

MONITORING: AN ESSENTIAL TOOL IN BEE ECOLOGY AND CONSERVATION

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ABSTRACT

Our research group has used several methods to monitor solitary bees in the wildlands of California and Costa Rica. In this paper we review these methods, the questions that directed them, and the usefulness and limits of the methods for current and future studies. The simplest methods are presented first, followed by the more complex methods. We emphasise that monitoring to record trends in pollinator frequencies over time requires a thoughtful and well-designed plan. We also propose that these trends must be accompanied with associated ecological information in order to assist in their interpretations. These interpretations become important if and when decision-makers attempt to use pollinator trends and associated ecological information for land management planning that includes protection and enhancement of pollinators. Biologists must also become more actively involved in promoting awareness and implementing plans to conserve these vital biological elements.

INTRODUCTION

Several recent reports strongly suggest that numbers of crop pollinators around the world are declining, consequently, diminishing yields of some crops (Banaszak 1995; Buchmann and Nabhan 1996; Nabhan and Buchmann 1997; Allen-Wardell *et al.* 1998). The problem also extends to wildlands where numbers of pollinators of native flora may also be declining to levels where reproduction of an unknown number of plant species is or maybe negatively affected (Janzen 1974; Cuddihy and Stone 1990; Royte 1995; Frankie *et al.* 1997). There are ample reasons to believe that these reports are offering the first warnings of more serious future problems as more pollinator nesting/immature habitats and wild floral resources are destroyed by ever-increasingly human development.

The above reports are mostly anecdotal, and thus at this time it is difficult to find hard, convincing evidence to begin taking the necessary steps to reverse the apparent decline in pollinators. Implementing such action requires much more biological information from a variety of researchers who are just now beginning to ask new questions about pollinator diversity and ecology; how to quantitatively monitor pollinators over long periods; reasons for their fluctuations and decline; how to protect and conserve them; how to convince decision makers to take action; and how far should biologists go in promoting pollinator conservation.

In this paper we are concerned with the issue of pollinator monitoring, more specifically with bees. With the exception of honeybees in agricultural (crop) pollination research, the scientific literature on bee pollinator monitoring is extremely sparse (Banaszak 1980; Dafni 1992; Kearns and Inouye 1993; Strickler *et al.* 1996; Frankie et al 1997, 1998). It is our belief that to make informed statements about pollinator trends for bees or for other pollinators in an area over time, there must be good monitoring data available.

Our research group has been developing and testing a variety of bee monitoring methods since 1972, although most of these studies were not designed specifically to assess trends in pollinators and their frequencies through time. The goals of this paper are to:

- Review bee monitoring techniques used by our research group in California and Costa Rica.
- Review monitoring results, analyses, and interpretations of selected case studies.
- Offer biological, socio-economic, and political perspectives on findings.

Study Sites

California. Six study sites were chosen in 1987 for bee monitoring studies in northern California. Three of these were in the San Joaquin valley in grassland-wetland and riparian habitats. Two were in central coastal inland mountains and one was in the southern Sierra Nevada foothills. The latter three sites each contained several diverse habitat types, ranging from grassland, to chaparral, to oak-woodland, to oak-gray pine forest. Details on the vegetation and habitats of all six sites are found in Frankie *et al.* (1998).

Costa Rica. Various study sites were used from 1972-present in the seasonal dry forest in and around the towns of Bagaces and Liberia in the Province of Guanacaste in northwestern Costa Rica. The main habitat types used were dry deciduous forest, riparian forest, savanna, mesic forest, regenerative forest, oak forest, oak riparian forest, and human-disturbed dry deciduous forest. These habitats are described in detail in Frankie *et al.* (1988, 1997).

Types of Monitoring

We have been systematically monitoring bees in Costa Rica since 1972 and in California since 1987. Several approaches and methods have been used for monitoring, depending on the questions or hypotheses posed. Each method was field tested several times prior to collection of the first data set. Usefulness and limits of data generated from each method are discussed. The studies reviewed below are presented in order of the simplest first (based on objectives and methods used) followed by more complex studies.

The first four of five monitoring types described here are based on collections and/or visual counts (or observations) of bees at flowers of selected host plants. Several basic conditions had to be met before these collections were made, which helped to standardise the methodology.

The conditions:

- Weather must be favourable for bees. Warm, sunny, no-wind days are optimal; breezy days are tolerated however. In California, daily high temperatures have to be at least (20° C) or higher; in Costa Rica they have to be (29 ° C) 85°F or higher. Further, days having high versus low pressure systems are preferred.
- Selected plant species should flower each year; avoid supra-annual flowering species.
- Selected plants must be in full flower.
- Large flowering individuals (trees) or patches of shrubs, herbs, etc. are selected for monitoring over small and/or isolated plants/patches.
- Monitor at time of day when plant is known to attract greatest number of visitors; that is, when floral resources are plentiful.
- Note type floral resource(s) sought by bees on selected plant species; that is, pollen, nectar, oil, etc.

The fifth monitoring type is based on trap-nesting data and is described later.

Monitoring Types

A: Monitoring Bees at Flowers

Concept 1: Monitoring from selected plant species that attract a wide variety of bees.

Questions posed:

- What is the diversity in guilds of bees on selected plant species that are known to attract a wide variety of bees?
- Are elements (taxa) of bee visitor guilds missing (or rare) at particular sites or times?

This simple method, which requires little preliminary field work, provides immediate information on which bee species are present or absent at any given time at a particular site. It is accomplished by collecting bees from flowers with an aerial net. With only modest field experience one can identify and select plant species that attract a variety of visitors from those that attract limited visitor diversity.

This is a useful method for making quick qualitative assessments of bees on plants to determine presence, relative abundance, or absence of species in an area. It is also a good method for comparing bee species diversity between areas and through time. In the latter case, it is necessary to standardise numbers of plants sampled, method of sampling, time frame used, size of aerial net, etc. (See Concept 3 below).

Examples of highly attractive bee plants in California and Costa Rica are as follows:

- California:** *Wislizenia refracta*; about 30 bee species known to visit flowers. *Marrubium vulgare*; about 25 bee species visit flowers.
- Costa Rica:** *Andira inermis*; up to 70 bee species visit flowers (Frankie *et al.* 1976). *Dalbergia retusa*; up to 60 bee species visit flowers. *Cassia biflora*; up to 30 bee species visit flowers.

Concept 2: Monitoring plant species that attract only selected bee taxa.

Question posed:

- Are known selected bee taxa present in an area where host plant is found?

This is also a simple method; however, it requires background knowledge and experience with given plant species and the specific bee taxa they attract. Once plant species and their limited pollinator guilds are identified, these systems can be useful for monitoring selected bee species. As with concept 1 monitoring, these plants can provide immediate qualitative information on presence, relative abundance, or absence of very specific bee species in an area (see also Thorp and Leong 1995). If the collections are systematically made and quantified, results on given plants can be compared spatially with other plants in adjacent areas, or compared through time on the same plants (see concept 3 below).

Examples of these plant species and their specific bees are as follows:

- California:** *Cordylanthus rigida* attracts almost exclusively *Bombus californicus* and *Megachile angelarum*
- Costa Rica:** *Byrsonima crassifolia* attracts primarily bees of the genera *Centris*, *Epicharis* and *Paratetrapedia* (Anthophoridae).
Licania arborea attracts primarily bees of the family Halictidae.
Miconia argentea attracts primarily stingless bees and a very few small anthophorid bee species.
Tabebuia ochracea and *T. rosea* attract primarily bees in the genus *Centris* (Anthophoridae).

Note: With the exception of *C. rigida*, *B. crassifolia* and *Tabebuia* species, honeybees are also common visitors to the above plant species.

Concept 3: Monitoring selected plant species for assessing diversity and frequency of bee species through time.

Question posed:

- What is bee species diversity and frequency on selected plant species (individuals) over more than one season?

This method requires considerable background work and experience and a quantifiable sampling technique. Further, in many cases, it requires that the same individual plant (in the case of trees) or patches (in the case of shrubs) be used. Thus, the prerequisites for using this approach are more restrictive than the previous two methods. The results, however, can be more useful for suggesting statistically significant trends in changing bee composition and bee frequency once baseline guild data have been established.

We are currently using this method to assess changing bee compositions and frequencies through time on two plant species in Costa Rica. These are *Cassia biflora* (Caesalpinaceae) and *Andira inermis* (Fabaceae). Only the case of *A. inermis* and its bees will be considered here as we have more data collected on this species over a longer time period.

The first systematic bee collections were made in 1972 from several trees of *A. inermis* along a roadside planting just south of the town of Liberia (Frankie *et al.* 1976). At that time the area around the trees was in the process of being developed for diverse agricultural uses, and there was still considerable native vegetation and habitat, even though it was fragmented. The bees were again systematically sampled in 1996 from the same stand of trees after 24 years had elapsed (Frankie *et al.* 1997). On the second occasion, greater attention was paid to land developments that had occurred over the 24-year period and to sampling from trees that were marked for future sampling. In 1972 about 70 bee species were collected from trees of *A. inermis*. By 1996, only 28 species were recovered and their frequencies were substantially lower (Frankie *et al.* 1997). More specifically, the average number of total bees collected on a single tree in 1972 for a half hour period was $824 \pm SD210$; in 1996 it was only $92 \pm SD59$, which represented an overall decline of slightly more than 90% of the bees (see also Frankie *et al.* 1993).

Increased agricultural development over 24 years in the area around the *A. inermis* trees, resulting in less native habitat and vegetation, is believed responsible for the sharp decline in bees. Further, introduction of non-native plant species, more frequent fires (all human-caused), and a more simplified agroecosystem have undoubtedly contributed to the reduction in bees (Vinson *et al.* 1993). The same trees at this site will continue to be monitored in the future years, in part to insure that the differences are not a result of annual variation (casual sampling on the Liberia trees during the interim years, however, suggested that it is a result of a steady decline (Frankie *et al.* 1993)).

With this type of systematic monitoring, a wide variety of new questions can be asked once a data base is established. For example, we observed that despite careful monitoring on each *A. inermis* tree, there were considerable differences in bee composition and frequency among sample trees. When the data were analysed to look specifically at this difference, it was observed that some trees were highly attractive to Africanised honeybees (AHB) and some were not; and, some had little attraction to any bees. Using Chi-square tests, we determined that there were statistically different proportions between AHB) and large native bee taxa (esp. *Centris* and *Epicharis*) on individual trees, suggesting that intraspecific variation in floral rewards appears to occur commonly in this tree. Examining conspecific trees that were growing side by side and had significantly different bees visiting their flowers further supported this observation. Intraspecific variation in floral rewards is suspected in the same forest in *Tabebuia rosea* (Frankie *et al.* 1983a) and in *Caesalpinia eriostachys*, *Dalbergia retusa*, *Gliricidia sepium*, and *Myrospermum frutescens* (all in Fabaceae) (see also Frankie and Haber 1983).

Concept 4: Monitoring wide range of plant species in a specific area to assess how bee species partition floral resources seasonally and spatially.

Questions posed:

- What bee species are probably the most important pollinators of given bee plants?
- How can systematic monitoring at flowers be used to assess potential competition between honeybees and native bees for floral rewards?

These kinds of questions require at least a season of pilot field research in an area to acquire experience on the bee taxa present and their relative frequencies on numerous representative plant species. With this experience an appropriate non-destructive monitoring program can be initiated that will be suitable for any plant species and its bees. In California and Costa Rica we have used the following scheme and replicated it up to a dozen times to assess bee type and frequency of visitation to a plant. We marked off a 2x2m square of flowering foliage and recorded numbers of bees that visit flowers in that specific space for 2 minutes. From replicated observations, we have determined low, medium, and high frequency visitation rates of solitary bee species versus honeybees. The only prerequisite for this study is a knowledge of all the families (and some genera) in an area and a strong personal sense of concentration and focus. A tape recorder can be used to assist in recording bee visits, especially when visitation is high and several bee species are present.

Results to date have been informative and provide evidence that honeybees (African and European) are apparently selective in taking floral resources that are also attractive to native bees. Honeybees have a range of preferences and definite non-preferences. After several years of monitoring in California and Costa Rica, the amount of overlap observed between native bees and honeybees approximates 40% in both areas, most subsites of which is a lower percentage than originally expected. A few California subsites have slightly higher percent overlap values, and that may be due, in part, to the high numbers of extant exotic weed species. Surveys of visitation frequencies of bees (see above methodology) on "bee flowers" were conducted to determine percent and level of overlap; that is, simultaneous visits or visits at different times by both honeybees and native bees to the same plant species. In the overlap cases, frequency of visitation may be rare, low, medium or high, depending on the plant species. Furthermore, honeybees may be spatially and temporally partitioned in an area, which may greatly reduce the potential for competition between native bees and honeybees, regardless of their monitored visitation frequency. Much work remains before we will know if honeybees and solitary bees regularly compete, sometimes compete, or coexist at our study sites.

B. Monitoring Bees in Trap Nests

Concept 5. Trap-nest monitoring for selected bee species in any given area.

Questions posed:

- What is diversity and frequency of cavity-nesting bees in an area?
- What are habitat nesting preferences for selected cavity-nesting bees in an area?
- What are changes in bee species composition and frequency through time in given areas?

This type of monitoring to answer most of these questions requires considerable preparatory field work, usually more than a year. In Costa Rica and California, two and three years, respectively, were required to determine; i) hole sizes that would attract extant cavity-nesting bees; ii) placement of trap nests in the most and least preferred habitats; iii) numbers of trap nests (or blocks of trap nests) to be used to sample common and occasional cavity nesters and; iv) length of trap nest season and intervals for periodic trap nest changes. After a season or two of this preparatory work, the first data sets can be gathered to answer the first question on bee diversity and relative bee frequency (Frankie *et al.* 1988; Thorp *et al.* 1992).

In the case of the second question on nesting habitat preference, two years of trial field work are desirable. In Costa Rica, we tested habitat preference for *Centris* species in several dry forest habitats in 1986, after two years of preparatory work (Frankie *et al.* 1988). Data were systematically collected and quantified in 1986 during the entire nesting season for six *Centris* species.

The results of trap-nest collections are best analysed using generalised linear models because the response variables are not continuous or normally distributed. For some questions the response variable is a discrete count (numbers of bees) with a Poisson error structure for which a Poisson regression is most appropriate. Other questions are best addressed with the data in the form of a proportion of used versus unused nesting holes, which has a binomial error structure and suggests a logistic regression. We have used several different statistical packages for these analyses: GLIM program (Baker and Nelder 1978), GLIM 3.77 (Payne 1986), BMDP (PLR for step-wise regression), and S-Plus, but there are many other programs that can be used for generalised linear models such as JMP, GENSTAT, some aspects of SAS, etc.

Using these types of analyses, we found that three *Centris* species (*C. bicornuta*, *C. nitida*, and *C. vittata*) had significant tendencies to use particular habitats whereas a fourth species (*C. analis*) showed no preferences (Frankie *et al.* 1988). With knowledge of habitat preferences, other studies were designed to answer further questions about nesting ecology. From 1987 to 1991, we studied preferred nesting habitats for seven cavity-nesting *Centris* species in the Costa Rican dry forest (Frankie *et al.* 1993). We found significant differences in frequency of nesting *Centris* bees in trap nests among sites and among habitats. Three of the common *Centris* species (*C. analis*, *C. nitida*, and *C. bicornuta*) preferred the closed oak forest in all five years of the study. These three species each showed significant changes in frequency through time, however, the overall frequency of nesting *Centris* bees in traps remained approximately the same from 1987 to 1991. Interestingly, the frequency of *C. bicornuta* went up through time; whereas the frequency went down in *C. nitida*. *Centris analis*, on the other hand, increased in numbers from 1987-89 before starting a downward trend. These kinds of frequency patterns also raised new questions about the ecological reasons why bee frequencies change through time (Frankie *et al.* 1993).

In California, we initiated a study in 1987 to record and monitor bee species diversity and changes in frequencies of selected species in six northern California sites (Thorp *et al.* 1992). The main impetus for this study was to record specific types of ecological data at these sites before arrival of the Africanised honeybees in the northern part of the state. For three years 1987-89, we gathered a wealth of qualitative data on cavity-nesting native and exotic solitary bees (Thorp *et al.* 1992), which was then used to design a quantitative study to examine bee frequencies and their possible changes through time. Results of this study (1990-92) were analysed using the Poisson regression (Frankie *et al.* 1998), as we had done in Costa Rica.

The California bee monitoring study has been ongoing constantly since 1990 at the six original study sites (Thorp *et al.* 1992). The first three years of this study clearly indicated significant differences among sites in bee diversity and composition; significant differences in bee frequency between sites; and significant differences in changes in bee frequency over the three year period (Frankie *et al.* 1998).

One of the most dramatic finds of the study occurred at the southern most site in the San Joaquin Valley-- Creighton Ranch Reserve, near Corcoran, California. At this site, we recorded the highest bee diversity in 1987 among all six study sites in our trial field work (Thorp *et al.* 1992). After that time, a long-term drought set in, and bee diversity and frequency declined precipitously and remained low through the winter of 1994-95 when the drought broke. Diversity and frequency of bees began to increase slowly in 1996 and then made a sharp increase in 1997, declining slightly in 1998. It is also noteworthy that cavity-nesting bees were extremely scarce on flowers at Creighton and at several other surrounding sites in the southern San Joaquin Valley during the drought period. Further, the drought had a much less severe effect on monitored bees at two other sites in the northern part of the San Joaquin Valley (Frankie *et al.* 1998). These findings raise new questions regarding weather and floral resource relationships to nesting biology of solitary bees, which must be taken into

account when assessing short-term and long-term trends in bee frequencies over time (see below).

Need for additional ecological information. Trap-nesting studies provide valuable quantitative information on selected bee species diversity and changes in bee frequencies through time. They do not, however, provide insight on cause and effects of changed frequencies. It is thus important to plan ahead with specific complementary ecological studies that should provide information for interpreting bee frequency patterns. Obvious examples of this kind of study would include: i) studies on natural mortality factors; ii) monitoring usual and unusual weather patterns (e.g. drought periods, extreme rainy periods, El Niño and La Niña years); and iii) monitoring human disturbances (e.g. such as new or changing agricultural developments, pesticides, loss of preferred bee nesting habitats, fire, changes in local/regional hydrology).

Another type of ecological information that can be obtained concerns the selection of bee taxa as bioindicators of habitat change or environmental health. In our comparative bee monitoring work on *Andira inermis* in Costa Rica, we observed that changes in agricultural development over a 24 year period may have had their greatest impact on megachilid bees and stingless bees as evidenced by their noticeable decline in species diversity and frequency (Frankie *et al.* 1997). Much more work is needed to document taxa that are most affected by ecological changes and reasons for their sensitivity.

Discussion

Bee monitoring in California and Costa Rica has proved to be a useful tool for answering a wide variety of questions concerning pollinator diversity, relative frequency, preferred habitats, and changes in frequency through time. The most important types of monitoring were those driven by questions that required quantitative collections of data, which could be replicated within seasons and annually. Information-filled monitoring programs, which are desirable, should contain the following kinds of characteristics:

- **Concept.** A well-defined concept stating the problems, goals and limits of monitoring study is a prerequisite.
- **Questions.** Good questions or hypotheses must drive each monitoring program. The scope of the question should be reasonable to insure that finding an answer is feasible.
- **Appropriate design and statistical analysis** of data should be well planned in advance of the first data collections. Pilot studies may be necessary. Consistency of collections through time is a must.
- **Emerging trends** of bee monitoring should be considered as a **first step** in a long-term monitoring program as the trends will almost surely generate new questions concerning cause and effect.
- **Complementary ecological information.** New questions that result from emerging trends should be anticipated. They will require interpretation from additional ecological information that should be gathered at the onset of the monitoring program.
- **Flexibility.** To design experiments to test new questions as they arise from emerging trends.

Very few studies exist in the literature on quantitative pollinator monitoring, especially as it relates to long-term trends. Yet, it is important for pollinator/pollination biologists to begin collecting this type of data at specific sites that can be followed through time. It is also desirable to select sites that have already received some past pollinator studies. In some cases there is probably enough data already collected to help generate questions and perhaps to provide some historical picture of bee diversity and relative frequency (Frankie *et al.* 1976, 1983, 1997; Barthell *et al.* 1997). Recent inventories by one of us (Thorp *et al.* 1994) at Santa Cruz Island, California provide a bee data base on selected plant species that is planned for future comparative surveys to assess bee diversity and frequency. Further,

extensive survey studies, such as those conducted in the mid 1970's by Hurd *et al.* (1980) on bee species diversity and frequency associated with sunflower, *Helianthus*, in the Southwestern United States, could also serve as a basis for future comparative surveys to assess the status of numerous bee species.

As recommended by New (1998, pp.21) and Scudder (1996), it is desirable to combine methods in assessing diversity and frequency of selected insect taxa whenever possible. Other workers have also advocated the use of 'sampling sets' in which several different methods are employed together to help compensate for bias of a specific approach or method (Disney 1986; Stork 1994).

We have begun to work with a combination of monitoring methods in Costa Rica to evaluate changes in forest-wide frequencies of large anthophorid bees during the dry season months of January through April. The bees, which include members of the genera *Centris* (most abundant), *Epicharis*, *Mesoplia*, *Mesocheira*, and *Xylocopa*, are considered to be the most important pollinators of a large number of plant species in this forest type (Frankie *et al.* 1976, 1983b). In a 10x10 km. site around the small town of Bagaces in Guanacaste Province, we have used the following before-mentioned methods to assess anthophorid frequencies:

- 1) 2x2m counts on three common primary pollen hosts and three common primary nectar hosts.
- 2) results of annual trap-nest studies on cavity-nesting *Centris* only.
- 3) results from quantitative bee sampling on *Andira inermis*.

We have also integrated selected ecological information with the bee frequency information to help in the interpretation of the findings to date.

Combined results of the three methods suggest the following anthophorid frequency pattern in the area between 1996-1999:

- large anthophorid bees were at relatively medium-high frequency levels in 1996 and 1997.
- dry El Niño conditions of 1998 severely limited flowering quantity (and probably quality) of most anthophorid bee hosts, which led to fewer provisioned nest cells.
- anthophorid bee frequencies were at extremely low overall levels in 1999, and this was probably due to sparse nest provisions from very limited floral resources available in 1998.

This assessment work will be continued at this site during the next five years with the goal of recording the likely recovery of large anthophorid bees in the area.

There remains the need to develop new statistical methods that will help evaluate the evidence collected by biologists. Any statistical methods utilised by pollinator researchers will, by logistical necessity, need to work well with what will most likely be limited sample sizes. Multivariate time series methods will inherently play important roles in assessing changes in bee frequencies through time. Of interest, for example, would be a study of the trends of competing bee species counts within the same region; likewise, counts of a bee species through time compared to concurrently collected qualitative ordinal data such as flower availability. Diversity indices are occasionally used by bee ecologists, but methods to quantify bee diversity for comparative purposes have received limited testing with mixed results (see Kevan *et al.* 1997). Other methods to quantify bee diversity have been attempted by Banaszak (1996) in Europe in both cultivated and natural seminatural environments (see also Banaszak 1980, 1995).

Where to monitor pollinators will depend to a great extent on the questions posed. Some say that only agricultural croplands should receive attention; others believe that natural areas should receive the attention. We propose that both areas are important, and wherever possible, croplands and natural areas, which are adjacent, should be monitored

simultaneously. Monitoring adjacent areas will also provide for a comparative approach on a wealth of information to be generated.

At some point in the monitoring studies, there will be enough data generated to suggest how pollinators will need to be protected and enhanced in the future for appropriate crop pollination. Pollinator biologists, in this regard, should always be thinking about enhancing native pollinator guilds or communities. One possible way might be to plant agriculture field edges with pollinator food plants as has been done for natural enemy populations of herbivorous insects (Long *et al.* 1998). This would be a challenging and worthwhile project to undertake.

Finally, pollinator/pollination biologists will need to become more proactive in the future and carry their findings beyond traditional scientific meetings and journals (O'Brien 1993). That is, they will need to become more interactive with land managers, engineers, planners, and other decision makers to insure scientific knowledge on pollinators is incorporated into land management plans. Further, there are other numerous audiences that need to be educated about the important services that pollinators provide (Nabhan and Buchmann 1997). Some of these audiences could be very helpful at assisting in promoting pollinator protection and enhancement in future decision making and even in possible policy and regulatory processes.

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REFERENCES

- Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, et al. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 1998; 12: 8-17.
- Baker RJ, Nelder JA. Generalised linear interactive modelling. Release 3. Oxford: The GLIM System Manual/Royal Statistical Society; 1978.
- Banaszak J. Studies on methods of censuring the numbers of bees. *Polish Ecological Studies* 1980; 6: 355-66.
- Banaszak J, editor. Changes in fauna of wild bees in Europe. Bydgoszcz: Pedagogical University; 1995.
- Banaszak J. Ecological bases of conservation of wild bees. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH, editors. The conservation of bees [Based on Symposium organized jointly by the International Bee Research Association and the Linnean Society of London, held in April, 1995]. London: Academic Press; 1996. (Linnean Society Symposium Series, 18).
- Barthell JF, Griswold TL, Frankie GW, Thorp RW. *Osmia* (Hymenoptera: Megachilidae) diversity at a site in central coastal California. *Pan Pacific Entomologist* 1997; 73: 141-51.
- Buchmann SL, Nabhan GP. The forgotten pollinators. Washington (DC): Island Press; 1996.

- Cuddihy LW, Stone CP. Alteration of native hawaiian vegetation: effects of humans, their activities and introductions. Honolulu: University of Hawaii Press; 1990.
- Dafni A. Pollination ecology: a practical approach. Oxford: IRL/OUP; 1992.
- Disney RHL. Assessments using invertebrates, posing the problem. In: Usher MB, editor. Wildlife conservation evaluation. London: Chapman and Hall; 1986. p.271-93.
- Frankie GW, Opler PA, Bawa KS. Foraging behaviour of solitary bees: implications for outcrossing of a neotropical forest tree species. *Journal of Ecology* 1976; 64: 1049-57.
- Frankie GW, Haber WA. Why bees move among mass flowering neotropical trees. In: Jones CE, Little RJ, editors. Handbook of experimental pollination biology. New York: Van Nostrand. Reinhold; 1983. p.360-72.
- Frankie GW, Haber WA, Baker HG, Baker I. A possible chemical explanation for differential foraging by anthophorid bees on individuals of *Tabebuia rosea* in the Costa Rican dry forest. *Brenesia* 1983a; 19/20: 397-405.
- Frankie GW, Haber WA, Opler PA, Bawa KS. Characteristics and organisation of the large bee pollination system in the Costa Rican dry forest. In: Jones CE, Little RJ, editors. Handbook of experimental pollination biology. New York: Van Nostrand. Reinhold; 1983b. p.411-47.
- Frankie GW, Vinson SB, Newstrom LE, Barthell JF. Nest site and habitat preferences in *Centris* bees in the Costa Rican dry forest. *Biotropica* 1988; 20: 301-10.
- Frankie GW, Newstrom LE, Vinson SB, Barthell JF. Nesting-habitat preferences of selected *Centris* bee species in Costa Rican dry forest. *Biotropica* 1993; 25: 322-33.
- Frankie GW, Vinson SB, Rizzardi MA, Griswold TL, O'Keefe S, Snelling RR. Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. *Journal of the Kansas Entomological Society* 1997; 70: 281-96.
- Frankie GW, Thorp RW, Newstrom-Lloyd LE, Rizzardi MA, Barthell JF, Griswold TL, et al. Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. *Environmental Entomology* 1998; 27: 1137-48.
- Hurd Jr. PD, LaBerge WE, Linsley EG. Principal sunflower bees of North America with emphasis on the Southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 1980; (310): 158.
- Janzen DH. The de-flowering of Central America. *Natural History* 1974; 83: 49.
- Kearns CA, Inouye DW. Techniques for pollination biologists. Niewot: Colorado University Press; 1993.
- Kevan PG, Greco CF, Belaoussoff S. Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. *Journal of Applied Ecology* 1997; 34(5): 1122-36.
- Long RF, Corbett A, Lamb C, Reberg-Horton C, Chandler J, Stimmann M. Beneficial insects move from flowering plants to nearby crops. *California Agriculture* 1998; 52: 23-6.
- Nabhan GP, Buchmann SL. Services provided by pollinators. In: Daily GC, editor. Nature's services: societal dependence on natural ecosystems. Covelo: Island Press; 1997.

New TR. Invertebrate surveys for conservation. New York: Oxford University Press; 1998.

O'Brien MH. Being a scientist means taking sides. *Bioscience* 1993; 43: 706-8.

Payne CD, editor. The generalised linear interactive modelling system. Oxford: The GLIM System Manual Royal Statistical Society; 1986.

Royte E. On the brink: Hawaii's vanishing species. *National Geographic* 1995; 188: 2-37.

Scudder GGE. Terrestrial and freshwater invertebrates of British Columbia: priorities for inventory and descriptive research. Victoria: Province of British Columbia/Ministry of Forests Research Program; 1996.

Stork NE. Inventories of biodiversity: more than a question of numbers. In: Forey PL, Humphries CJ, Vane-Wright RI, editors. *Systematics and conservation evaluation*. Oxford: Clarendon Press; 1994. p.81-100.

Strickler K, Scott VL, Fischer RL. Comparative nesting ecology of two sympatric leaf-cutting bees that differ in body size (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 1996; 69: 26-44.

Thorp RW, Frankie GW, Barthell JF, Gordon D, Newstrom L, Griswold T, et al. Long-term studies to gauge effects of invading bees. *California Agriculture* 1992; 46: 20-3.

Thorp RW, Leong JM. Native bee pollinators of vernal pool plants. *Femontia* 1995; 23: 3-7.

Thorp RW, Wenner AM, Barthell JF. Flowers visited by honeybees and native bees on Santa Cruz Island. In: Halvorson WL, Maender GJ, editors. *The Fourth California Islands Symposium: update on the status of resources*; 1994; Santa Barbara, USA. Santa Barbara: Santa Barbara Museum of Natural History; 1994. p.351-65.

Vinson SB, Frankie GW, Barthell JF. Threats to the diversity of solitary bees in a neotropical dry forest in Central America. In: La Salle L, Gauld I, editors. *Hymenoptera and biodiversity*. Wallingford: CAB International; 1993. p.53-81.