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Review article

Bees and pollination in our changing environment

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Summary — This is a review of the early literature demonstrating the adequacy of pollination by local bee populations before intensive and extensive agricultural practices. Although not always the best pollinators, honey bees were used in crops when populations of other bees crashed. Publications on managing and conserving pollen bees are included because interest in sustainable agriculture and biodiversity of bees and host plants is increasing.

Apoidea / pollination / sustainable agriculture / management

INTRODUCTION

Due to their fuzzy bodies and frequent, consistent flower-visiting habits, bees (Apoidea) are usually the most effective pollinators of the numerous crops and wild plants that are not wind-pollinated. The study of this important subject is difficult, due to the complex interactions between the bees, their hosts, and various environmental and economic conditions; also, existing knowledge is widely dispersed in the biological and other literature (for example, Clements and Long, 1923; Grant, 1949; Schmid, 1975). This review of interesting and still timely publications was compiled because many of the early reports are not accessible by computerized literature search, and others are in journals not searched by pollination biologists. Thus, there have been many oversights and omissions. In spite of many published reports to the contrary, most people continue to simplistically credit the common honey bee (*Apis mellifera* L) with nearly all of the insect pollination in nature (for example, Barclay and Moffett, 1984) and agricultural crops (Anonymous, 1973; Cheung, 1973; McGregor, 1976; Levin, 1983; Robinson *et al,* 1989; references in Southwick and Southwick, 1992).

At issue is the logical valuation of publicly shared assets (bees), most species and populations belonging to nobody, yet benefiting all of us through pollination (in economics, a condition referred to as an 'externality'). Honey bees and certain stingless honey bees were brought into domestication or management long ago, but for the

purpose of their honey and wax production rather than for any superior pollinating abilities. Pollination of crops was not a consideration at that time. Because they were owned by beekeepers and thus already had value in the economic system (in economic terms, were 'internalized') and could be managed, honey bees began to be used as pollinators when populations of other bees (= pollen bees) and crop yields declined, due to new adverse agronomic and environmental impacts. The challenge of bee and pollination economics even launched J K Galbraith's distinguished career in economics (Voorhies *et al,* 1933). The honey bee is a good general pollinator, but not for all crops, under all conditions, just as the prolific freshwater carp is a good fish, but others may be more suited to different environments such as the sea, tastier, or less bony. The pollination need is similar to that in fisheries and aquaculture, where, as 'free' wild fish populations decline, fish prices rise, and ever more species are brought into domestication (aquaculture). Since the Roman empire, the common carp has been the world's major cultured food fish, but due to recently reduced populations of wild fish there are now many more (in the Washington DC area, farm-raised fish now predominate in shops).

The rational assessment and valuation of things that have been historically considered 'free', such as clean air, adequate water, fish, and pollinators, has become a major concern in ecology, as scarcities of such things increase (Meyer and Turner, 1992; Vitousek, 1994). It seems to be human nature to unwittingly use up or destroy our resources, unless they can be specifically identified as worth saving, for economic reasons, or as ultimately beneficial to human life. Economic rationales such as, "what is it good for?" may be disguised as environmental, religious and aesthetic values in many cultures.

Thus, it is time to protect our native beneficial Apoidea through habitat conservation and sustainable agriculture, and to augment them with selected, managed pollinators that are best adapted to most efficiently pollinate the flowers of our crops.

DELAYED RECOGNITION

The bias in favor of maladapted but manageable honey bees is clearly illustrated by alfalfa (lucerne) pollination. Henslow (1867) first reported the tripping mechanism of the flower, and he noted that honey bees took only nectar, without tripping (pollinating). This was confirmed repeatedly (Müller, 1873; Brand and Westgate, 1909; Westgate, 1911; Piper *et al,* 1914; Hadfield and Calder, 1936; Tysdal, 1940; Knowles, 1943; Linsley, 1946; Akerberg and Lesins, 1949; Stephen, 1955; Semmens *et al,* 1993; many more recent authors). Other species of bees (especially *Megachile)* tripped the flowers and were soon found by astute observers to be efficient pollinators (Brand and Westgate, 1909; Piper *et al,* 1914; Archer, 1917; Sladen, 1918; Helmbold, 1929; Hadfield and Calder, 1936; Salt, 1940; Tysdal, 1940; Knowles, 1943; Stapel, 1943; Linsley, 1946; Akerberg and Lesins, 1949). Recommendations for conservation of habitats where bees could nest (Vansell, 1951; Franklin, 1952; Stephen, 1955), and the rearing or management of selected bee species (Knowles, 1943; Peck and Bolton, 1946; Bohart, 1972) began to be made as populations of native bees crashed, due to the new use of insecticides and the continuing destruction of habitat. In 1943, a Canadian grower, WD Clarke, first raised *Megachile* for alfalfa pollination (Peck and Bolton, 1946). Nevertheless, because honey bees were manageable and could distribute pollen from heat-stressed, open flowers, they still were promoted by scientists and others for alfalfa pollination everywhere (Akerberg and Lesins, 1949; Vansell, 1951; Franklin, 1952; Anon, 1973; Levin, 1983; Olmstead and

Wooten, 1987; Robinson *et al,* 1989). Recently, economic data confirming the superiority of managed *Megachile rotundata* F and *Nomia melanderi* Ckll were published (Olmstead and Wooten, 1987; Peterson *et al,* 1992; Wichelns *et al,* 1992).

A similar situation exists in apples and related orchard crops. Before the introduction of insecticides, early observers reported adequate pollination by native bees alone, and most of them recommended the conservation of uncultivated lands in or near orchards to provide habitat for their nesting (Sax, 1922; Hutson, 1926; Wilson, 1926, 1933; Atwood, 1933; Voorhies *et al,* 1933; Brittain and Newton, 1934; Howlett, 1934; Musychenko, 1937; Orsono-Mesa, 1947). Musychenko (1937) first recommended the management of pollen bees to augment their populations, and a Japanese apple grower, E Matsuyama, seems to have been the first to do so, using *Osmia cornifrons* (Rad) in the 1930s (Maeta and Kitamura, 1981). At present, this superior bee is managed to pollinate a third of Japan's apples (Sekita and Yamada, 1993) and its use has spread to other countries (Parker *et al,* 1987). Although polylectic honey bees are used in orchards, they obtain little nectar, and, having a long flight range, they tend to stray, to forage elsewhere (Voorhies *et al,* 1933; Cheung, 1973). Growers thus pay for hive rentals that may benefit their neighbors or even undesirable weeds (Voorhies *et al,* 1933; Loring, 1981; Goltz, 1987; MacFawn, 1993). Because most managed pollen bees are gentle, easy to keep, prefer the crop host, have short flight ranges, stay in the orchard, work rapidly, and collect and distribute pollen efficiently, interest in keeping them is increasing. *O lignaria propinqua* Cr, *O cornuta* (Latr), and other *Osmia* spp are now being managed (Parker *et al,* 1987; Torchio, 1990, 1991; Bosch, 1994; Bosch and Blas, 1994; Marquez *et al,* 1994).

Blueberries and cranberries (*Vaccinium* spp) are other crops that are better pollinated by pollen bees than honey bees, as discovered by Shaw *et al* (1939), and repeatedly confirmed (Wood, 1961, 1979; Boulanger *et al,* 1967; Bigras-Huot and Jobin, 1972; Kevan *et al,* 1983; Parker *et al,* 1987; Harder and Thomson, 1989). The management of several new pollinators is recently developing (Parker *et al,* 1987; Batra, 1994; Stubbs *et al,* 1994). New techniques for mass rearing bumble bees (Ptacek, 1985; Röseler, 1985; van Heemert *et al,* 1990; Vogel and Westerkamp, 1991) permit their field use in blueberries and cranberries, and their widespread use in glasshouses on other crops, such as the hothouse tomato. For best yields, these crops require buzz-pollination, which honey bees have long been known to be unable to perform (Fink, 1896; Herbst, 1918; Orsono-Mesa, 1947; Rick, 1950). Unfortunately, the findings of these authors were ignored for decades, and instead of efforts to manage the best pollinators, honey bees were used.

Different pollinators have different pollinating abilities, which vary with the bee species (its size, hairiness, quickness, fidelity, longevity, learning ability, flight range, cold tolerance, season, flower handling ability, *etc*). The appropriate match between each bee species and its host is critical, because a poorly adapted pollinator may even function as a parasite by removing nectar and pollen, without achieving pollination. Some early reports were relatively neglected (Allard, 1911; Green, 1955; Fronk and Slater, 1956; Medler, 1956;), but as knowledge of ecosystem dynamics and change increased, more attention was paid to this subject, especially the relationships between native bees, honey bees and plants (Primack and Silander Jr, 1975; Schemske and Horvitz, 1984; Herrera, 1987, 1989; Harder and Thomson, 1989; Thomson and Thomson, 1989, 1992; Young and Stanton, 1990; Westerkamp, 1991a,b; Willmer, 1991; Wilson and Thomson, 1991; Chagnon *et al,*

1993; Kunin, 1993; Cresswell, 1994; Marquez *et al,* 1994a,b).

THE CONSERVATION OF NATIVE BEES

Because unmanaged native bees are so important as pollinators of crops and wild plants, and interest in maintaining biodiversity is growing (Prescott-Allen and Prescott-Allen, 1986; Parker *et al,* 1987; Torchio, 1991), general awareness of the diversity of bee species and public knowledge of their value to ecosystems is increasing (Morse, 1960; Malyshev, 1963; Michener, 1979; Schreck and Schedl, 1979; Westrich, 1983b, 1990; MacKenzie and Winston, 1984; Scott-Dupree and Winston, 1987; Zöckler, 1988; Banaszak, 1989a; O'Toole, 1993; Adams and Senft, 1994). The impacts of various human activities on populations of bees and on their habitats have been studied, especially in Europe, where long and detailed records have been kept (Westrich, 1990). Impacts in Europe include forestry, cultivation patterns, pollution, drainage, irrigation, construction, parks as refuges, urbanization, herbicides and insecticides, road traffic, weed invasions, and host plant destruction (Emeis, 1964; Pawlikowski, 1967; Benedek, 1970, 1972; Haeseler, 1972, 1978, 1982; Peters, 1972; Jacob-Remacle, 1976, 1984, 1992; Williams, 1982, 1986, 1989; Banaszak, 1983, 1985, 1987, 1989b; Prescott-Allen, 1986; Banaszak and Manole, 1987; Kosior, 1987; Tanacs, 1987; Archer, 1989; Kratochwil and Klatt, 1989; Pawlikowski, 1989a, b; Torres *et al,* 1989; Fussell and Corbet, 1991; Schwenninger, 1992; Westrich, 1983a; Osborne *et al,* 1991; Vogel and Westerkamp, 1991; Lagerlöf *et al,* 1992; Donath, 1994).

Recent studies have documented similar impacts and population changes in Japan (Munakata, 1984) and in North and Central America (Plowright *et al,* 1978; Miliczky and Osgood, 1979; Wood, 1979; Ginevan *et al,* 1980; Johansen *et al,* 1983; Hansen and Osgood, 1984; Thomson *et al,* 1985; Kevan *et al,* 1990b; Vinson and Frankie, 1990; Johansen and Mayer, 1990; Kevan *et al* 1990a).

EXOTIC POLLINATORS

The accidental or deliberate importation of pollinators into new geographic regions has lately become a concern to some environmentalists. The widespread European honey bee and bumble bees imported into some regions (Dunning, 1886) may be displacing native bees or other pollinators of the native flora, or they may provide unsatisfactory pollination of these plants (Pyke and Balzer, 1983; Vogel and Westerkamp, 1991; Westerkamp, 1991; Wilson and Thomson, 1991; Thomson and Thomson, 1992; Kato, 1993; Paton, 1993). *Bombus terrestris* L is now widely distributed for pollination of crops and is another potential competitor (Donovan, 1990; Semmens *et al,* 1993; Kato, 1993). Although several species of solitary bees have been distributed to new regions for pollinating crops, they are less likely to displace native bees than is the ubiquitous European honey bee, due to their greater host-specificity, climatic limitations, shorter foraging ranges, specific conditions for nesting, and brief adult life (Donovan, 1990).

The principles that apply to the importation and establishment of exotic pollinators resemble those of classical biological control (Batra, 1982), in which beneficial organisms are sought near the center of origin of the problem-causing organism in a similar climate, observed and tested for lack of harm to other beneficial or rare organisms, imported into quarantine where their parasites can be eliminated, tested with hosts again, in confinement and then released for a specific purpose into their new environments. Considerable effort has gone into identifying the most efficient pollinators of

several Eurasian crops that may be worthy of importation into North America, South America, Australia and New Zealand where native pollinators are not well adapted to pollinate these crops (reviewed in Parker *et al,* 1987). Conversely, American pollinators of sunflowers, cotton, passion fruit, squashes and gourds, avocado, tomato, chili, blueberries and cranberries have been studied in areas where these crops are believed to have originated, the goal being to introduce their pollinating bees into areas where the crops are now grown without their most efficient pollinators (Parker *et al,* 1987).

Large human populations can currently only be maintained by agriculture, which must alter native environments. Humans, like all organisms, may be expected to increase in population (absent natural enemies), until all available resources are fully exploited, either directly (as in agriculture), or indirectly, for example, when biota and other natural resources have been assessed and then reserved for possible future value (in economic terms, internalized). The impact of humans is large, complex, and irreversible (Vitousek, 1994). One way to provide for more habitat in which to conserve native bees and other biodiversity, as well as nonrenewable resources, would be to improve the yields on existing crop lands. This can be accomplished, in part, by introducing the most efficient pollinators for these crops.

Résumé — Les abeilles et la pollinisation dans un environnement changeant. Les recherches antérieures ont montré que, avant le développement de l'agriculture intensive, des monocultures et l'utilisation des pesticides, la pollinisation des fleurs par les populations d'abeilles indigènes (Apoïdés) était satisfaisante. Quand ces populations d'abeilles ont décliné, des abeilles moins efficaces (principalement l'abeille domestique *Apis mellifera*) ont été utilisées pour la pollinisation parce qu'elles étaient déjà utilisées pour la production de miel et de cire. Il y a des dizaines d'années des chercheurs ont identifié les insectes pollinisateurs les mieux adaptés et décrit leurs habitats et leurs modes d'élevage. La prise de conscience actuelle de la destruction de leurs habitats, le besoin de biodiversité parmi les pollinisateurs, une plus grande connaissance de la spécificité insecte–plante, la valeur économique des pollinisateurs choisis, et les menaces pesant actuellement sur les populations d'abeilles domestiques ont fait de la pollinisation par les apoïdés en général un sujet d'actualité.

Cette publication présente une revue des références les plus intéressantes en incluant les recherches antérieures qui sont rarement citées mais cependant encore très actuelles. Elle décrit également les conditions historiques qui ont favorisé l'utilisation de l'abeille domestique, les implications économiques de la pollinisation, les changements dans l'environnement et dans les populations d'apoïdés, l'impact des abeilles domestiques étrangères et l'importance qu'il y a à comprendre le comportement des insectes pollinisateurs sur les fleurs.

apoïdés / pollinisation / gestion des pollinisateurs / agriculture

Zusammenfassung — Bienen und Bestäubung in unserer sich wandelnden Umwelt: ein kurzer Überblick über alte und neue Literatur. Frühere Untersuchungen vor Entwicklung der intensiven Landwirtschaft mit Monokulturen und Pestiziden haben ergeben, daß die heimische Bienenpopulation eine adäquate Bestäubung geleistet hat. Nachdem die Wildbienenpopulation zurückging, wurden die Honigbienen vermehrt für die Bestäubung eingesetzt, obwohl sie weniger leisteten. Ein Hauptgrund war wohl, daß zu diesem Zeitpunkt bereits eine Technik der Bienen-

haltung zur Erzeugung von Wachs und Honig vorhanden war. Alternative Bestäuber wurden bereits vor Jahrzehnten von problembewußten Wissenschaftlern bestimmt und Empfehlungen für ihre Haltung und den Schutz ihres Lebensraums gegeben. Zur Zeit rückt die Zerstörung der Umwelt immer deutlicher in unser Bewußtsein. Außerdem erkennen wir, daß die Biodiversität der Bestäuber notwendig ist und daß eine genaue Kenntnis über die Pflanze-Bestäuber-Spezifität gebraucht wird. Der ökonomische Wert von selektierten Bestäubern und die Bedrohung der Honigbienenpopulation hat neuerdings die Bestäubung durch Apoidea zu einem wichtigen Diskussionsthema gemacht. Es werden einige interessante Literaturzitate aufgelistet, in denen auch selten zitierte, aber immer noch gültige ältere Forschungen über Bestäubung enthalten sind. Weiter läßt sich die historische Entwicklung der Ausrichtung der Bestäubungspraxis vorwiegend auf Honigbienen verfolgen. Auch die Ökonomie der Bestäubung, die Veränderungen in der Umwelt und in der Population der Apoidea, die Wirkung der in vielen Erdteilen ursprünglich nicht heimischen *Apis mellifera* und die Wichtigkeit unseres Verständnisses für das Verhalten auf den Blüten wird durch die Literaturzitate deutlich.

Apoidea / Bestäubung / nachhaltige Landwirtschaft / Bewirtschaftung

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