

Conservation of Asian honey bees

Benjamin P. Oldroyd, Piyamas Nanork

▶ To cite this version:

Benjamin P. Oldroyd, Piyamas Nanork. Conservation of Asian honey bees. Apidologie, 2009, 40 (3), 10.1051/apido/2009021 . hal-00892024

HAL Id: hal-00892024 https://hal.science/hal-00892024

Submitted on 11 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Review article

Conservation of Asian honey bees*

Benjamin P. OLDROYD¹, Piyamas NANORK²

¹ Behaviour and Genetics of Social Insects Lab, School of Biological Sciences A12, University of Sydney, NSW 2006, Australia

² Department of Biology, Mahasarakham University, Mahasarakham, Thailand

Received 26 June 2008 - Revised 14 October 2008 - Accepted 29 October 2008

Abstract – East Asia is home to at least 9 indigenous species of honey bee. These bees are extremely valuable because they are key pollinators of about 1/3 of crop species, provide significant income to some of the world's poorest people, and are prey items for some endemic vertebrates. Furthermore, Southeast Asian Dipterocarp forests appear to be adapted to pollination by honey bees. Thus long-term decline in honey bee populations may lead to significant changes in the pollinator ecology of these forests, exacerbating the more direct effects of deforestation and wood harvesting on forest health. Although complete extinction of any honey bee species is seen as unlikely, local extinction is likely to occur across extensive areas. The most significant threats to local honey bee populations are deforestation and excessive hunting pressure. Conservation of East Asian honey bees requires immediate action to determine what rate of colony harvesting by honey hunters is sustainable. This requires information on the demography of hunted populations, particularly the intrinsic growth rates and the rates of harvest.

Apis / Conservation / Honey hunting / demography / sustainable harvest / pollination / dipterocarp forests

1. INTRODUCTION

In the 100 years between 1880 and 1980 the South and Southeast Asian nations of India, Bangladesh, Sri Lanka, Myanmar, Thailand, Laos, Cambodia, Vietnam, Malaysia, Singapore, Brunei, Indonesia and the Philippines, grew in human population by 262%, the area of cultivated land by 86%, the area bearing grass and shrub vegetation by 20%, while total forest cover decreased by 29% (Flint, 1994), Deforestation has continued unabated during the last 25 years (Sodhi et al., 2004). The region has developed an extremely high human population density, and in some countries such as Pakistan, Nepal and Bangladesh, rapid population growth continues today (Anon, 2004). Increasing hu-

Corresponding author: B.P. Oldroyd, boldroyd@bio.usyd.edu.au

man population size, especially when coupled with increased affluence and per capita consumption inevitably causes increased pressures on natural ecosystems. (Nonetheless a better-educated and wealthier population may have greater capacity and desire to do something about conservation than a desperately poor one). Of particular concern for honey bee conservation is broad scale conversion of primary forest to short-cycle forestry, rubber and oil palm plantation, agriculture, and urban areas (Kevan and Viana, 2003; Sodhi et al., 2004). All these activities involve removal of mature trees suitable for nesting, and often involve reduction in food resources and the use of pesticides. In some cases, direct interactions with humans can result in nest destruction (Underwood, 1992). Increasing population and affluence coupled with a desire for natural products harvested from the wild can also increase economic incentive for hunting and gathering within the remaining forests

^{*} Manuscript editor: Mark Brown

(Nath et al., 1994; Chen et al., 1998; Wilkie and Carpenter, 1999; Nath and Sharma, 2007).

Despite the foregoing, indigenous honey bees remain common throughout much of their original range. The red dwarf honey bee Apis florea is actually expanding its range into the Middle East (Mossagegh, 1993) and the Eastern hive bee A. cerana into New Guinea (Anderson, 1994). In Hong Kong, one of the most urbanized and altered landscapes on the planet, A. cerana remains common, and is an important pollinator of remnant vegetation (Corlett, 2001). Nonetheless there are obvious signs of threatening processes at work (see below) on some species in some areas, and we suspect that these processes either have or soon will drive local extinctions. Perhaps this has already occurred in the dwarf bees on the island of Hong Kong where they are apparently absent (Corlett, 2001). The red honey bee A. koschevnikovi is now extremely rare on peninsular Malaysia and the south of Thailand (Otis, 1996). Whether complete extinction of a particular species is likely or possible is not clear, but the threat is real and potential consequences of such an extinction are significant.

In this review we aim to document the ecological, economic and social values of Asian honey bees and identify the main threats to them. We follow with a brief introduction to sustainable yield theory. Much of this material was reviewed in the monograph Asian honey bees: Biology, conservation and human interactions (Oldroyd and Wongsiri, 2006), but we re-present it here for completeness and to expand and update it. We then identify the critical data and studies of life history traits that are required to understand the demography of a honey bee population (Seeley, 1978; Oldroyd et al., 1997). Remarkably little is known about the reproductive behaviour of Asian species, and this lack renders our understanding of Asian honey bee demography little more than educated guesses (Oldroyd and Wongsiri, 2006). We then discuss what steps can and should be taken to help conserve honey bees. Many of these, such as a reduction in deforestation, are common to broader conservation goals, but some, such as less destructive hunting techniques, are unique to honey bees. Finally we discuss the opportunity of exploiting new molecular-based means of rapidly assessing population size (Moritz et al., 2007a, b), even in the most impenetrable forest. This technique promises to provide a sound basis for the understanding demography of wild honey bee populations everywhere, but will be particularly useful for Asian honey bees in remote jungles.

2. DIVERSITY IN APIS: WHAT HAVE WE GOT TO CONSERVE?

Planning for species conservation requires (among other things) an understanding of the phylogenetic relationships among the species of concern (Vane Wright et al., 1991; Crozier, 1992; May, 1994; Humphries et al., 1995). This is because we should like to preserve biodiversity in its broadest sense. Thus a species that is phylogenetically distant from all others is generally reckoned to be of higher conservation value than a subspecies (Crozier, 1992). For example, we should be more concerned about the loss of highly novel species like the tuatara (*Sphenodon* spp.) than by the loss of morphological variant of an otherwise widespread taxon.

The taxonomy of the honey bees has been given considerable attention and we now understand the broad evolutionary history of the genus well (Raffiudin and Crozier, 2007) (Fig. 1). Broadly, there are three groupings, which have sometimes been regarded as subgenera (Maa, 1953). These are the dwarf bees, which build a single comb surrounding a twig or small branch, the medium-sized cavity nesting bees which build a series of parallel combs, usually within a defendable cavity, and the giant bees which build a single comb suspended beneath a rock overhang or tree branch. Each group has two or more species, with the cavitynesting bees being the most speciose (Otis, 1996; Oldroyd and Wongsiri, 2006).

The species and subspecies joined by solid lines in Figure 1 are strongly supported as being taxonomically distinct based on sequence divergence of nuclear and mitochondrial genes (Raffiudin and Crozier, 2007; De La Rúa et al., 2009). In addition, there are probably other species of honey bee that are not yet described.

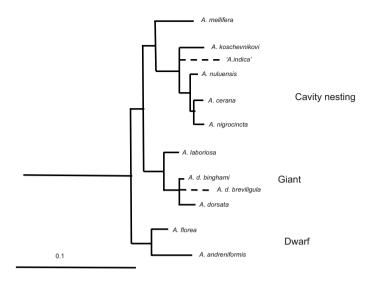


Figure 1. Phylogeny of the honey bees (after Raffiudin and Crozier, 2007). Dotted lines indicate unconfirmed species.

Two likely candidates are indicated by dashed lines on the phylogeny of Figure 1: the yellow 'plains' cavity nesting honey bee of south India (Oldroyd et al., 2006), and the giant honey bee of the Philippines *A. d. breviligula* (Maa, 1953). The latter has not been analysed genetically, but is almost certainly a distinct species from *A. dorsata* based on its dark coloration (personal observations of BPO), absence of nest aggregations (Morse and Laigo, 1969), and geographical isolation.

We suggest that all the species of Figure 1 are deserving of conservation effort, and encourage investigations exploring the broader diversity of honey bees.

3. VALUE OF HONEY BEES

Although we would argue that honey bees have intrinsic value, it is often useful in the conservation context to be armed with the tangible benefits of a species so that they may be given higher priority for conservation policy and perhaps funding (Chardonnet et al., 2002).

3.1. Pollination services

Although most of the heavily traded agricultural commodities derive from plants that are self pollinated, wind pollinated or propagated vegetatively, up to a third of the food we eat is derived from plants which are either dependent on or benefit from insect pollination, especially by honey bees (e.g. Williams, 1996; Richards, 2001; Klein et al., 2007). The value of crops pollinated by the western honey bee *A. mellifera* is staggeringly large (eg Scott-Dupree et al., 1995; Morse and Calderone, 2000; Gordon and Davis, 2003), but unfortunately, no estimates are available for the value of honey bee pollination for Asian counties or for Asia in aggregate.

Natural ecosystems are also heavily dependent on animals for pollination (Bawa, 1990; Corlett, 2004). There is increasing concern that anthropogenic disruption of plantpollinator mutualisms will lead to a wave of plant extinctions (Bond, 1994; Buchmann and Nabhan, 1996; Biesmeijer et al., 2006). Because of their dance language and large foraging range, honey bee colonies can rapidly identify and exploit ephemeral floral resources over a wide area (Koeniger et al., 1982; Dyer, 1985; Punchihewa et al., 1985; Dyer and Seeley, 1991; Dornhaus and Chittka, 1999; Sen Sarma et al., 2004; Dornhaus et al., 2006; Beekman and Lew, 2007; Beekman et al., 2008), often resulting in inter-specific competition for food (Koeniger and Vorwohl, 1979; Oldroyd et al., 1992; Rinderer et al., 1996; Köppler et al., 2007). Perhaps for this reason, the non-Apis bee fauna of Asia is depauperate relative to tropical forests in Australia

and America (Michener, 1979; Corlett, 2004; Batley and Hogendoorn, 2009). The forest communities of tropical Asia evolved with two or more honey bee species present, and may therefore be particularly vulnerable to a reduction in the density of honey bees (Corlett, 2004).

The low land forests of Asia are dominated by the family Dipterocarpaceae – a family of some 17 genera notable for its two-winged wind-dispersed fruit, and often-massive trees that emerge above the surrounding rainforest canopy (Ashton, 1988). The pollination ecology of this region is characterised by infrequent (2–10 years) general flowering (GF) events in which most trees of most tree species flower simultaneously at more or less random times of year (Appanah, 1985; Ashton et al., 1988). Two major hypotheses have been proposed for the evolution of GF in this region (Maycock et al., 2005). First, GF may lead to a 'mast' fruiting event in which fruit are so abundant that frugivores are satiated and recruitment of seedlings is high (Janzen, 1971; Janzen, 1974). Second, GF may act to attract migratory pollinators such as honey bees to the area, thereby enhancing pollination success and outcrossing (Sakai, 2002). Regardless of which hypothesis is more likely to be correct, the spatial separation of conspecifics and the intense competition amongst individual plants for the attention of pollinations during a GF strongly suggest that many Dipterocarp tree species of the South-east Asian lowland forests are adapted for pollination by migratory honey bees which can rapidly increase in population size by both reproductive and migratory swarming (Itioka et al., 2001). No other pollinators have both these capacities. Within the period of a MF event, pollinating vertebrates such as bats and birds can only increase population densities by migration. Because most bat species have fixed roosts, and because many birds are territorial, migration is unlikely to significantly increase population densities of these pollinators during MF. Stingless bees and solitary bees that are nonmigratory can only increase population densities via reproduction.

Another reason why the Dipterocarp forests may be especially reliant on honey bee pollina-

tion is the need for long distance movement of pollen between spatially separated conspecific trees that are often self-incompatible or dioecious (Bawa, 1990). Even when trees are selffertile, restriction of gene flow among trees potentially results in inbreeding depression and a reduction in vigor (Slatkin, 1985). Transfer of pollen over long distances requires an animal vector that has species fidelity while foraging, a large foraging range, and visits multiple trees, either as individual foragers, or via transfer of pollen among foragers in the nest. Honey bees have all these characteristics (deGrandi-Hoffman and Martin, 1995). Microsatellite studies of paternity in various Asian tree species show strong outcrossing rates, and average mating distances greater than 500 m (Konuma et al., 2000; Kenta et al., 2004), far further than is seen in the neotropical species Pithecellobium elegans (Crane, 1991).

It is difficult to imagine that mating distances of this magnitude are achieved by anything other than *Apis*. Furthermore, forest fragmentation for forestry and agriculture my raise the importance of *Apis* pollinators still further, as trees become ever more isolated, and alternative pollinators are adversely affected (Nanson and Hamrick, 1997; Ghazoul, 2005; Kremen et al., 2007)

3.2. Honey bees as prey

Asian honey bees are prey for a variety of insect, mammalian and bird predators (Oldroyd and Wongsiri, 2006). Several bird species are specialist predators of honey bees including the Orange-rumped honey guide (*Indicator xanthonotus*), the Malaysian honey guide (*I. archipelagicus*) and the Oriental (*Pernis ptilorhyncus*) and Barred (*P. celebensis*) honey buzzards. Still others, particularly the bee-eaters (*Merops* spp.) and drongos (*Dicrurus*), are opportunistic hunters of Asian honey bees. These species would either be imperilled or driven to extinction if Asian honey bees were themselves made extinct.

3.3. Social and religious values

Many Asian people revere honey bees, and are concerned for their welfare. The arrival of an *A. dorsata* swarm in garden of a temple or house is often regarded as a good omen. Honey bees play an important role in two of the main religions of Asia. In the Hindu religion honey represents the 'blendedness of everything' and is often mixed with clarified butter, sugar, milk and curd to produce one blended mixture, which is shared amongst participants in ceremonies.

Although not as central, honey bees feature in a variety of religious stories from Buddhism as well. Stories about bees are used to teach people the value of working hard, flying low (being modest), being clean, clever in collecting and being united as a family.

Buddhists believe in life after death and that a deceased person will be reborn. To be a happier and healthier person in the next life, a person must perform good deeds. Giving alms to monks is one of the most expressive ways that an individual can perform a good deed, so many Buddhists like to provide alms to their local monks every day. Monks are permitted only two meals per day: breakfast and lunch. But the Buddha allowed monks to consume 5 things: clarified butter, dense butter, vegetable oil, sugar cane juice and honey as 'tonics' at any time of day. Thus these items are welcomed offerings and are regarded as being particularly meritorious.

At the beginning of the rainy season, Buddhists observe the Vassutanavikadivasa, a time during which the monks are confined to their temples. Traditionally the monks were presented with beeswax candles during Vassutanayikadivasa so that they could continue study into the night. (These days people tend to give a light bulb instead!) The end of Vassutanayikadivasa is celebrated by the Pavaranadivasa festival, which in Thailand includes the honey ceremony or Tak bat nam peung. In northeastern Thailand, Pavaranadivasa parades often include massive and elaborately decorated beeswax candles, and villages often have competitions for the biggest and best candles.

The central place of bees, honey and beeswax in both Buddhism and Hinduism, imbues honey bees with a special place in the minds of many Asian people. We hope that these beliefs will help to give urgency to conservation efforts.

4. MAIN THREATS

4.1. Deforestation

Sodhi et al. (2004) outline the depressing reality of deforestation in Southeast Asia. This region has the highest rate of tropical deforestation in the world, and is predicted to lose three quarters of its original forest and 42% of its biodiversity in the next hundred years.

The impacts of deforestation on honey bees are poorly understood. Liow et al. (2001) used honey baits to trap bees along transects in disturbed and relatively undisturbed sites in Singapore and Jahor in peninsular Malaysia. The proportion of Apidae (stingless bees and honey bees) was very low in oil palm plantations and very high in undisturbed sites. This strongly suggests that oil-palm plantations do not favour honey bees. This is understandable: the palms do not produce nectar, which is only available from ground flora, and suitable nesting sites are rare within the plantations. No hollows are available for cavity nesting bees, and the dense leaves of the palm fronds render them unsuitable for nest building by A. dorsata. Presumably dwarf bees can nest in the palm fronds.

4.2. Hunting

Asian people have been hunting honey bees for more than 40000 years (Crane, 1999) and bee hunting is still widely practiced throughout the region. To take an *A. florea* or *A. andreniformis* colony, the hunter merely shakes the bees off, snips the branch holding the colony, and carries the comb home. We assume that provided there is plenty of food available, the colony recovers from the theft of its comb more often than not. Hunting *A. dorsata* and *A. laboriosa* is much more brutal, and

often involves burning the bees with a smoldering torch of tightly-bound brush (e.g. Valli and Summers, 1988; Lahjie and Seibert, 1990; Nath et al., 1994; Crane, 1999; Tsing, 2003). Some harvested colonies may be able to regroup, especially if the hunt occurs in daylight. Often, however, the hunt is conducted in darkness. The hunter bangs his torch on the branch supporting the colony to create a shower of sparks. The bemused bees follow the sparks to the forest floor (Tsing, 2003; Oldroyd and Wongsiri, 2006) where they crawl about, often with singed wings. Many queens must be lost during these harvests, and their colonies perish along with them. Night hunting is preferred by many hunters because it reduces the number of stings received. This method of hunting kills many if not most colonies. For example, BPO witnessed a harvested tree in the Nigris Hills of Tamil Nadu, India, in which over 100 colonies were killed by hunters in a single night. Of late we have even heard of 'hunters' using insecticides to kill bees prior to harvesting honey.

The level of hunting pressure is most likely increasing in many areas. Even the poorest people (who are more likely to engage in hunting than land owners) have increasing access to motorized transport so that they can access nests over a broad area. Conversion from a barter/subsistence economy to a cash-based economy increases the incentive to produce a high value, easily-transported product like honey (Nath et al., 1994; Tsing, 2003; Nath and Sharma, 2007). Increasing affluence in the cities and rural towns may increase the demand for wild honey which is perceived some as being more natural, pesticide free, healing and delicious than honey produced from domestic colonies. Finally, decreasing areas of forested land increases the hunting pressure on the remaining forested pockets (Nath et al., 1994).

4.3. Loss of nest sites

Cavity nesting bees require cavities for nesting. A. cerana is able to nest in manmade structures, or in the hollows of coconut palms (*Cocus nucifera*), and we think it likely that cavities are rarely a limiting resource. Nonetheless Inoue et al. (1990) found that when *A. cerana* nests in the small cavities of coconut palms, their growth is limited, and this may hinder their ability to produce reproductive swarms of viable size.

Of greater concern is the removal of nesting trees of the giant honey bee, *A. dorsata. A. dorsata* colonies are highly philopatric, often migrating over large distances, but returning to the same nesting site every year (Butani, 1950; Koeniger and Koeniger, 1980; Underwood, 1990; Dyer and Seeley, 1994; Kahona et al., 1999; Neumann et al., 2000; Paar et al., 2000; Sheikh and Chetry, 2000; Thapa et al., 2000; Itioka et al., 2001; Paar et al., 2004). Moreover, *A. dorsata* tend to nest in large aggregations, sometimes with more than 100 colonies on a single tree (Oldroyd et al., 2000; Paar et al., 2004).

We do not understand why particular trees are used year after year as nest sites (Oldroyd et al., 2000; Oldroyd and Wongsiri, 2006), but it may be assumed that these trees are of considerable importance to the welfare of a population (Paar et al., 2004). Anecdotal discussions with students at the Indian Institute of Science in Bangalore suggested that when a major bee tree is felled to make way for a building or other structure, the colonies attempt to build their nests on the structure. Depending on the structure, this may cause undesirable interactions with humans, and the killing of the colonies.

4.4. Parasites and pathogens

Honey bee colonies can be affected by a variety of fungal, viral and bacterial infections, and can be infested by various insect and mite parasites (Morse and Nowogrodzki, 1990; Bailey and Ball, 1991; Oldroyd and Wongsiri, 2006). Wild populations are not normally threatened by the parasites and pathogens with which they co-evolved, and most wild colonies we have encountered are pictures of robust health. However adverse effects of pests and diseases may arise when wild populations are stressed by environmental degradation. For example, Allen et al. (1990) found a Nepalese population of *A. laboriosa* that was severely infected with European foulbrood (*Mellisococcus pluton*), which they attributed to environmental stress brought on by deforestation.

Of potentially greater significance than environmental stress is the anthropogenic movement of honey bee populations between countries which potentially exposes wild populations to novel parasites and pathogens to which they have no resistance. *A. mellifera* has been introduced into most Asian countries at one time or other, almost certainly exposing wild Asian *Apis* to novel pathogens. Thus the European Foulbrood observed by Allen et al. (1990) may well have had its origins in the *A. mellifera* colonies introduced into Kathmandu by well meaning but incompetent aid agencies.

Since the 1980s many populations of *A. cerana* have been severely infected by so-called Thai Sac Brood virus, which kills early pupal stages and is often lethal to colonies (Abrol and Bhat, 1990; Verma et al., 1990; Nath et al., 1994; Chinh, 1998; Abrol, 2000). The origins of this pathogen are unknown, but potentially it arose from the anthropogenic movement of temperate strains of *A. cerana* into tropical areas, or from introduction of *A. mellifera*. European foul brood is also known from *A. cerana* (Bailey, 1974).

A Conopid fly *Physocephala parralleliven*tris Kröber (Diptera: Conopidae) parasitizes *A. cerana, A. koschevnikovi* and *A. dorsata* in Borneo (Tingek et al., 2004). It grasps flying bees in flight and deposits a tiny larva on the integument. The larva penetrates the bee's cuticle, consuming the bee from the inside. We suspect that this fly or a close relative is also present in Thailand, because we have seen fly larvae in the abdomens of *A. florea* workers. Spread of this fly to populations which have not previously been exposed to it could potentially be devastating.

An emerging threat to Asian *Apis* is the small hive beetle *Aethina tumida*. Originally from sub-Saharan Africa (Dietemann et al., 2009), this pest has recently spread to Australia, the United States of America and Egypt (Mostafa and Williams, 2002; Neumann and Elzen, 2004; Ellis and Hepburn, 2006) where it causes significant damage, especially in warm, wet climates. The pest normally

lives saprophitically on falling debris from a honey bee colony. Mostly the bees confine the adult beetles to unreachable crevices (Ellis and Hepburn, 2006). Occasionally, however, the beetles are able to overwhelm the host colony's defences. The floor of the hive becomes a seething mass of beetle larvae, which apparently attracts more adult beetles. Within a day or so the larvae invade the brood comb at which point the colony will either abscond or be killed.

It is worryingly likely that A. tumida could become successful parasites of some or all of the Asian cavity-nesting species. When A. tumida was introduced to colonies of Bombus impatiens it was able to complete its life cycle (Stanghellini et al., 2000), suggesting that the species could potentially swap hosts to the Asian honey bee species which are far more closely related to the original host than *Bombus.* Optimistically, the adult beetles may fail to recognize the Asian species as suitable hosts, or the Asian species with their long history of association with parasitic mites will be adept at locating and killing A. tumida. Hopefully this optimism is warranted because exposure is likely: package bees were shipped from Australia to several Asian countries for a short period after the arrival of the beetles in 2000, and at least some of these shipments were likely infested with A. tumida.

4.5. Climate change and forest fire

The Intergovernmental Panel on Climate Change Fourth Assessment Report (2007) suggests that due to a 70% increase in greenhouse gas emissions over the 100 years from 1906, the average temperature of the Earth has risen 0.74 °C, and that this has decreased precipitation in parts of south east Asia. With expected increases in greenhouse gas emissions over the next two decades, global temperatures will most likely increase by a further 0.4 °C. In Southeast Asia, peak years for wildfire coincide with severe ENSO-induced droughts (Duncan et al., 2003), which are anticipated to occur more frequently with global warming. Drought combined with extreme wild fire events, and human impacts including

deliberate fire setting associated with slash and burn agriculture (Brown, 1998; Nath and Sharma, 2007) are altering the structure of plant communities across the Asian region (Taylor et al., 1999).

The impacts of these changes on honey bee populations is not easy to assess (Murray et al., 2009). In some ways, oligolectic, migratory species such as the Asian honey bees will be better able to adapt to environmental change and changes in ecotones than most other insects. However there is anecdotal evidence that some species (notably A. andreniformis (Wongsiri et al., 1997) and A. koschevnikovi (Otis, 1996)) are obligate forest dwellers whose range will become more restricted with the retreat of the rainforest. On the other hand both these species inhabit disturbed areas including cities and towns in Borneo (personal observations of BPO) and so the exact cause of the decline of A. koschevnikovi in Malaysia and the rarity of A. andreniformis in most of Thailand is unclear. Perhaps competition from A. florea is important.

4.6. Pesticides

Exposure to most insecticides kills individual foragers, and can kill whole colonies (Desneux et al., 2007). Some commercial fruit crops, particularly longan (Dimocarpus longan), litchie (Litchi chinensis) and citrus are major honey producers which are highly attractive to honey bees (Crane et al., 1984). Other orchard trees like mangosteen, Garcinia mangostana and rambutan, Nephphelium lappaceum, make ideal nesting sites for dwarf bees (Oldroyd and Wongsiri, 2006). These orchards are regularly sprayed with insecticides, which kills all colonies nesting in the tree canopy (personal observations). Spraying during flowering may also affect colonies nesting outside the crop but foraging in the crop. Some tree crops such as oil palm, *Elaeis* spp., are regularly sprayed, and this may contribute to the observed paucity of bees within oil palm plantations.

Regulation of pesticide use is lax in some Asian countries, and this can increase the possibility of bee exposure to pesticides, for example by contamination of streams.

4.7. Street lighting

When open nesting species like A. dorsata and A. andreniformis nest near sources of light, foragers are attracted to the lights at night (personal observations). Many bees are killed in this way. This may be of limited consequence for colony survival, but cannot be helpful to an already-stressed nest. We do not know if A. dorsata queens on mating flights are attracted to lights, but if so, queens may also be lost in this way.

4.8. Competition with introduced *A. mellifera*

Concerns have sometimes been raised about the possibility that introduced A. *mellifera* may out compete and displace indigenous honey bees in Asia (see for example Verma, 1991). We think this unlikely. Feral populations of A. mellifera are unknown in Asia, and in our view are unlikely to be formed. First, in tropical regions with small variation in day length, European honey bees have difficulty regulating their rates of brood production and so they rarely reach swarming strength (Rinderer, 1988). Second, wherever A. dorsata is endemic, its parasitic mite Tropilaelaps clareae is also present, and likely to infest any feral A. mellifera colonies and kill them. Even where T. clareae is absent, feral colonies are likely to be killed by Varroa destructor. Host shifts between Varroa destructor to A. mellifera are rare (Anderson and Trueman, 2000; Solignac et al., 2005), and so indigenous Varroa are usually unlikely to infest A. mellifera colonies transplanted in to Asia. However, most A. mellifera populations world wide, including transplanted Asian ones are already infested with V. *destructor*. Thus, establishment of a feral population from a domesticated one already infested with Varroa seems unlikely (Anderson, 1994; Anderson and Sukarsih, 1996; Oldroyd and Wongsiri, 2006).

Despite the foregoing it is clear that A. *mellifera* beekeeping has replaced A. *cerana*

beekeeping in large parts of India, Japan, Pakistan, China, and Thailand, reducing population sizes of *A. cerana* in these regions. There is some evidence that very high densities of *A. mellifera* drones could interfere with *A. cerana* matings (Ruttner and Maul, 1983) though in Japan at least the times of mating flights do not overlap (Yoshida et al., 1994).

4.9. Anthropogenic movement

Only 10000 years ago much of the Indonesian archipelago, the Andaman Islands, Taiwan and Hong Kong were connected to mainland Asia (Heaney, 1991). Rising sea levels caused by the current phase of global warming created thousands of islands, some large, some small, and in doing so the once contiguous populations of honey bees were separated into isolated populations (Smith et al., 2000; Smith, 2002; Oldroyd and Wongsiri, 2006). This isolation has contributed to the rich diversity of honey bee ecotypes we see today, particularly in *A. cerana* and its related species (Hepburn et al., 2001; Radloff et al., 2005).

Anthropogenic movement of honey bees between regions potentially erodes biodiversity by homogenizing the gene pool. For example, the 'mainland Asia' mitotype of *A. cerana* is ubiquitous across Asia, often alongside a regional mitotype (Smith and Hagen, 1996; Smith et al., 2000). This suggests that humans have moved preferred strains of *A. cerana* among the some of the islands of the South China Sea. Not only do such movements potentially reduce biodiversity, they can also spread pests, pathogens and diseases.

4.10. Tourism

While tourism is sometimes regarded a positive force for conservation (Wynberg, 2002), more often than not it is negative (Noss et al., 1996; Pickering and Hill, 2007), especially when it involves hunting (Anon, 1991). A Google search of 'Honey hunting tour' reveals dozens of companies offering guided tours of honey hunting sites including operations in Nepal (more than 50 web sites), Thailand (1), Bangladesh (1), Tibet (1) and Bhutan (2), and we aware of similar enterprises in Malaysia which do not yet have a web presence. These practices are very likely to increase the number of colonies killed, and to foster hunting at inappropriate times of year when colonies are stressed and unlikely to recover.

5. WHAT SHOULD BE DONE TO CONSERVE ASIAN HONEY BEES?

It is undeniable that forest clearing contributes to honey bee decline, and the cause of honey bees can only add to the chorus of plants and animals that are similarly afflicted. Clearing of old growth forest on this planet should simply be stopped. Nonetheless conservation strategies must be rooted in pragmatism as well as good science, so we should also focus on those issues where something can realistically achieved in the shorter term, and that that will also be useful.

5.1. Quarantine

No doubt local people will continue to move *A. cerana* nests among neighbouring islands, and there is little that can be done about this. Most of the ports and airports of Asia give priority to the free flow of goods and people in the belief that the economic benefits of doing so outweigh the potential costs to agriculture and the environment. There are some exceptions. Malaysia, for example, does not allow importation of *A. mellifera* into Borneo. South Korea and Japan have banned imports of queens and packages from countries where *A. tumida* is now endemic. We applaud these measures.

5.2. Hunting

The impact of hunting on species viability depends on population size and growth rate, the proportion of colonies which survive a typical harvest, the proportion of colonies which are harvested, rates of migration from adjacent regions, the length of life of colonies, their

reproductive rate and so on (e.g. Caughley and Sinclair, 1994). Almost no information is available on any of these parameters, so assessing the impact of hunting on the viability of honey bee populations is difficult. Based on the assumptions of indefinite survival of established colonies, production of 2.5 swarms per year and 100 colonies per square kilometer, Oldroyd and Wongsiri (2006) suggested hunting of A. florea is unlikely to threaten populations because the level of harvesting is likely to be far less than the potential for population growth (i.e. a potential growth rate of 250 colonies per square kilometer). However densities of A. dorsata are likely to be much lower than this, perhaps 10 colonies per square kilometer, allowing a maximum harvest of much less than 25 colonies, which may often be exceeded. If so, and assuming that the harvest rate remains unchanged, the population will be driven to extinction. Hunters in Tamil Nadu report that A. dorsata is becoming more rare (Nath et al., 1994), and we assume that hunting in excess of the sustainable yield is the primary cause of this decline.

We urgently need to know the key demographic parameters for hunted honey bee populations. The critical parameters are:

H Harvest rate. The proportion of colonies that are harvested.

N Population size. The total population size.

r Growth rate, the change in the number of colonies per season if the population were unharvested.

S Survival rate. The proportion of colonies that survive harvest to reproduce.

With these parameters in hand one can calculate the intrinsic growth rate of a population relative to its current size. The goal is to maintain H much less than r.

These parameters cannot be readily determined directly, but they can be inferred. The growth rate can be estimated by determining the number of surviving daughter colonies a typical established colony produces. For the giant bees we need someone to study a nesting site for a complete reproductive season, counting the number of established colonies at the beginning of the season, the number of migrants that join the nesting site, the number of daughter colonies, and the survival of all of these. For the dwarf bees, which do not form dense aggregations as the giant bees do (Rinderer et al., 2002; Wattanachaiyingcharoen et al., 2008), such a study may not be feasible. However the number of daughter colonies can be estimated by determining the average number of reproductive swarms that are cast by typical colonies in a typical season, and estimating a failure rate from a sample of swarms.

Estimates of S can potentially be determined experimentally. For example, A. flo*rea* nests could be harvested in the traditional way: shaking the bees off and harvesting the comb. The adult bees and queen should then form a cluster, which could be monitored for its survival. Various extensions of this simple idea could include establishing study plots that are regularly surveyed and the location of all colonies noted. Colonies could be harvested in some plots and not in others, and the recolonization rate determined (Oldroyd et al., 1997). If worker samples were taken from all colonies for genetic analysis it may be possible to build a picture of what happens to harvested nests.

Estimating N by survey and physical counting of colonies (Oldroyd et al., 1997) is likely to severely underestimate the total number of colonies present (Hepburn and Radloff, 1998) so new genetic methods (Baudry et al., 1998; Moritz et al., 2007a, b) of estimating the number of colonies present in a population are preferred (Zayed, 2009). The innovation in this method is to genotype males at a series of tightly linked microsatellite loci. Males can be sampled directly from a population by using a drone trap fitted with a sex attractant, or the genotypes of the fathering males of workers can be inferred from a sample of workers from a single colony. The use of tightly linked loci means that it is much easier to distinguish brother drones from unrelated drones - two unrelated drones are less likely to share a haplotype of linked loci by chance than a multilocus diplotype. Software is available to estimate the number of colonies represented in a sample of drones (Wang, 2004). All that remains then is to estimate the area from which the drones may have been drawn in order to find

a good estimate of the density of colonies in a region. The efficacy of the method was demonstrated by showing that the estimated relative density of colonies in South Africa was much higher than in Europe (Moritz et al., 2007b). It should be noted that we doubt that this genetic method provides an accurate picture of the absolute number of colonies in a region, but it should provide a good estimate of the relative density between two regions.

5.3. Encouraging harvesting of wild colonies in a more sustainable manner

Harvest of *A. dorsata* and *A. laboriosa* is often a destructive process, but this need not be so. Bee hunters are often conservationists as well as being hunters, and are receptive to ideas that may help conserve bees. They are often strong advocates for forest protection (Nualsanong, 2000).

In Vietnam, Cambodia, Kalamantan and some other parts of Indonesia, efforts are being made to encourage harvesting of honey from A. dorsata nests in a non-destructive manner (Crane et al., 1993; Tan et al., 1997; Purwanto et al., 2000; Tan and Ha, 2002; Waring and Jump, 2004). This involves using bee smokers and protective clothing to shield hunters from stings so that harvesting can be done in daylight, rather than burning or smoking the bees at night. Second, bee hunters can construct 'rafters' in the forest to attract migrating A. dorsata swarms. Rafters are stout boards about 2 m long that are suspended at a 45° angle in a forest clearing (Tan et al., 1997; Tan and Ha, 2002). It is much easier to take honey from a colony nesting on a rafter 1 m from the ground than from a wild colony nesting in a 20 m tall Koompasia tree.

We applaud efforts to encourage more sustainable honey harvesting, but note that in many areas hunters have insufficient funds to purchase smokers and bee veils, relying almost exclusively on materials gathered from the forest to construct their simple hunting equipment.

5.4. Should we encourage keeping native honey bees?

Clearly if thousands of beekeepers each kept hundreds of colonies of a native honey bee like A. cerana, then the bee would be unlikely to go extinct. Should we therefore encourage keeping native A. cerana rather than European A. mellifera? The answer is 'it depends'. First the benefits to beekeepers. There is no doubt that A. cerana is resistant to parasites and pathogens likely to be encountered, whereas throughout Asia, A. mellifera must be regularly treated to manage mite infestations. Furthermore, A. cerana can live happily in rough boxes or tree trunks with little or no need for expensive equipment (Oldroyd and Wongsiri, 2006). On the other hand, there is no argument that in side by side trials A. mellifera will always provide more honey, and provide a higher return on investment than can A. cerana (even if start up costs are higher) (Magsaysay et al., 2004). So if the capital is available, it is not really justifiable to encourage a less profitable form of agriculture. Poor beekeepers should not be expected to bear the burden of conservation, which is the responsibility of us all.

One important reason to encourage *A. cer*ana beekeeping over *A. mellifera* beekeeping is that *A. mellifera* seems more vulnerable to predation by bee-eating birds than are the indigenous honey bees. Thus some *A. mellifera* beekeepers in East Asia take steps to reduce bird predation by placing nets over apiaries. As many birds become entangled in the nets, there can be many bird deaths.

In Thailand, much of the honey available in local markets is wild honey harvested from open-nesting species, and this seems to be preferred to bottled honey which is often of poor quality. Perhaps the best thing to do, then, is to encourage sustainable and hygienic harvesting of wild honey from dwarf bees, rather than encouraging a transition to *A. mellifera* or *A. cerana* beekeeping.

6. CONCLUSIONS

Our review has shown that some Asian honey bee species are severely threatened by a combination of alteration to habitat, overhunting, and potentially climate change. Of particular concern are species like *A. andreniformis* and *A. koschevnikovi*, which are apparently confined to heavily forested areas, at least in mainland South East Asia. *Apis laboriosa*, denizen of mountainous regions, may be threatened by over-hunting, land clearing for cropping, and exotic disease.

We emphasise the urgent need for research into the demography of wild honey bee populations. We recommend a moratorium on destructive harvesting of giant bee nests wherever this can be legally enforced.

ACKNOWLEDGEMENTS

The authors are supported by the Australian Research Council and the Thailand Research Fund respectively. We thank Nadine Chapman, Gudrun Koeniger and Madeleine Beekman for comments on the manuscript.

La conservation des abeilles asiatiques.

Apis / protection / démographie / récolte soutenable / pollinisation / forêt à dipterocarpe / récolte de miel sauvage / chasseur de miel

Zusammenfassung – Der Schutz asiatischer Honigbienen. Asien ist eine Region mit hoher Bevölkerungswachstumsrate und zunehmendem Einkommen, in Verbindung mit hohen Entwaldungsraten. Besondere Beachtung für den Schutz der Honigbienen muss dabei auf grossangelegte Umwandlungen von Primärwald in kurzzyklische Waldwirtschaft, in Landwirtschaft und in städtische Gebiete gelegt werden. Nichstdestotrotz sind Honigbienen in ihren ursprünglichen Verbreitungsgebieten nach wie vor mehr oder weniger häufig anzutreffen. Allerdings gibt es inzwischen Anzeichen für lokale Rückgänge, insbesondere von A. koschevnikovi auf der malayischen Halbinsel und von A. andreniformis in den landwirtschaftlich genutzten Gebieten Thailands. Auch die Riesenhonigbienen A. dorsata und A. laboriosa scheinen in Grossteilen der Region unter Druck zu geraten. Diese lokalen Auslöschungen und der generelle Rückgang in der Dichte an Honigbienennestern wird vermutlich Konsequenzen haben, sowohl für die Natur als auch für die Menschen in der Region.

An erster Stelle zu nennen wäre, dass ein Drittel unserer Nahrung pflanzlichen Ursprungs ist und dass diese Pflanzen von der Bestäubung insbesondere durch Honigbienen entweder abhängig sind oder davon profitieren. Auch in natürlichen Ökosystemen besteht ein starker Bedarf nach Bestäubern. Aufgrund ihrer Tanzsprache und ihres weiten Sammelradius können Honigbienenvölker kurzfristig verfügbare Trachtquellen schnell erkennen und ausbeuten. Solch schwankende und unvorhersehbare Blühereignisse sind in den Pflanzengemeinschaften der tropischen asiatischen Wälder die Regel. Wir gehen davon aus, dass diese Fortpflanzungsstrategien in der Gegenwart von zwei oder mehr Arten wandernder Honigbienen evoluieren konnten, da diese in der Lage sind ihre lokalen Populationsgrössen schnell zu steigern und somit genügend Bestäuber verfügbar sind. Der Verlust an Honigbienen kann deshalb die bestäubungsabhängige Ökologie der südostasiatischen Wälder stark beeinflussen. An zweiter Stelle steht die Tatsache, dass die asiatischen Honigbienen vielen Insekten, Säugern und Vögeln als Beute dienen. Verschiedene Vogelarten sind sogar auf Honigbienen spezialisiert, wie zum Beispiel der Gelbbürzelhoniganzeiger (Indicator xanthonotus), der Malaienhoniganzeiger (I. archipelagicus), sowie der Schopfwespenbussard (Pernis ptilorhyncus) und der Celebeswespenbussard (P.

celebensis). Diese Arten wären entweder bedroht oder würden ganz aussterben, wenn die asiatischen Honigbienen aussterben würden. An dritter Stelle steht, dass Honigbienen bei vielen asiatischen Völkern hohes Ansehen geniessen und dass sie um ihr Wohlbehalten bemüht sind. Honigbienen spielen auch in der Religion in den asiatischen Hauptregionen eine wichtige Rolle.

Die hauptsächlichen Ursachen für die Bedrohung der Populationen der Honigbienen stellen die Rodungen, die exzessive Honigjagd, die Ausbreitung von Parasiten und Pathogenen, der imkerliche Transport von Völkern zwischen den Inseln, mögliche Klimaveränderungen und der Verlust an Nistgelegenheiten dar. Letzteres betrifft vor allem die von *A. dorsata* bevorzugten grossen Bäume.

Anstrengungen zum Schutz der Honigbienen sollten die Honigjagd im Auge haben, für die nachhaltige Nutzungskriterien erarbeitet werden sollten. Hierzu müssen dringend Daten erhoben werden zur Abschätzung des Umfangs der ausgebeuteten Völker und deren Überlebensraten. Gleichzeitig müssen Honigerntemethoden entwickelt und propagiert werden, die die Völker nicht vernichten. Wir empfehlen auch ein Moratorium gegen die destruktive Honigernte bei Riesenhonigbienen, dort wo dies rechtlich möglich und durchsetzbar ist, bis wir Daten zur nachhaltig möglichen Honigernte in den betreffenden Gebieten haben.

Apis / Schutz / Honigjagd / Demographie / nachhaltige Ernte / Bestäubung / Dipterocarpen-Wälder

REFERENCES

- Abrol D.P. (2000) Beekeeping with *Apis cerana* in Jammu and Kashmir: present status and future prospects, Bee World 81, 149–152.
- Abrol D.P., Bhat A.A. (1990) Studies on 'Thai sac brood virus' affecting indigenous honeybee *Apis cerana indica* Fab. colonies – Prospects and future strategies – I, J. Anim. Morphol. Physiol. 37, 101–108.
- Allen M.F., Ball B.V., Underwood B.A. (1990) An isolate of *Melissococcus pluton* from *Apis laboriosa*, J. Invertebr. Pathol. 55, 439–440.
- Anderson D.L. (1994) Non-reproduction of Varroa jacobsoni in Apis mellifera colonies in Papua New Guinea and Indonesia, Apidologie 25, 412–421.
- Anderson D.L., Sukarsih (1996) Changed Varroa jacobsoni reproduction in Apis mellifera colonies in Java, Apidologie 27, 461–466.
- Anderson D.L., Trueman J.W.H. (2000) Varroa jacobsoni (Acari: Varroidae) is more than one species, Exp. Appl. Acarol. 24, 165–189.
- Anon (1991) Does game cropping serve conservation a reexamination of the African data, Can. J. Zool.-Rev. Can. Zool. 69, 2283–2290.
- Anon (2004) World Population Prospects. The 2004 revision, in: The Department of Economic and Social Affairs of the United Nations, New York.
- Appanah S. (1985) General flowering in the climax rain forests of South-East Asia, J. Trop. Ecol. 1, 225–240.
- Ashton P.S. (1988) Dipterocarp biology as a window to the understanding of tropical forest structure, Annu. Rev. Ecol. Syst. 19, 347–370.
- Ashton P.S., Givnish T.J., Appanah S. (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics, Am. Nat. 132, 44–66.
- Bailey L. (1974) An unusual type of *Streptococcus plu*ton from the Eastern hive bee, J. Invertebr. Pathol. 23, 246–247.
- Bailey L., Ball B.V. (1991) Honey bee pathology, 2nd ed., Academic Press, London, 124 p.
- Baudry E., Solignac M., Garnery L., Gries M., Cornuet J.-M., Koeniger N. (1998) Relatedness among honeybees (*Apis mellifera*) of a drone congregation, Proc. R. Soc. Lond. B 265, 2009–2014.
- Batley M., Hogendoorn K. (2009) Diversity and conservation status of native Australian bees, Apidologie 40, 347–354.
- Bawa K.S. (1990) Plant-pollinator interactions in tropical rain forests, Annu. Rev. Ecol. Syst. 21, 399– 422.
- Beekman M., Lew J.B. (2007) Foraging in honey beeswhen does it pay to dance? Behav. Ecol. 19, 255– 261.

- Beekman M., Gloag R.S., Even N., Wattanachaiyingcharoen W., Oldroyd B.P. (2008) Dance precision of *Apis florea* – clues to the evolution of the honey bee dance language? Behav. Ecol. Sociobiol. 62, 1259–1265.
- Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemüller R., Edwards M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J., Kunin W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands, Science 313, 351–354.
- Bond W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction, Philos. Trans. R. Soc. Lond. B 344, 83–93.
- Brown N. (1998) Out of control: fires and forestry in Indonesia, Trends Ecol. Evol. 13, 41.
- Buchmann S.L., Nabhan G.P. (1996) The forgotten pollinators, Island Press, Washington DC, p. 292.
- Butani D.K. (1950) An *Apis dorsata* colony in New Delhi, Indian Bee J. 12, 115.
- Caughley G., Sinclair A.R.E. (1994) Wildlife ecology and management, Blackwell Science, Cambridge, p. 334.
- Chardonnet P., des Clers B., Fischer J., Gerhold R., Jori F., Lamarque F. (2002) The value of wildlife, Rev. Sci. Tech. Office International des Epizooties 21, 15–51.
- Chen P.P., Wongsiri S., Jamyanya T., Rinderer T.E., Vongsamanode S., Matsuka M., Sylvester H.A., Oldroyd B.P. (1998) Honey bees and other edible insects used as human food in Thailand, Am. Entomol. 44, 24–29.
- Chinh P.H. (1998) Thai sac brood virus disease control in *Vietnam*, in: Matsuka M., Verma L.R., Wongsiri S., Shrestha K.K., Partap U. (Eds.), Asian Bees and Beekeeping. Proc. 4th Asian Apic. Association Int. Conf. Science Publishers, Enfield, New Hampshire, Kathmandu, Nepal, pp. 57–59.
- Corlett R.T. (2001) Pollination in a degraded tropical landscape: a Hong Kong case study, J. Trop. Ecol. 17, 155–161.
- Corlett R.T. (2004) Flower visitors and pollination in the Oriental (Indomalayan) Region, Biol. Rev. 79, 497–532.
- Crane E. (1991) Apis species of tropical Asia as pollinators, and some rearing methods for them, Acta Hortic. 288, 29–48.
- Crane E. (1999) The world history of beekeeping and honey hunting, Routledge, New York, p. 720.
- Crane E., Walker P., Day R. (1984) Directory of important world honey sources, International Bee Research Association, London, p. 384.
- Crane E., van Luyen V., Mulder V., Ta. T.C. (1993) Traditional management system for *Apis dorsata* in submerged forests in southern Vietnam and central Kalimantan, Bee World 74, 27–40.

- Crozier R.H. (1992) Genetic diversity and the agony of choice, Biol. Conserv. 61, 11–15.
- deGrandi-Hoffman G., Martin J.H. (1995) Does a honey bee (*Apis mellifera*) colony's foraging population on male-fertile sunflowers (*Helianthus annuus*) affect the amount of pollen on nestmates foraging on male steriles? J. Apic. Res. 34, 109–114.
- De La Rúa P., Jaffé R., Dall'Olio R., Munozi I., Serrano J. (2009) Biodiversity, conservation and current threats to European honeybees, Apidologie 40, 263–284.
- Desneux N., Decourtye A., Delpuech J.M. (2007) The sublethal effects of pesticides on beneficial arthropods, Annu. Rev. Entomol. 52, 81–106.
- Dietemann V., Pirk C.W.W., Crewe R. (2009) Is there a need for conservation of honeybees in Africa, Apidologie 40, 285–295.
- Dornhaus A., Chittka L. (1999) Evolutionary origins of bee dances, Nature 401, 38.
- Dornhaus A., Klugl F., Oechslein C., Puppe F., Chittka L. (2006) Benefits of recruitment in honey bees: effects of ecology and colony size in an individualbased model, Behav. Ecol. 17, 336–344.
- Duncan B.N., Martin R.V., Staudt A.C., Yevich R., Logan J.A. (2003) Interannual and seasonal variability of biomass burning emissions constrained by satellite observations, J. Geophys. Res. 108, 4040.
- Dyer F.C. (1985) Mechanisms of dance orientation in the Asian honey bee *Apis florea*, J. Comp. Physiol. A 157, 183–198.
- Dyer F.C., Seeley T.D. (1991) Dance dialects and foraging range in three Asian honey bee species, Behav. Ecol. Sociobiol. 28, 227–233.
- Dyer F.C., Seeley T.D. (1994) Colony migration in the tropical honey bee *Apis dorsata* F. (Hymenoptera: Apidae), Insectes Soc. 41, 129–140.
- Ellis J.D., Hepburn H.R. (2006) An ecological digest of the small hive beetle (*Aethina tumida*), a symbiont in honey bee colonies (*Apis mellifera*), Insectes Soc. 53, 8–19.
- Flint E.P. (1994) Changes in land-use in South and Southeast-Asia from 1880 to 1980 – a data-base repared as part of a coordinated research-program on carbon fluxes in the tropics, Chemosphere 29, 1015–1062.
- Ghazoul J. (2005) Pollen and seed dispersal among dispersed plants, Biol. Rev. 80, 413–443.
- Gordon J., Davis L. (2003) Valuing honeybee pollination. Rural Industries Research and Development Corporation, Canberra, p. 36.
- Heaney L.R. (1991) A synopsis of climatic and vegetational change in Southeast Asia, Climatic Change 19, 53–61.
- Hepburn H.R., Radloff S. (1998) Honeybees of Africa. Springer-Verlag, Berlin, 370 p.

- Hepburn H.R., Smith D.R., Radloff S.E., Otis G.W. (2001) Infraspecific categories of *Apis cerana*: morphometric, allozymal and mtDNA diversity, Apidologie 32, 3–23.
- Humphries C.J., Williams P.H., Vane Wright R.I. (1995) Measuring biodiversity value for conservation, Annu. Rev. Ecol. Syst. 26, 93–111.
- Inoue T., Adri, Salmah S. (1990) Nest site selection and reproductive ecology of the Asian honey bee, *Apis cerana indica*, in central Sumatra, in: Sakagami S.F., Ohgushi R.-i., Roubik D.W. (Eds.), Natural history of social wasps and bees in equatorial Sumatra, Hokkaido University Press, Sapporo, Japan, pp. 219–232.
- IPCC (2007) Intergovernmental Panel on Climate Change, Fourth assessment report, in: World Meterological Organization, Geneva.
- Itioka T., Inoue T., Kaliang H., Kato M., Nagamitsu T., Momose K., Sakai S., Yumoto T., Mohamad S.U., Hamid A.A., Yamane S. (2001) Six-year population fluctuation of the giant honey bee *Apis dorsata* (Hymenoptera: Apidae) in a tropical lowland dipterocarp forest in Sarawak, Ann. Entomol. Soc. Am. 94, 545–549.
- Janzen D. (1974) Tropical backwater rivers, animals, and mast fruiting by the Dipterocarpaceae, Biotropica 6, 69–103.
- Janzen D.H. (1971) Seed predation by animals, Annu. Rev. Ecol. Syst. 2, 465–496.
- Kahona S., Nakamura K., Amir M. (1999) Seasonal migration and colony behavior of the tropical honeybee *Apis dorsata* F. (Hymenoptera: Apidae), Treubia 31, 283–297.
- Kenta T., Isagi Y., Nakagawa M., Yamashita M., Nakashizuka T. (2004) Variation in pollen dispersal between years with different pollination conditions in a tropical emergent tree, Mol. Ecol. 13, 3575–3584.
- Kevan P.G., Viana B.F. (2003) The global decline of pollination services, Biodiversity 4, 3–8.
- Klein A.M., Vaissiere B.E., Cane J.H., Steffan-Dewenter I., Cunningham S.A., Kremen C., Tscharntke T. (2007) Importance of pollinators in changing landscapes for world crops, Proc. R. Soc. B-Biol. Sci. 274, 303–313.
- Koeniger N., Vorwohl G. (1979) Competition for food among four sympatric species of Apini in Sri Lanka: Apis dorsata, Apis cerana, Apis florea and Trigona iridipenis, J. Apic. Res. 18, 95–109.
- Koeniger N., Koeniger G. (1980) Observations and experiments on migration and dance communication of *Apis dorsata* in Sri Lanka, J. Apic. Res. 19, 21– 34.
- Koeniger N., Koeniger G., Punchihewa R.K.W., Fabritius M., Fabritius M. (1982) Observations and experiments on dance communication in *Apis florea* in Sri Lanka, J. Apic. Res. 21, 45–52.

- Konuma A., Tsumura Y., Lee C.T., Lee S.L., Okuda T. (2000) Estimation of gene flow in the tropical-rainforest tree *Neobalanocarpus heimii* (Dipterocarpaceae) inferred from paternity analysis, Mol. Ecol. 9, 1843–1852.
- Köppler K., Vorwohl G., Koeniger N. (2007) Comparison of pollen spectra collected by four different subspecies of honey bee *Apis mellifera*, Apidologie 38, 341–353.
- Kremen C., Williams N.M., Aizen M.A., Gemmill-Herren B., LeBuhn G., Minckley R., Packer L., Potts S.G., Roulston T., Steffan-Dewenter I., Vazquez D.P., Winfree R., Adams L., Crone E.E., Greenleaf S.S., Keitt T.H., Klein A.M., Regetz J., Ricketts T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change, Ecol. Lett.10, 299–314.
- Lahjie A.M., Seibert B. (1990) Honey gathering by people in the interior of East Kalimantan, Bee World 71, 153–157.
- Liow L.H., Sodhi N.S., Elmquist T. (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia, J. Appl. Ecol. 38, 180–192.
- Maa T. (1953) An inquiry into the systematics of the tribus *Apidini* or honeybees (Hym.), Treubia 21, 525–640.
- Magsaysay J.F., Lucero R.M., Manila-Fajardo A.C., Tapay N.E. (2004) Economics of raising honey bees in the Philippines, in: Camaya E.N., Cervancia C.R. (Eds.), Bees for new Asia, Proc. 7th Asian Apic. Association Conference, University of the Philippines: Los Baños, pp. 305– 310.
- May R.M. (1994) Conceptual aspects of the quantification of the extent of biological diversity, Philos. Trans. R. Soc. Lond. B 345, 13–20.
- Maycock C.R., Thewlis R.N., Ghazoul J., Nilus R., Burslem D. (2005) Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest, J. Veget. Sci. 16, 635–646.
- Michener C.D. (1979) Biogeography of the bees, Ann. Missouri Bot. Gard. 66, 277–347.
- Moritz R.F.A., Dietemann V., Crewe R. (2007a) Determining colony densities in wild honeybee populations (*Apis mellifera*) with linked microsatellite DNA markers, J. Insect Conserv. 11, 391–397.
- Moritz R.F.A., Kraus F.B., Kryger P., Crewe R.M. (2007b) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees, J. Insect Conserv. 11, 391–397.
- Morse R.A., Laigo F.M. (1969) *Apis dorsata* in the Philippines, Philippines Association of Entomologists, Laguna, p. 96.

- Morse R.A., Nowogrodzki R. (1990) Honey bee pests, predators and diseases, Cornell University Press, Ithaca, p. 474.
- Morse R.A., Calderone N.W. (2000) The value of honey bees as pollinators of U.S. crops in 2000, Glean. Bee Cult. Suppl., 1–15.
- Mossagegh M.S. (1993) New geographical distribution line of *Apis florea* in Iran, in: Conner L.J., Rinderer T., Sylvester H.A., Wongsiri S. (Eds.), Asian Apiculture. Wicwas Press, Cheshire, pp. 64–66.
- Mostafa A.M., Williams R.N. (2002) New record of the small hive beetle in Egypt and notes on its distribution and control, Bee World 83, 99–108.
- Murray T.E., Kuhlmann M., Potts S.G. (2009) Conservation ecology of bees: populations, species and communities, Apidologie 40, 211– 236.
- Nanson J.D., Hamrick J.L. (1997) Reproductive and genetic consequences of forest fragmentation: Two case studies of neotropical canopy trees, J. Hered. 88, 265–276.
- Nath S., Sharma K. (2007) Honey trails in the Blue Mountains: Ecology, people and livelihood in the Nilgiri Biosphere Reserve, India. Keystone Foundation, Kotagiri.
- Nath S., Roy P., Leo R., John M. (1994) Honeyhunters and beekeepers of Tamil Nadu. A survey document. Keystone, Pondicherry, p. 86.
- Neumann P., Elzen P.J. (2004) The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): Gaps in our knowledge of an invasive species, Apidologie 35, 229–247.
- Neumann P., Koeniger N., Koeniger G., Tingek S., Kryger P., Moritz R.F.A. (2000) Home-site fidelity of migratory honeybees, Nature 406, 474–475.
- Noss R.F., Quigley H.B., Hornocker M.G., Merrill T., Paquet P.C. (1996) Conservation biology and carnivore conservation in the Rocky Mountains, Conserv. Biol. 10, 949–963.
- Nualsanong K. (2000) Traditional knowledge and natural resources management [in Thai], Taksinkadee 5, 130–138.
- Oldroyd B.P., Wongsiri S. (2006) Asian Honey Bees. Biology, Conservation and Human Interactions, Harvard University Press, Cambridge, Ma., p. 340.
- Oldroyd B.P., Rinderer T.E., Wongsiri S. (1992) Pollen resource partitioning by *Apis dorsata*, *A. cerana*, *A* andreniformis and *A. florea* in Thailand, J. Apic. Res. 31, 3–7.
- Oldroyd B.P., Thexton E.G., Lawler S.H., Crozier R.H. (1997) Population demography of Australian feral bees (*Apis mellifera*), Oecologia 111, 381–387.
- Oldroyd B.P., Osborne K.E., Mardan M. (2000) Colony relatedness in aggregations of *Apis dor-sata* Fabricius (Hymenoptera, Apidae), Insectes Soc. 47, 94–95.
- Oldroyd B.P., Reddy M.S., Chapman N.C., Thompson G.J., Beekman M. (2006) Evidence for reproductive isolation between two colour morphs of cavity

nesting honey bees (*Apis*) in south India, Insectes Soc. 53, 428–434.

- Otis G.W. (1996) Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; *Apis*) in Asia, J. Kans. Entomol. Soc. 69, 311–333.
- Paar J., Oldroyd B.P., Kastberger G. (2000) Giant honey bees return to their nest sites, Nature 406, 475.
- Paar J., Oldroyd B.P., Huettinger E., Kastberger G. (2004) Genetic structure of an *Apis dorsata* population: the significance of migration and colony aggregation, J. Hered. 95, 119–126.
- Pickering C.M., Hill W. (2007) Impacts of recreation and tourism on plant biodiversity and vegetation in protected areas in Australia, J. Environ. Manage. 85, 791–800.
- Punchihewa R.K.W., Koeniger N., Kevan P.G., Gadawaski R.M. (1985) Observations on the dance communication and natural foraging ranges of *Apis cerana*, *Apis dorsata*, and *Apis florea* in Sri Lanka, J. Apic. Res. 24, 168–175.
- Purwanto, Didik B., Hadisoesilo S., Kasno, Koeniger N., Lunderstädt J. (2000) Sunggau system: A sustainable method of honey production from Indonesia with the giant honey bee *Apis dorsata*, in: Wongsiri S. (Ed.), Proc. 7th Int. Conf. on tropical bees: Management and diversity, International Bee Research Association: Cardiff, Chiang Mai, Thailand, pp. 201–206.
- Radloff S.E., Hepburn H.R., Hepburn C., Fuchs S., Otis G.W., Sein M.M., Aung H.L., Pham H.T., Tam D.Q., Nuru A.M., Ken T. (2005) Multivariate morphometric analysis of *Apis cerana* of southern mainland Asia, Apidologie 36, 127–139.
- Raffiudin R., Crozier R.H. (2007) Phylogenetic analysis of honey bee behavioral evolution, Mol. Phylogenet. Evol. 43, 543–552.
- Richards A.J. (2001) Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? Ann. Bot. 88, 165–172.
- Rinderer T.E. (1988) Evolutionary aspects of the Africanization of honey-bee populations in the Americas, in: Needham G., Page R.E. Jr., Delfinado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood, Chichester, pp. 1–12.
- Rinderer T.E., Marx B.D., Gries M., Tingek S. (1996) A scientific note on stratefied foraging by Sabahan bees on the yellow flame tree (*Peltophorum ptercarpum*), Apidologie 27, 423–425.
- Rinderer T.E., Oldroyd B.P., de Guzman L.I., Wattanachaiyingcharoen W., Wongsiri S. (2002) Spatial distribution of the dwarf honey bees in an agroecosystem in southeastern Thailand, Apidologie 33, 539–543.

- Ruttner F., Maul V. (1983) Experimental analysis of the interspecific isolation of *Apis mellifera* L and *Apis cerana* Fabr., Apidologie 14, 309–327.
- Sakai S. (2002) General flowering in lowland mixed diterocarp forests of South-east Asia, Biol. J Linn. Soc. 75, 233–247.
- Scott-Dupree C., Winston M.L., Hergert G., Jay S.C., Nelson D.L., Gates J., Termeer B., Otis G.W. (1995) A guide for managing bees for crop pollination, in: Canadian Association of Professional Apiculturists [online] http://www.capabees.com (accessed on 30 January 2009).
- Seeley T.D. (1978) Life history strategy of the honey bee, *Apis mellifera*, Oecologia 32, 109–118.
- Sen Sarma M., Esch H., Tautz J. (2004) A comparison of the dance language in *Apis mellifera carnica* and *Apis florea* reveals striking similarities, J. Comp. Physiol. A 190, 49–53.
- Sheikh M.S., Chetry G. (2000) Distribution of honey bees in Assam, Environ. Ecol. 18, 236–234.
- Slatkin M. (1985) Gene flow in natural populations, Annu. Rev. Ecol. Syst. 16, 393–430.
- Smith D.R. (2002) Biogeography of Apis cerana: southeast Asia and the Indo-Pakistan subcontinent, in: XIV Int. Congr. IUSSI, Hokkaido University, Sapporo, Japan, p. 233.
- Smith D.R., Hagen R.H. (1996) The biogeography of *Apis cerana* as revealed by mitochondrial DNA sequence data, J. Kans. Entomol. Soc. 69, 294–310.
- Smith D.R., Villafuerte L., Otis G., Palmer M.R. (2000) Biogeography of *Apis cerana* F. and *A. ni-grocincta* Smith: insights from mtDNA studies, Apidologie 31, 265–279.
- Sodhi N.S., Koh L.P., Brook B.W., Ng P.K.L. (2004) Southeast Asian biodiversity: an impending disaster, Trends Ecol. Evol. 19, 654–660.
- Solignac M., Cornuet J.M., Vautrin D., Le Conte Y., Anderson D., Evans J., Cros-Arteil S., Navajas M. (2005) The invasive Korea and Japan types of Varroa destructor, ectoparasitic mites of the Western honeybee (*Apis mellifera*), are two partly isolated clones, Proc. R. Soc. B-Biol. Sci. 272, 411–419.
- Stanghellini M.S., Ambrose J.T., Hopkins D.I. (2000) Bumble bee colonies as potential alternative hosts for the small hive beetle (*Aethina tumida* Murray), Am. Bee J. 140, 71–75.
- Tan N.Q., Ha D.H. (2002) Socio-economic factors in traditional rafter beekeeping with *Apis dorsata* in Vietnam, Bee World 83, 165–170.
- Tan N.Q., Chinh P.H., Thai P.H., Mulder V. (1997) Rafter beekeeping with *Apis dorsata*: some factors affecting occupation of rafters by bees, J. Apic. Res. 36, 49–54.

- Taylor D., Saksena P., Sanderson P.G., Kucera K. (1999) Environmental change and rain forests on the Sunda shelf of Southeast Asia: drought, fire and the biological cooling of biodiversity hotspots, Biodiv. Conserv. 8, 1159–1177.
- Thapa R., Wongsiri S., Oldroyd B.P., Prawan S. (2000) Migration of *Apis dorsata* in northern Thailand, in: Matsuka M., Verma L.R., Wongsiri S., Shrestha K.K., Partap U. (Eds.), Asian Bees and Beekeeping, Proc. 4th Asian Apic. Association Int. Conf., Science Publishers, Enfield, New Hampshire, Kathmandu, pp. 39–43.
- Tingek S., Koeniger G., Koeniger N., Gries M. (2004) *Physocephala paralliventris* Kröber (Conopidae), a parasitic fly of three *Apis* species in northern Borneo, in: Bees for new Asia, Proc. 7h Asian Apic. Association Conf., Los Baños, Philippines, pp. 364–365.
- Tsing A.L. (2003) Cultivating the wild: Honey-hunting and forest management in Southeast Kalimantan, in: Zerner C. (Ed.), Culture and the question of rights. Forests coasts and seas in Southeast Asia. Duke University Press, Durham, pp. 24–55.
- Underwood B.A. (1990) Seasonal nesting cycle and migration patterns of the Himalayan honey bee *Apis laboriosa*, Natl. Geogr. Res. 6, 276–290.
- Underwood B.A. (1992) Impact of human activities on the Himalayan honeybee, *Apis laboriosa*, in: Verma L.R. (Ed.), Honey bees in mountain agriculture, Westview Press, Boulder, pp. 51–58.
- Valli E., Summers D. (1988) Honey hunters of Nepal. Harry N. Abrams, Inc., New York, p. 104.
- Vane Wright R.I., Humphries C.J., Williams P.H. (1991) What to protect – Systematics and the agony of choice, Biol. Conserv. 55, 235–254.
- Verma L.R. (1991) Beekeeping in integrated mountain development, Aspect publications, Edinburgh, p. 367.

- Verma L.R., Rana B.S., Verma S. (1990) Observations on *Apis cerana* colonies surviving from Thai sacbrood virus infestation, Apidologie 21, 169– 174.
- Wang J. (2004) Sibship reconstruction from genetic data with typing errors, Genetics 166, 1963–1979.
- Waring C., Jump D.R. (2004) Rafter beekeeping in Cambodia with Apis dorsata, Bee World 84, 14– 18.
- Wattanachaiyingcharoen W., Wongsiri S., Oldroyd B.P. (2008) Aggregations of unrelated *Apis florea* colonies, Apidologie 39, 531–536.
- Wilkie D.S., Carpenter J.F. (1999) Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation, Biodiv. Conserv. 8, 927– 955.
- Williams I.H. (1996) Aspects of bee diversity and crop pollination in the European Union, in: Matheson A., Buchman S.L., O'Tool C., Westridge P., Williams I.H. (Eds.), The conservation of bees, Academic Press, London.
- Wongsiri S., Lekprayoon C., Thapa R., Thirakupt K., Rinderer T.E., Sylvester H.A., Oldroyd B.P., Boocham U. (1997) Comparative biology of *Apis* andreniformis and *Apis florea* in Thailand, Bee World 78, 23–35.
- Wynberg R. (2002) A decade of biodiversity conservation and use in South Africa: tracking progress from the Rio Earth Summit to the Johannesburg World Summit on Sustainable Development, S. Afr. J. Sci. 98, 233–243.
- Yoshida T., Saito J., Kajigaya N. (1994) The mating flight times of native Apis cerana japonica Radoszkowski and introduced Apis mellifera L in sympatric conditions, Apidologie 25, 353–360.
- Zayed A. (2009) Bee genetics and conservation, Apidologie 40, 237–262.