

## WHAT POLLINATOR DISPERSAL STUDIES CAN DO FOR POLLINATOR-CROP SYSTEMS.

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### ABSTRACT

Theoretical and empirical researches have shown the need to associate landscape structure and dynamics to population dispersal mechanisms in a series of management scenarios. The knowledge of generalized dispersal patterns in agricultural settings is particularly welcome in studies of optimal foraging and plant gene flow because they have direct applications in practical issues such as crop yield, crop isolation, and pest control. The degree of genetic isolation of a crop which is animal pollinated is tightly associated with the foraging strategy of the animal. The analysis of individual pollinators' foraging behaviour is the basis of our understanding of crop isolation (in the sense of maintaining the purity of a stand), and of bee-hive management in the field. Likewise, data on the foraging flight of pollinators should ideally become part of risk assessment protocols when dealing with genetically modified crops, in order to reduce unwanted crop-weed hybridization and other potential problems. Simple quantitative methods for analysing pollinator movement could be widely adopted to compare the effectiveness of prospective pollinators. I review empirical and theoretical data available on pollinator foraging behaviour and pollen flow, and discuss the patterns that emerged from the most common pollination features measured.

### INTRODUCTION

The foraging behavior of insect pollinators has long been regarded as a highly useful system for the study of plant-insect interactions. It has been used as a model system in optimal foraging theory (Levin and Kerster 1974; Pyke 1978; Dukas and Real 1993) and in evaluating plant gene flow (Levin and Kerster 1974; Schmitt 1980; Rasmussen and Broedsgaard 1992). In addition, data on pollinator movements can provide fundamental information to a variety of agroecosystem studies. For example, a classical growers' challenge is the arrangement (amount and location) of beehives in the field to increase seed and fruit production, that is, to optimize crop pollination (recent experimental examples in Dag and Eisikowitch 1995; Vaissière and Froissart 1996). Another important economic issue is the maintenance of crop purity for seed production, which requires that a commercial stand be effectively isolated from the pollen of nearby relatives, wild or cultivated. The reverse situation has become increasingly problematic in recent years, with the prospective commercial release of a variety of genetically modified (transgenic) organisms (Ellstrand 1988; Klingner *et al.* 1991; Dale 1992; Kareiva *et al.* 1994).

Although the foraging strategies of pollinators are complex, a common assumption is that individuals --particularly bees-- follow the nearest neighbour pollination rule (Levin and Kerster 1974; Zimmerman 1981; Rasmussen and Broedsgaard 1992). According to it, bees foraging for nectar or pollen move to the nearest neighbouring flower or plant of the same species, if it has proved rewarding. This rule is appealing because it conforms to optimal foraging theories, and seems to be consistent (Turner *et al.* 1982).

It has been shown that bees are flexible enough to accommodate to landscape changes and therefore their flight pattern reflects resource spacing (Morris 1993, Morris *et al.* 1994). However, the rule might not apply as strongly to all landscapes. This relaxation could occur because the perception of neighbours may be influenced by factors such as floral display in a single plant, distance to other floral resources in the area, and density of the preferred floral resource. Studies on how the density and distribution of resources affect pollinator flight are common (Pyke 1978; Zimmerman 1982; Geber 1985; Fenster 1991; Pyke and Cartar 1992;

Morris 1993). The response of pollinators to floral display and patch size is also intrinsically related with plant reproductive strategies. For example, plants have the option of mass blooming --which increases the chance of self-pollination-- or gradual blooming over extended periods, with the risk of reduced appeal to pollinators (de Jong *et al.* 1992).

A series of methodological approaches are currently used to evaluate individual pollinator efficiency and pollen transfer. This paper reviews the applications of these methods in several aspects of pollination research in agriculture. The usefulness and limitations of some widely-used techniques are discussed with special reference to agricultural settings.

### **Patterns of Individual Foraging Behaviour**

The individual foraging behaviour of a pollinator species affects pollination efficiency and hence crop yield. Knowledge of these patterns is essential in any decision aiming at optimization or containment measures. The patterns of foraging behaviour can be described by a list of components, most of which are tightly associated with the response of pollinator to resource display. I comment on the most common parameters measured and the patterns that emerged from these studies.

Quantitative information on pollinator response to floral landscapes has been obtained in two different ways: by manipulating both landscape and bee visits in a very artificial ways, usually in one dimension (e.g. Manasse 1992; Morris 1993), and by measuring flight parameters in large-scale landscapes, with little or no manipulation of floral arrays or bee visits (e.g. Danka *et al.* 1990).

Observations of individual movement have been made in natural, artificial and agricultural settings (Plowright and Galen 1985; Ginsberg 1986; Kipp 1987; Collevatti *et al.* 1997). Most of the quantitative data available regarding foraging of insect pollinators in crops refer to the honey bee, *Apis mellifera* L. ( Kipp 1987; Danka *et al.* 1990; Greco *et al.* 1995), although there are some data available on the performance of other species, particularly bumble bees (e.g. Plowright and Galen 1985; Goulson 1994; MacKenzie 1994). Overall, bumble bees have proved to be more directional than honeybees, and perform longer inter-plant flights, therefore potentially increasing pollen flow.

Regarding the role of individual foraging in optimal pollen transfer, there is ample field evidence that only a few flowers out of those available in a plant are visited by any single pollinator (references in Di Pasquale and Jacobi 1998). This visiting strategy enhances the amount of outcross pollen and reduces that of self pollen, which is crucial for seed set in the case of self-incompatible species.

Another important pattern related to optimal foraging is the well documented preference of insects for high densities of resources. Thus, in natural systems, closely packed conspecific plants are seen as one single patch of resources and benefit from outcrossing. A large-scale monoculture would then be seen as an endless patch of the same resource. Commercial crops are extremely homogeneous landscapes compared to natural populations, as a result of the dominance of a single, synchronously available resource and the systematic distribution of individual plants. These features are typical of agricultural landscapes.

On a more detailed scale, however, each crop grows or needs to be planted in a particular way. This results in rewards like pollen and nectar being offered to pollinators in a variety of patterns, of which the most common is a landscape composed of alternating strips of high (crop rows) and low (intercrop rows) resources.

When the crop landscape is composed of distinctive alternating strips of high and low resources, it has been observed that most bees tend to forage in the same row, and have a strong forward tendency (Greco *et al.* 1995; Roumet and Magnier 1993; but see Currie *et al.* 1990). This information leads to practical horticultural measures, like in the case of

asparagus, a dioecious species for which the recommendation was to grow a sequence of female plants separated by one male plant in the same row to optimize seed yield (Greco *et al.* 1995). Other crops induce directionality in the insect because of their specific growth habit. In cucurbits such as the cantaloupe *Cucumis melo*, bees seldom change rows because they visit sequential flowers along a vine (Jacobi *et al.* 1995).

Besides flight path characteristics among resources, a very important parameter to evaluate pollinator efficiency is the extent of pollen carryover, i.e. the number of sequential plants or flowers that receive pollen from a focal plant. Pollen carryover is a function of physical and behavioural characteristics of the insect related to pollen handling. Carryover has usually been estimated based on the percentage of stigmas marked at different distances from a donor plant, the mark being either differentiated pollen, or pollen analogues like powder dyes (Thomson *et al.* 1986; Cresswell *et al.* 1995). Typically most pollen is transferred to the first few flowers (Cresswell *et al.* 1995; Mogie and Stamp 1995).

Finally, pollinator efficiency depends also on the fidelity to a floral resource. Although flower constancy is the rule in pollination, heterospecific pollen transfer (i.e. a single bee carrying mixed loads of pollen) is not uncommon in natural habitats and can affect the reproductive success of plant populations (Campbell 1985). High levels of resources, typical of crops, significantly reduces heterospecific pollen transfer (McLernon *et al.* 1996). Still, there is some controversy over the comparative degree of floral constancy of honeybees and other bees. At least in some crops like cranberry, honeybees have proved to be inferior as pollinators compared to bumble bees (MacKenzie 1994) and leafcutter bees (Cane *et al.* 1996), on account not only of slowness and the percentage of illegitimate visits, but also of heterospecific pollen loads.

### **Estimating Pollen Flow Via Flight Patterns**

Pollination is the most important component of gene flow because it is during this process that genes are exchanged among individuals. The combined knowledge of flight patterns of a pollinator and pollen carryover can give an estimate of genetic neighbourhood and gene flow of a plant species. The adoption of measures aiming at crop isolation will depend on studies of pollen flow.

Methods related to containment strategies are of several kinds, varying from genetic modifications (e.g. male-sterility) of a cultivar to physical barriers such as surrounding a crop with barren land or with a related variety that will act as a pollen-trap. The purpose in both cases is to hamper unwanted pollen flow, be it from wild populations to a cultivar that has to maintain its genetic purity, or from a transgenic crop to populations of non-transgenic commercial varieties or wild relatives.

Recent studies (e.g. Klinger *et al.* 1991; Rasmussen and Broedsgaard 1992; Antrobus and Lack 1993) have shown that gene flow in seed plants is not as limited as suggested by earlier techniques. However, it is still considered restricted, because of the short-range movement of most pollen and seeds (Bos *et al.* 1986; Golenberg and Nevo 1987; Gouyon *et al.* 1987; Jackson and Clarke 1991).

There are two kinds of methods for quantifying gene flow in the field: a) direct methods based on tracking marked individuals or their vectors (e.g. Philipp *et al.* 1992; Rasmussen and Broedsgaard 1992; Eguiarte *et al.* 1993) and b) indirect methods that infer patterns of gene flow from the spatial distribution of genetically marked offspring (e.g. Handel 1982; Fenster 1991; Klinger *et al.* 1991; Ranker 1992; Eguiarte *et al.* 1993).

Indirect methods have the disadvantage of not disclosing the dynamics of gene dispersal, nor the identity of its agents. It is thus difficult to adopt any sort of containment measure of pollen movement, which is the phenomenon to be focused on in the case of temporary populations such as crops. Estimates of pollen movement based on pollinator behaviour, on the other

hand, give a clear picture of the dynamics of pollen flow, since the agents are known (Cresswell *et al.* 1995), and have a more robust predictive power. Because the degree of isolation of an entomophilous plant population is linked to the flight characteristics of its main pollinators, data on pollinator foraging behaviour have been incorporated into quantitative models that specifically aim to predict pollen dispersal (Morris 1993, Morris *et al.* 1994).

A widely used method, proposed by Kareiva and Shigesada (1983) consists in following individual bees from flower to flower for several steps. Visited flowers are numbered consecutively. The flight path is then reconstructed by measuring step lengths between two consecutive stops, and the turning angle between these two. These two measures can be incorporated into equations to obtain information on the distance covered after a certain amount of visits, or net squared displacement. In order to simplify the model, an important assumption is that the organism exhibits the same probability of turning left or right, in which case the expected net squared displacement is

$$E(R_n^2) = nE(l^2) + E(l)^2 \frac{c}{1-c} \left( n - \frac{1-c^n}{1-c} \right) \quad (1)$$

Where:

$l$  is the mean step length

$c$  is the mean cosine of the turning angle

$n$  is the number of steps.

This method uses meaningful biological parameters that are relatively easy to measure in the field (e.g. McCullough and Cain 1989; Turchin *et al.* 1991; Cresswell 1997). It also simplifies comparative approaches of pollen flow by different insects.

If some measure of flight time is also recorded in addition to calculating the two variables (step length and turning angle) mentioned above, then the necessary requirements are completed for the eventual use in what are known as diffusion or diffusion-advection models (refs. in Cresswell *et al.* 1995), with the general equation

$$\frac{dP}{dt} = -c \frac{dP}{dx} + D \left[ \frac{d^2P}{dx^2} \right] \quad (2)$$

Where

$P$  is the probability of finding an individual forager at point  $x$  and time  $t$

$c$  is the advection velocity

$D$  is the diffusion coefficient

The results are useful in deciding upon the necessary containment measures of genetically engineered crops, and complement gene flow studies based on indirect methods. Cotton, for example, is one of the leading transgenic target crops, so assessment of containment measures in different geographical and ecological settings is mandatory (Kareiva *et al.* 1994). As part of these studies, I compared the flight behaviour of bumble bees and honeybees, each being the main pollinator of a particular commercial cotton field. I assumed that the bees faced similar conditions of resource display, as a result of the standardization of commercial plantations. My results confirm the general view that bumble bees are more directional and perform longer flights between plants than honeybees. This behaviour increases the chances of long-distance pollen transfer, consequently aggravating the risk of transgenic gene invasiveness through hybridization with unmanaged populations.

## DISCUSSION

There are two scales at which insect dispersal parameters can subsidize pollinator management techniques. One is the population scale, encompassing aspects of habitat, nesting sites, home range and territoriality, which can affect management of hives, and can give support to decisions concerning marginal land use. The second is the individual scale at which the pollinator transfers pollen among individual plants or flowers of the target crop. At this level, assessment of pollinator efficiency is made through parameters related to individual foraging such as behaviour on the flower, pollen packing, legitimate visits, flower constancy and pollen carryover. Few single studies, however, measure and associate more than two or three of these parameters, and even these have concentrated on honeybees.

Crop pollination throughout the world faces the risks of a very high dependence on a single pollinator, *A. mellifera* (Torchio 1990). One of the solutions to these risks has been to encourage research projects that develop breeding systems and appropriate bee management techniques with bees other than *A. mellifera*. Another reason for proposing greater investments in using pollinators other than *A. mellifera* is that this species has shown to be a poorer pollinator than managed bumble bees (MacKenzie 1994) or leafcutter bees (Cane *et al.* 1996) in various crops (Torchio 1990, Richards 1993). A recent review (Heard 1999) has confirmed that in the tropics, stingless bees (Apidae:Meliponini) are the effective pollinators of nine crop species and contribute to the pollination of some 60 other, but evidence is still lacking for many plant species (see also Roubik (ed) 1995).

Although a large amount of research has been devoted to test the ability of a few non-*Apis* bees as pollinators of commercially important crops (e.g. Richards 1993, 1995; Rahman and Chopra 1994; Cane *et al.* 1996), data are still inconclusive to effectively support the adoption of a series of non-*Apis* pollinators in many areas of agriculture. One of the main items to investigate is how native bees react to the attractiveness of particular crops. At the scale of a commercial plantation patch attractiveness is obviously not an issue, so concern switches to evaluate the capacity of bees to reach plants in central positions or away from pollinator nesting sites, the attractiveness of the resources offered compared to nearby wildflowers, and the flight behaviour in a landscape of rows and furrows. Brookes *et al.* (1994) found that the extent of alfalfa pollination by native bees is highly dependent on the resources offered in marginal lands, and that some of them do not visit the central part of the crop.

It was also flight studies that indicated that africanized honeybees could be as effective of pollinators as European honeybees (Danka *et al.* 1990), so that the problem of their invasiveness should be looked for elsewhere than in crop yield. These examples demonstrate that it would be useful to extend these type of studies to other potential pollinators, preferably with standardized techniques or protocols, because many studies in natural landscapes have shown a large differences in gene flow depending on the main pollinator (e.g. Schmitt 1980).

## CONCLUSION

Studies of pollinator foraging movements have proven useful in a series of agricultural problems, particularly related to crop isolation and yield. Most of these studies, however, have focused on a single species, *A. mellifera*, or have used a methodology that rendered comparisons with other studies difficult. A series of quantitative methods are available that could be applied more frequently or even be introduced in protocols so as to facilitate comparisons between prospective pollinators and different agricultural landscapes.

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## REFERENCES

- Antrobus S, Lack AJ. Genetics of colonizing and established populations of *Primula veris*. *Heredity* 1993; 71: 252-8.
- Bos M, Harmens H, Vrieling K. Gene flow in *Plantago* I. Gene flow and neighbourhood size in *P. lanceolata*. *Heredity* 1986; 56: 43-54.
- Brookes B, Small A, Lefkovitch LP, Damman H, Fairey DT. Attractiveness of alfalfa (*Medicago sativa* L.) to wild pollinators in relation to wildflowers. *Canadian Journal of Plant Sciences* 1994; 74: 779-83.
- Campbell DR. Pollen and gene dispersal: the influences of competition for pollination. *Evolution* 1985; 39: 418-31.
- Cane JH, Schiffhauer D, Kervin LJ. Pollination, foraging, and nesting ecology of the leaf-cutting bee *Megachile (Delomegachile) addenda* (Hymenoptera: Megachilidae) on cranberry beds. *Annals of the Entomological Society of America* 1996; 89: 361-7.
- Collevatti RG, Campos LAO, Schoereder JH. Foraging behaviour of bee pollinators on the tropical weed *Triumfetta semitriloba*: departure rules from flower patches. *Insectes Sociaux* 1997; 44: 345-52.
- Cresswell JE. Spatial heterogeneity, pollinator behaviour and pollinator-mediated gene flow: bumble bee movement in variously aggregated rows of oil-seed rape. *Oikos* 1997; 78: 546-56.
- Cresswell JE, Bassom AP, Bell SA, Collins SJ, Kelly TB. Predicted pollen dispersal by honey-bees and three species of bumble-bees foraging on oil-seed rape: a comparison of three models. *Functional Ecology* 1995; 9: 829-41.
- Currie RW, Jay SC, Wright D. The effects of honeybees (*Apis mellifera* L.) and leafcutter bees (*Megachile rotundata* F.) on outcrossing between different cultivars of beans (*Vicia faba* L.) in caged plots. *Journal of Apicultural Research* 1990; 29: 68-74.
- Dag A, Eisikowitch D. The influence of hive location on honey bee foraging activity and fruit set in melons grown in plastic greenhouses. *Apidologie* 1995; 26: 511-9.
- Dale PJ. Spread of engineered genes to wild relatives. *Plant Physiology* 1992; 100: 13-5.
- Danka RG, Hellmich RL, Collins AM, Rinderer TE, Wright VL. The flight characteristics of foraging Africanized and European honeybees (Hymenoptera: Apidae). *Annals of the Entomological Society of America* 1990; 83: 855-9.
- De Jong TJ, Waser NM, Price MV, Ring RM. Plant size, geitonogamy and seed set in *Ipomopsis aggregata*. *Oecologia* 1992; 89: 310-5.
- Di Pasquale C, Jacobi CM. Dynamics of pollination: a model of insect-mediated pollen transfer in self-incompatible plants. *Ecological Modelling* 1998; 109: 25-34.
- Dukas R, Real LA. Effects of recent experience on foraging decisions by bumble bees. *Oecologia* 1993; 94: 244-6.

- Eguiarte LE, Burquez A, Rodriguez J, Martinez-Ramos M, Sarukhan J, Pinero D. Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution* 1993; 47: 75-87.
- Ellstrand NC. Pollen as a vehicle for the escape of engineered genes? *Trends in Biotechnology* 1988; 6: S30-2.
- Fenster CB. Gene flow in *Chamaecrista fasciculata* (Leguminosae) I. Gene dispersal. *Evolution* 1991; 45: 398-409.
- Geber MA. The relationship of plant size to self pollination in *Mertensia ciliata*. *Ecology* 1985; 66: 762-72.
- Ginsberg H. Honey bee orientation behaviour and the influence of flower distribution on foraging movements. *Ecological Entomology* 1986; 11: 173-8.
- Golenberg EM, Nevo E. Multilocus differentiation and population structure in a selfer, wild emmer wheat, *Triticum dicoccoides*. *Heredity* 1987; 58: 451-56.
- Goulson D. A model to predict the influence of insect flower constancy on interspecific competition between insect pollinated plants. *Journal of Theoretical Biology* 1994; 168: 309-14.
- Gouyon PH, King EB, Bonnet JM, Valdeyron E, Vernet P. Seed migration and the structure of plant populations. An experimental study on *Thymus vulgaris* L. *Oecologia* 1987; 72: 92-4.
- Greco CF, Banks P, Kevan PG. Foraging behaviour of honeybees (*Apis mellifera*) on asparagus (*Asparagus officinalis*). *Proceedings of the Entomological Society of Ontario* 1995; 126: 37-43.
- Handel SN. Dynamics of gene flow in an experimental population of *Cucumis melo* (Cucurbitaceae). *American Journal of Botany* 1982; 69: 1538-46.
- Heard TA. The role of stingless bees in crop pollination. *Annual Review of Entomology* 1999; 44: 183-206.
- Jackson JF, Clarke GR. Gene flow in an almond orchard. *Theoretical and Applied Genetics* 1991; 82: 169-73.
- Jacobi CM, Gryj EO, Banks J. Measuring foraging movements of honeybees in different floral landscapes: is perception of nearest neighbors a safe rule? [Manuscript]; 1995.
- Kareiva PM, Morris W, Jacobi CM. Studying and managing the risk of cross-fertilization between transgenic crops and wild relatives. *Molecular Ecology* 1994; 3: 15-21.
- Kareiva PM, Shigesada N. Analyzing insect movement as a correlated random walk. *Oecologia* 1983; 56: 234-8.
- Kipp LR. The flight directionality of honeybees foraging on real and artificial inflorescences. *Canadian Journal of Zoology* 1987; 65: 587-93.
- Klinger T, Elam D, Ellstrand N. Radish as a model system for the study of engineered gene escape rates via crop-weed mating. *Conservation Biology* 1991; 5: 531-5.

- Levin D, Kerster HW. Gene flow in seed plants. *Evolutionary Biology* 1974; 7: 139-220.
- MacKenzie KE. The foraging behaviour of honeybees (*Apis mellifera* L.) and bumble bees (*Bombus* spp.) on cranberry (*Vaccinium macrocarpon* Ait). *Apidologie* 1994; 25: 375-83.
- Manasse R. Ecological risks of transgenic plants: effects of spatial dispersion on gene flow. *Ecological Applications* 1992; 2: 431-8.
- McCullough CE, Cain ML. Analyzing discrete movement data as a correlated random walk. *Ecology* 1989; 70: 383-8.
- McLernon SM, Murphy SD, Aarssen LW. Heterospecific pollen transfer between sympatric species in a midsuccessional old-field community. *American Journal of Botany* 1996; 83: 1168-74.
- Mogie M, Stamp AJ. Pollen carryover and neighbourhood in *Ranunculus bulbosus*. *Experientia* 1995; 51: 381-3.
- Morris WF. Predicting the consequences of plant spacing and biased movement for pollen dispersal by honeybees. *Ecology* 1993; 74: 493-500.
- Morris WF, Kareiva P, Raymer P. Do barren zones and pollen traps reduce gene escape from transgenic crops? *Ecological Applications* 1994; 4: 157-65.
- Philipp M, Madsen HES, Siegismund HR. Gene flow and population structure in *Armeria maritima*. *Heredity* 1992; 69: 32-42.
- Plowright RC, Galen C. Landmarks or obstacles: the effects of spatial heterogeneity on bumble bee foraging behavior. *Oikos* 1985; 44: 459-64.
- Pyke GH. Optimal foraging: movement patterns of bumble bees between inflorescences. *Journal of Theoretical Biology* 1978; 13: 72-98.
- Pyke GH, Cartar RV. The flight directionality of bumble bees: do they remember where they came from? *Oikos* 1992; 65: 321-7.
- Rahman A, Chopra NP. Three new species of bee pollinators of the genus *Megachile* Lat. (Hymenoptera:Apoidea: Megachilidae) together with their foraging plants and periods of activity. *Journal of Entomological Research* 1994; 18: 369-76.
- Ranker TA. Genetic diversity, mating systems, and interpopulation gene flow in neotropical *Hemionitis palmata* L. (Adiantaceae). *Heredity* 1992; 69: 175-83.
- Rasmussen IR, Broedsgaard B. Gene flow inferred from seed dispersal and pollinator behaviour compared to DNA analysis of restriction site variation in a patchy population of *Lotus corniculatus* L. *Oecologia* 1992; 89: 277-83.
- Richards KW. Non-apis bees as crop pollinators. *Revue Suisse de Zoologie* 1993; 100: 807-22.
- Richards KW. The alfalfa leafcutter bee, *Megachile rotundata*: a potential pollinator for some annual forage clovers. *Journal of Apicultural Research* 1995; 34: 115-21.
- Roumet P, Magnier I. Estimation of hybrid seed production and efficient pollen flow using insect pollination of male sterile soybeans in caged plots. *Euphytica* 1993; 70: 61-7.

- Schmitt J. Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). *Evolution* 1980; 34: 934-43.
- Thomson JD, Price MV, Waser NM, Stratton DA. Comparative studies of pollen and fluorescent dye transport by bumble bees visiting *Erythronium grandiflorum*. *Oecologia* 1986; 69: 561-6.
- Torchio PF. Diversification of pollination strategies for U.S. crops. *Environmental Entomology* 1990; 19: 1649-56.
- Turchin P, Odendaal FJ, Rausher MD. Quantifying insect movement in the field. *Environmental Entomology* 1991; 20: 955-63.
- Turner ME, Stephens JC, Anderson WW. Homozygosity and patch structure in plant populations as a result of nearest-neighbor pollination. *Proceedings of the National Academy of Sciences* 1982; 79: 203-7.
- Vaissière BE, Froissart R. Pollination of cantaloupes under spunbounded row cover by honeybees (Hymenoptera:Apidae). *Journal of Economic Entomology* 1996; 89: 1213-22.
- Zimmerman M. Optimal foraging, plant density and the marginal value theorem. *Oecologia* 1981; 49: 148-53.
- Zimmerman M. The effect of nectar production on neighborhood size. *Oecologia* 1982; 52: 104-8.