KEY WORDS:—Fruit – pollination – seed shadow – gene flow – pollen shadow – fitness – animal-plant interaction.

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INTRODUCTION

Seeds and pollen are moved about by animals as surface and food contaminants and as potential food items. Both transport events may raise, lower, or not affect the parent plant's fitness. The reviews and books on pollination and seed dispersal (e.g. Ridley, 1930; Grant, 1965; Faegri & van der Pijl, 1966; Baker & Hurd, 1968; Janzen, 1970, in press a; van der Pijl, 1972; Morton, 1973; Proctor & Yeo, 1973; Levin & Kerster, 1974; Richards, 1978; Fleming, 1979; Thompson & Willson, 1979; Wheelwright & Orians, 1982)

make it quite clear that within both fields, attention has been very lopsided. Pollination biology traditionally focuses on the incoming pollen because of its obvious agricultural importance and its ease of tally. We know next to nothing of the biology of pollen donation or dispersal (Levin & Kerster, 1974), or how the male half of plant reproductive biology views the world. For example, the question of whether a plant tries to sire as many seeds as possible, be a father in as many clutches as possible, or something in between (Janzen, 1977a), is almost unapproached in field biology (but see Bertin, 1982). The biology of seed dispersal by animals, studied almost exclusively by zoologists, has focused on the animals that arrive at a fruit crop and, more recently, on how they treat that crop. The seed shadow thereby generated and what recruitment it yields to the female parent is *terra incognita* in field studies.

In conversations, if not much yet in writing, pollination biology and seed dispersal biology are reputed to have been subjected to some fairly detrimental analogies of one onto the other. Indeed, Wheelwright & Orians (1982) found it quite inappropriate to view them as essentially the same process. However, it is my impression that we need not so much a discussion of misleading analogies as a closer look at what these processes have in common. This quickly leads to the awareness that much of their process in common is not understood for *either* pollination *or* seed dispersal by animals. I cannot hope to provide a factual comparison of the two (e.g. what fraction of the plants in Costa Rica are animal-dispersed and what fraction animal-pollinated, how much greater is the average weight of seed dispersers than pollinators, what is the average size of a disperser coterie, etc.). Generally these kinds of facts have not been gathered. Rather, here I focus on the structure of similarity.

TERMINOLOGY

Seed dispersal, via animal(s) or otherwise, is movement away from the maternal parent plant. Behavioural shedding of a fruit to present it, or its seeds, to an earth-bound vertebrate disperser coterie is not seed dispersal. A seed that travels away from a tree in a bird's gut, but returns to the ground below the tree via that bird's faeces, has been dispersed. Most dispersed seeds land in sites lethal to the seed or seedling. In almost all seed crops evolutionarily moulded by past fitness-enhancement through animal-mediated seed dispersal, some seeds are also dispersed by abiotic factors. Some seeds in almost all seed crops are never dispersed, and some species have seed crops in which the majority of seeds are usually not dispersed. Both states, and the states in between, may be selected for (may be 'normal'), may be the consequence of immediate capricious nature acting on an individual plant (or population), or may be the consequence of the genotype having not yet been completely moulded by new selective pressures brought about through a change in the environment. Seed dispersal is a quantitative trait and seed shadows display strong variation at the level of the habitat, population and the individual's crop.

Seed dispersal is nothing more than eruptive emigration of offspring away from parents. Just as with animal offspring, the highest parental fitness does not occur with the largest possible number of emigrants but rather occurs with some complex function of number, size, placement, timing, subsidy, etc. The frequent

use of the misnomer 'bird-dispersed fruit', 'monkey fruit', etc. has turned our attention away from the fate of the *offspring* and onto the nature of the attractant for the dispersal agent. Fruits are not dispersed; fruits are maternal parental subsidy (as are seed coats) whose adaptive function is to be digested, rotted, scarified, etc. What now needs to become of interest is not what animal likes to eat the fruit of this or that plant, but rather questions such as what is the adaptive significance of multi-seeded fruits, what traits influence seed spitting, what is the ideal germination pattern of the clutch of seeds that emanate from the rears and fronts of the disperser coterie, etc.

Seed dispersal has to be one of the greyest words in biology. Everybody knows what it is yet we know next to nothing about it. Perhaps the largest mistake of all is to view only those seeds that land where you think they should have landed as having been 'dispersed'. We do not begin to know enough about the biology of wild plants to know what dispersal timing and location gives the highest parental and offspring fitness (and all the computer and theoretical modelling in the world will not provide that knowledge).

Pollination by animals is pollen arriving at the stigma of a conspecific plant via an animal. Immediately it is clear that this is not parallel to the definition of seed dispersal, where no implication of seed fate is contained in the definition (and see Wheelwright & Orians, 1982). A seed swallowed and digested has been dispersed; a seed defecated in the dark depths of a dry cave has been dispersed. A pollen grain that falls from a flying bee or is fed to a bee larva has not participated in pollination. This difference in terminology originates in the fact that the targets of dispersing seeds do not have the unambiguous morphology of a stigma (though a conspecific stigma is not a conspecific stigma is not a . . .). We should perhaps speak of pollen dispersal; pollination is arrival. While tempted to coin a word for seed arrival at sites where there seems at least some chance of growing into an adult with some fitness (in part the 'safe sites' of Harper, 1977), I refrain because the application of the term is essentially impossible. Perhaps when we know much more of the biology of individual wild plants. . .

The differences between seed dispersal and pollination are made even more severe by the fact that pollination also involves obtaining the right pollen (as well as generating pollen shadows). The question appears of whether a maternal parent wants one, few, or many parents for her clutch (Janzen, 1977). Pollination biology has traditionally ignored the question of the source of the pollen that is brought to wild plants by animals (but see Janzen *et al.*, 1980; Bertin, 1982); what kinds of seeds the animals bring *to* a fruit crop is likewise undiscussed in dispersal biology, but I suspect that at least for perennial plants it is of relatively small concern to the maternal parent. The trick in pollen reception is to bring in the animals carrying the right pollen (i.e. to some degree those that have previously been to the right plants). The trick in seed dispersal is to send the seeds *away* in the right animals, and where they have been previously may also be of great import. For example, if a newly awakened bee goes directly from her nest to a tree's flower crop, it may be useless in bringing in pollen (though of value in taking some away to another plant). If a newly awakened bird goes to a fruit crop, it may be of great value in arriving with an empty stomach that can carry away many seeds. In fact, I will hazard that pollination probably cannot be discussed as a single phenomenon. The biology of pollen

reception is sufficiently different from pollen dispersal to have generated monoecious and dioecious modes of sexuality, and these same differences require that we speak of pollen reception and pollen donation as separate events. Lumping the two under the word pollination obfuscates that fact that we are usually talking about one or the other (usually pollen reception in the traditional literature).

There are two other discordances in our ways of thinking about seed dispersal and pollination biology. First, the concept of a seed shadow (the area mapped out by the dispersed seeds of a seed crop) and how it maps onto environmental heterogeneity is not difficult to grasp (e.g. Janzen *et al.*, 1976; Vander Wall & Balda, 1977; Stapanian & Smith, 1978; Darley-Hill & Johnson, 1981; Herrera & Jordano, 1981). However, the parallel concept in pollen donation or dispersal does not even have a name (pollen shadow?). A pollen shadow blankets two kinds of habitat. One is very small (and perhaps analogous in part to single small tree falls in a large expanse of primary forest) and consists of conspecific stigmas (where there is at least *some* chance of survival). The other is the area in between, where the pollen is unambiguously dead. By contrast, in almost no part of a seed shadow is a seed unambiguously dead (except in dry caves, and even here there may be a chance for secondary dispersal). Part of the art of being a sexually reproducing plant is to focus portions of the pollen shadow onto a certain set of stigmas. However, the set of all conspecific stigmas does not define the target of the pollen shadow. Even if there is no other complication, the paternal plant has to cope with the question mentioned earlier of whether to sire a maximum number of seeds, be a parent in a maximum number of crops, or something in between.

Second, pollen is much more a plant product than is a seed. Pollen is parental tissue much like nectar, fruit and leaf epidermis, except to the degree it has been changed by mutations, inversions, etc. Its impact on parental fitness is expressed almost entirely through the fitness of its ensuing zygote and the fitness of a parent's collective suite of offspring. Selection may therefore mould those pollen traits (and the other floral traits) that lead to a pollen shadow of a specific kind with no conflicts other than those that generate the answer to the question why you don't have eyes on the ends of your fingers. Seeds, however, are independent organisms as much as are their parents. The parent-offspring relationship is also moulding their biology. May I illustrate the potential conflict by asking what would be the effect on human parent-offspring interactions if each child was provided by the state with a moderate or small bank account which could not be directly drawn from by parents but whose funds could be used by the child in dealings with sibs and parents? To complicate things even more, I should note that seeds are very peculiar organisms. Not only are they an individual wrapped in a portion of the parent, but the resources that the zygote obtains from the mother pass through the hands of a committee, the endosperm, which is made up of 2-5 or more identical twins of the mother and 1 identical twin of the father (the pollen genotype). Furthermore, how would human relationships be altered if children appeared in equal-aged, sub-batches of multi-fathered sibs, and to rid herself of one child, the mother had to abandon numerous or all of the members of the batch? Photosynthesizing embryos (Janzen, 1982a), polyploid endosperm, and multi-seeded fruits provide the commonplace examples for the above generalizations.

To examine the subject in detail, I will make what appear to be widely held and simple generalizations about pollination or seed dispersal by animals, and then examine the similarities more closely.

GENERALIZATIONS

(1) *The parent plant cannot assay the success of all fruiting and most flowering events*

A parent plant can know how many of which flowers are pollinated, and it can know the amount and other morphological traits of the seeds (fruits) it produces, and modify other activities accordingly. However, the parent plant cannot assay *any* aspect of the consequences of its physiological and morphological behaviours that have been selected for through the fitness enhancement of seed dispersal. The plant is as if it were a deaf and blind person shooting at buffalo on an undulating plain. There are gun placements and firing frequencies that will maximize the number of buffalo hit, but none can be directly modified in response to the number of buffalo hit. If fruits are picked when ripe by an animal, the parent may be able to know how many have been removed, but it cannot know by whom or where the seeds went. If the fruits are shed as part of a behavioural presentation to dispersers, it cannot even know how many have been removed.

Pollen dispersal is nearly identical to the situation described for seed dispersal, but pollen reception is very different. The maternal parent has a multitude of developmental stages in which it can evaluate the potential or actual zygotes that it is subsidizing (the products of the pollen it received), and it has many ways that it can respond to various degrees of 'success' in pollen reception (e.g. fruit or seed abortion, Stephenson, 1981; changes in supra-annual fruiting phenology).

The pattern of flower and fruit (seed) output is, however, almost entirely dependent on some kind of averaging of what worked for previous generations—in strong contrast to vegetative traits, traits that are so much moulded to match the ecological realities of the present. However, there are some inconspicuous feed-back systems. How much pollen is dispersed is to some degree related to how much is received, and it is at least conceivable that flower crop size and other traits are modified accordingly. For seed dispersal however, the feedback is more tenuous; fruit crops do not increase and decrease in size (within a season) depending on how many animals there are in the habitat—though they may change in the size perceived by one animal as another removes the fruits. However, the appropriate sites for seed arrival may be more tightly linked to the plant, if the dispersal agents are instrumental in making such sites as well as dispersing seeds into them. For example, more elephants may mean both more thorough removal of *Balanites* fruits (nuts) and the creation of more places for them to become saplings. Bison may not only disperse herb seeds as they consume prairie foliage, but create the breaks in the perennial plant cover in which seedlings can establish (Janzen, in prep.).

(2) *Pollination and seed dispersal are the means by which plant genes flow*

Yes, pollen donation is simply insemination with an unattached penis, and genes may flow to a menagerie of distances from one plant's flower crop. But *flow* is not what is being selected for. What is being selected for is the value of siring

offspring of another plant. Likewise pollen reception (being pollinated) is really physiological and morphological sorting through the catch of a pollen trap; what is being selected for is not amount or flow *per se*, but rather those pollen parents the maternal plant deems best (assuming the pollen grain to be incompetent at raping the maternal parent). Seed dispersal is quite different from either of the above processes. It is emigration, eruptive emigration. Seed dispersal is no different from any other kind of juvenile dispersal away from the parent. Movement of genotypes about the habitat occurs through seed dispersal; the movement itself is not what is of value to parent or offspring, but rather movement to or away from particular sites or to particular patterns of proximity to other plants.

(3) *Pollination and seed dispersal are mediated by animals ranging from very dependent on the bait to those where the bait is a quite trivial part of the diet*

If we think only of bees, then it seems easy to feel that pollinators are more tightly linked to flowers than are vertebrate seed dispersers to fruits and seeds. But a moment of reflection shows that heteromyid rodents, cedar waxwings, manakins and quetzals, spider monkeys, etc., are the bees of the world of vertebrates and seeds. Further, just as the lepidopteran pollinators are only in part dependent on flower products (caterpillars eat a lot of leaves), many seed dispersers quite thoroughly mix fruit with other diets ranging from carrion to grass blades. From the plant's viewpoint, it is evident that most flower crops and most fruit crops are used by multispecific pollen and seed disperser coteries (and see Wheelwright & Orians, 1982, for emphasis on this). However, there are some plants, such as those serviced by mistletoe birds on the one hand, and elephants on the other, that are about as restricted in their seed dispersal interactions as are certain species of orchids in their dependence on orchid bees. At the extreme end are the ant mutualist rubiaceae epiphytes *Hydnophytum* and *Myrmecodia* which are probably as tightly tied to the ants for dispersal (Janzen, 1974) as *Catasetum* orchids are tied to *Eulaema* and *Euglossa* for pollination (e.g. Janzen, 1981b).

(4) *Complex and evolved arrays of animal-flower fruit interactions have on occasion been disrupted severely by losses of major sets of animals*

For example, the New World lost a major set of seed dispersers about 10 000 years ago (Janzen & Martin, 1982). At first glance there does not appear to be a comparable event in the history of pollinators. However, one can identify many potential ripple effects on the pollinators and their plants brought about by the above-mentioned loss of the large seed dispersers. The ensuing changes in density of this or that large plant should in turn affect the pollinator pool available to other plants in the habitat. Furthermore, the large mammals, through browsing, grazing and trampling should have altered the ratios of flowering to vegetative parts and the ratios of herbaceous to woody plants. Finally, the large mammals were undoubtedly dispersers of many small plant seeds (Janzen, in prep.) of the kinds of herbaceous plants that provide much of the nectar and pollen for bees and other flower visitors. This way of looking at the world makes of special interest the study of the present-day invasion of Central America by the African honey bee, which is very busily taking over the floral resources of native bees and other insects (D. W. Roubik, pers. comm.). In

other words, in this area of ecology, pollination and seed dispersal have much in common.

(5) *Pollen and seeds make secondary movements among landing sites*

It is clear that some pollen is moved from stigma to stigma by animal pollinators (e.g. Levin & Kerster, 1968) but in the vacuum of information on the subject, it is tempting to suggest that it is trivial compared to the secondary movement of seeds. Not only are animal-dispersed seeds commonly moved again by erosion, water and wind, but rodents are particularly adept at displacing dispersed seeds one or more times from their point of deposition (e.g. Janzen, 1982b). Of course such seed predators kill many seeds in the process of moving them, but nonetheless they are major forces in altering seed shadow configurations.

(6) *Most pollen and seeds die because they land in the wrong place*

Such a generalization is extremely hard to examine because it is not the tradition to determine where and how pollen and seeds die, but rather on which sites they survive. There is a strong temptation to label an animal that digests 50–90% of the seeds it swallows as a poor dispersal agent. However, if it defecates the few survivors in tree falls of high quality it may be vastly superior to a shade-loving animal with a much more gentle digestive system. Flowers offer the same example, only more so. It is certain that many species of female bees kill most of the pollen grains that they carry off yet are generally thought of as high quality pollinators. In other words, most attempts at pollen donation as well as seed dispersal fail. However, a seed crop has two components. First, there is the literal failure of the seed not being picked up by a dispersal agent. Second, there is the failure of having the seed(s) dumped at the wrong place. Flowers as well as fruits and seeds are susceptible to this dichotomy.

(7) *Dispersal and pollinator syndromes can be operationally identified*

There is a strong temptation for those who work with flower visitors to feel that floral syndromes are not as 'tight' as are fruit syndromes, and those who study visitors to fruit crops often feel the opposite. In fact, the application of syndromes to either flowers or fruits is fraught with pitfalls. While it is a reasonable guess that a flower with a long thin white fragrant nocturnal corolla is visited by sphinx moths and pollinated by a subset of these visitors, it is most decidedly bad biology to assume that the majority of sphinx moth nectar intake comes from such flowers or that sphinx moths are not to be expected among the major pollinators of other kinds of flowers. Likewise, it is a reasonable guess that a large-nutted drupe was evolutionarily moulded by the attention of large herbivorous vertebrates over millions of years yet at present some miniscule mouse may be the tree's sole means of highly effective seed dispersal. Red fruits may be eaten by a multitudinous coterie of seed dispersers; which of the members raise the fitness of the plant how far will be left to researchers long in the future to determine (and cannot be determined by the colour of the fruit or number of seeds eaten by any specific member of the disperser coterie).

I can identify no clear way in which flowers are more appropriate for syndrome biology than are fruits. In both cases, the description of a syndrome,

and the placement of a species within it, are only rough approximations, the utility of which will partly disappear as we come to know more of the details of nature.

(8) *Selection operates to maximize pollen movement and seed dispersal*

The most is never the best in pollination and seed dispersal, just as in other areas of biology. No animal runs as fast as it can all of the time. No plant photosynthesizes as much as it can all of the time. In pollination, it is quite evident that having maximum pollen reception (dump the anther contents onto the stigma and be done with it) or maximum pollen removal (as achieved by wind-pollinated plants) is often unlikely to yield maximum fitness. The distribution of pollen among the array of visitors is a complex game where the selective pressures probably never fully manipulate the traits to where ecological reality generates maximum fitness for the resources available. This is of course true for seed dispersal systems as well, but there is still a pervasive feeling among zoologists that one measures the 'goodness' of a dispersal agent by how many seeds it carries off. It is quite possible for a tapir that dumps a few seeds on a creek bank to produce more adult trees than a herd of horses that defecates thousands of seeds in open grassland. However, by virtue of the heterogeneity of tapirs and horses in the habitat, fruit traits of interest to both sets of animals will be selected for. And even given that selection, it may well be that the phenotype that eventually appears is that which guides more seeds into the poorer disperser because its traits are more compatible with other traits of the plant.

(9) *Since at least some portion of a flower and fruit crop is evolutionarily designed to be eaten by one or more animals, it is not likely that all 'unwanted' animals can be kept out (and who is 'wanted' varies with the ecological circumstance)*

The importance of distinguishing between visitors and pollinators, at least in theory if not in practice, has been in fashion for some time with pollination studies. However, it is clear that no studies have been able to map who is carrying the pollen that gives the highest fitness to a wild plant. Much more recently, it has become fashionable to begin to differentiate between those frugivorous vertebrates that do, and those that do not, carry off seeds (e.g. Howe & Primack, 1975). However, since the plant's desired seed shadow is unknown, it is still impossible to know which of those that carry off seeds are as much fruit thieves or parasites of the mutualism as are those that spit them below the parent plant.

It is striking that the fountains of nectar and fruit are not taken over by animals that are avid collectors of sugars, such as ants at flowers (Janzen, 1977b) and monkeys for fruits. While Haber *et al.* (1982) are impressed with the occasional presence of an ant taking nectar from a flower I am much more impressed with the general failure of ants (and stingless bees—*Trigona*) to take over these calorie-rich food sources and defend them territorially. The answer has to lie in nectar toxicity, difficulty of entering flowers, the 'on/off' nature of nectar flow, nectar dilution, and nectar inadequacy as a pure diet. To pretend that ants fully use flower nectar (Haber *et al.*, 1982) is to ignore a potentially very interesting phenomenon. Likewise, the analogous case must apply with large crops of ripening fruits, except that they lack the intermittent presentation of resources found in flowers. I suspect that such intermittent presentation has

not been selected for in a fruit crop because the consumers are generally not abundant enough to truly monopolize the crop and because it would be too risky to do so for the frugivore, *vis à vis* exposure to predators and diet balancing.

(10) *Floral and fruit rewards are evolutionarily adjusted to the 'needs' of the animals concerned, and vice versa*

Almost all species of plants are pollinated or dispersed by an array of animals (and certainly they have been over evolutionary time), and the desires of the members of a disperser or pollinator coterie are not identical. Furthermore, the traits that will exclude the unwanted visitors vary from animal to animal. The same applies to fruits and the dispersers of their seeds. Finally, what an animal needs from a flower or a fruit depends in part on environmental traits beyond the control or perception of the plant, and therefore the selective pressures on a fruit crop vary from day to day, site to site, tree to tree, year to year, etc. The phenotype outcome, for both flowers and fruits (seeds) should be an object that is optimal for no animal but rather the collective result of these somewhat opposing and supporting selective forces. That is to say, flowers and fruits are no different from any other set of organs called upon to generate a single output, say, such as shooting a gun or laying an egg. While a flower or a fruit may appear to be a relatively single-minded, unipurpose structure, the portions of the environment with which it interacts directly or one step removed are substantially more diverse than those of importance to say a single leaf, block of xylem, etc. I see no sign that this is more so for flowers than fruits.

(11) *Seed and pollen are dispersed as contaminants to food (or vestiture) except when explicitly harvested for food*

Seeds are large and this is why seeds are largely dispersed by large animals. Pollen is small and therefore dispersed by a much greater range of sizes of animals. However, the rules for dealing with contaminants apply to both seeds and pollen. Seed spitting and seed regurgitation have their analogues in body cleaning and pollen filters in the bee digestive tract. Seed digestion is sometimes a side product of consuming contaminated food, just as may be the case with pollen. I see no way in which pollinators as a group are more fastidious than are seed dispersers. There may even be differential worry over contaminant pollens of different sizes, colour and stickiness (e.g. Dressler, 1971), just as seeds of different physical traits are differentially noticed by fruit eaters (e.g. Janzen, 1981a).

(12) *Neither seed dispersal nor outcrossing are absolutely necessary for the persistence of nearly all of those many plant populations that are normally serviced by animals*

However, it is easy to imagine that if the animals are removed, substantial changes in population structure and genetic structure will quickly occur (and vice versa). With seed dispersal, it should be the density of plants, the juxtaposition of plants, and the number of habitats in which they are found, that will be most immediately affected by the removal of dispersal agents (e.g. Janzen & Martin, 1982). With the removal of pollinators, the consequences of inbreeding should apply and seed crops should be affected by the economics of reduced resource output to pollinators. The latter should occur with fruits and

seeds as well, but in both cases it is over an evolutionary time scale. I am often asked 'but if the Pleistocene extinctions eliminated major dispersal agents for some trees, why didn't the trees become extinct?' The answer is (1) some may have, and (2) there is no reason to expect them to be extinguished. Rather, they should persist in those habitats where conditions for recruitment are such that dispersal by other means generates a seed shadow adequate for the survival of the population. The analogous case is represented by the removal of pollinators. Those individual plants that can self-pollinate keep the population going while selection acts severely to favour selfing, or to generate new phenotypes that attract new pollinators.

CONCLUSION

This is an intellectually straightforward subject; finding out what is happening in nature is the difficult part. It is difficult because unlike the wind, animals tend to be removed by mankind. Further, a toucan retains its bill in a zoo but does not retain (or acquire) its foraging patterns. You cannot study seed rain into a treefall in a small patch of virgin forest in a national park if that patch is imbedded in an ocean of second growth generating millions of times more seeds of the species that occupy treefalls than could all the treefalls in millions of square kilometres of virgin forest (Janzen, in press b). It is hard to study the seasonal biology of male bees that pollinate primary forest orchids if plants of neighbouring croplands are subsidizing the females.

It is also difficult because we simply lack the technical machinery to follow dispersing pollen and seeds. And if (when) we have that machinery, we lack the people who can think enough like a wild plant to understand what placements of pollen and seeds will give what fitness results. Let me close with a question to illustrate what I mean.

Why do humans think flowers smell 'good'? Surely it is not because we still retain the genes from a time when we hovered at night in front of white-flowered tubular corollas. Floral fragrances presumably function to influence the speed and ease with which flowers are found by pollinators. That is to say, floral fragrances are messages that have long been subject to selection and are received by sensory systems likewise evolved to perceive them. As such, floral fragrances should have characteristics allowing them to be recognized over long distances under nocturnal weather conditions, distinguished from the multitude of other odours in nature, followed through vegetation and other generators or air turbulence, etc. Likewise, they have to do this within the bounds of sensory capabilities of the appropriate animals. The fragrances of ripe fruits dispersed by large mammals are subject to exactly the same kinds of selective pressures. Humans are undeniably part of one of the numerous mammal lineages that have been dispersers of the seeds of fleshy fruits for a very long time. Since the signal systems of nocturnally-pollinated flowers and fleshy fruits evolutionarily designed for mammals fulfil approximately the same function in nature, it is reasonable for them to converge on each other. It is likewise not surprising for the recipient of one signal system to be attracted to the signals of the other, especially if that recipient is a rather omnivorous beast. To put it more crudely, a perfumed and painted member of our society is quite unconsciously a fruit mimic.

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