Synergistic interactions between an exotic honeybee and an exotic weed: pollination of *Lantana camara* in Australia

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Summary

Lantana camara, a woody shrub originating in south and central America, is among the most widespread and troublesome exotic weeds of the old-world tropics. It invades pasture, crops and native ecosystems, causing substantial economic losses and environmental degradation. In Australia alone, *L. camara* is currently estimated to cover *c.* 40 000 km^2 . In glasshouse studies we demonstrate that *L. camara* requires cross-pollination to set fruit, and that honeybee visits result in effective pollination. Field studies carried out in Queensland, Australia, suggest that fruit set is limited by pollinator abundance, and that the main pollinator of *L. camara* throughout a substantial portion of its Australian range appears to be the honeybee, *Apis mellifera*. Seed set was strongly correlated with honeybee abundance, and at many sites, particularly in southern Queensland, honeybees were the only recorded flower visitors. Of 63 sites that were visited, seed set was highest at five sites where only honeybees were present. Hives are frequently stationed within and adjacent to areas such as National Parks that are threatened by this noxious weed. Management of honeybee populations may provide a powerful tool for cost-effective control of *L. camara* that has previously been overlooked. We suggest that there are probably many other weeds, both in Australia and elsewhere, that benefit from honeybee pollination.

Keywords: *Apis mellifera*, fruit set, introduced bees, invasion, *Lantana camara*, Australia.

Introduction

Lantana camara L. (Verbenaceae) is an aggregate species, containing several hundred wild and cultivated strains. It is a woody perennial shrub native to southern and Central America which has become naturalized in the Caribbean, the Pacific islands, Australia, New Zealand, Africa and southern Asia (Morton, 1994; Baars & Neser, 1999; Anon., 2000). It has become a major environmental weed, invading areas of native vegetation to the exclusion of native plants. *Lantana camara* is also an important weed of agriculture and forestry, encroaching on plantations, orchards and on pastures, where it forms dense thickets that livestock cannot penetrate. The leaves are toxic when ingested by most domestic livestock or native mammals, although toxicity varies greatly between strains (Ide & Tutt, 1998; Johnson & Jensen, 1998; Tokarnia *et al.*, 1999).

Lantana camara was first recorded in Australia in 1941 in the Adelaide Botanic Gardens, and by the 1860s was naturalized around Brisbane and Sydney (Swarbrick *et al.*, 1998). It now covers *c.* 40 000 km^2, and is still spreading (Anon., 2000). Some National Parks, such as Forty Mile Scrub NP in north Queensland, are now more or less entirely covered in *L. camara* (Fensham *et al.*, 1994). Each year an estimated Aus$10 million is spent on control, and the losses to the livestock industry alone are estimated at Aus$7.7 million, through decreased stocking densities and deaths of *c.* 1500 cattle per year through *L. camara* poisoning (Anon., 2000).

In attempts to control *L. camara*, 38 different species of biocontrol agents have been released in 29 countries to date (Broughton, 1999a). Twenty-eight species have been introduced to Australia (Anon., 2000). Several of the most effective control agents are seed predators, as *L. camara* reproduces primarily through seed (rather

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than vegetatively) (Broughton, 1999b). However, the degree of control achieved varies greatly according to local climate and the strains of *L. camara* that are present, and in many regions control agents of *L. camara* have little effect.

Biological invasions are often facilitated by the establishment of mutualistic interactions between the invader and other organisms already established in the system. Invading weeds may benefit from mutualistic interactions with mycorrhizal fungi, nitrogen fixing microbes, pollinators and seed dispersers (Richardson *et al*., 2000). In this study, we focus on the pollination of *L. camara*. Despite the importance of seed production to the spread of this weed, little is known about its pollination requirements. It is thought to require cross-pollination, and the pollinators are usually said to be butterflies or other long-tongued insects (Barrows, 1976; Anon., 2000). The pink or orange florets are narrow and tubular (depth *c*. 1 cm), and inflorescences consist of 20–40 clustered florets, with those in the centre opening first. Stamens and stigma are held approximately halfway down the corolla tube. Here we investigate the pollination system, attempt to determine what the main pollinators are, and quantify other factors affecting seed set of *L. camara* in Queensland, Australia.

Methods

Pollination requirements of L. camara

Seeds were collected from Brisbane Forest Park and sown in a glasshouse in the UK (16–25°C, natural lighting). Once the resulting plants flowered (in *c*. 18 months), inflorescences were bagged prior to opening and then subjected to one of the following treatments:

(a) Control; no pollination.
(b) Selfed; hand-pollinated with pollen taken from another inflorescence on the same plant.
(c) Cross-pollinated; hand-pollinated with pollen from a different plant.

Hand pollination was carried out using a wooden toothpick. Each inflorescence was only pollinated on one occasion. In *L. camara* because only a small proportion of the florets on the inflorescence are open at any one time, only the open florets were pollinated. Each treatment was replicated 30 times. Each treatment was repeated a maximum of three times on any one plant. Particular pairs of donor and recipient plants were used only once for cross-pollination. A Kruskal–Wallis test was used to compare the proportion of florets setting fruit in each treatment.

Effectiveness of honeybees as pollinators

Plants were obtained as above. Several flowering plants were placed outside on the Southampton University campus in September 2002, and were soon being regularly visited by honeybees (whether these were from apiaries or wild colonies was not known). A second group of plants were kept in an insect-free glasshouse, and further protected from pollination by enclosing inflorescences in netting before they opened. Single honeybees were captured while foraging and introduced to a 1 m^3 cage containing a flowering *L. camara*. If they did not continue foraging, they were released. If they commenced foraging, then a branch of a second *L. camara* plant supporting five inflorescences that had previously been bagged was inserted into the cage through a slit in the netting. The experiment continued until the foraging bee had visited all five of the test inflorescences (1–22 min). The bee was then marked and released, and the five inflorescences bagged once more. For controls, a second branch of the same plant supporting a further five inflorescences was then inserted into the cage for 10 min (with no bee present). This procedure was repeated with 16 plants.

The proportion of florets setting seed was recorded for the five test and five control inflorescences, and a single mean calculated from each for use in analyses.

Insect visitation and fruit set in wild populations

To determine which insect species were responsible for pollination of *L. camara* in natural situations in Australia, insect visitation and fruit set were recorded at sites along a transect *c*. 2000 km in length, from Vennman's Bushland National Park in southern Queensland to the Daintree National Park on the Cape York Peninsula. All localities used were National Parks or part of the Wet Tropics World Heritage Area, and were visited between 28 March and 16 May 2000 (Table 1). Each park was searched for at least 2 h or until *L. camara* was located either in the park or within one km of the boundary. Searches were made by vehicle along roads passing through parks, where present, or on foot. In total 29 parks were visited, of which *L. camara* was found in, or adjacent to, 25. We cannot be certain that *L. camara* does not occur in the four National Parks in which we found none, as it was not possible to search more than a small proportion of the total area.

In large National Parks where *L. camara* was abundant, more than one site was sampled for insect abundance and fruit set. Each sample site was located at least 2 km from other sites. The number of sites sampled per National Park varied between 1 and 10, with a total of 63 sites sampled from the 25 parks. Because of the

Table 1 National Parks searched for *Lantana camara*, arranged in the order of decreasing latitude. Abundance of *L. camara* is indicated by the approximate number of plants found, but undoubtedly at most sites more were present than were located. *Apis mellifera* abundance was crudely quantified as: absent; rare (< 5 observed); moderately common (5–20 observed); abundant (> 20)

Name	Abundance of *L. camara*	No. of sample sites	Latitude (°N)	Sample date(s)	*A. mellifera*
Daintree NP	~50	1	16.4	28/4	Rare
Mossman section of WHA	~50	3	16.6	28/4	Absent
Barron Gorge NP	~100	4	16.9	28/4	Absent
Fitzroy Island NP	0	0	17.0	30/4	Absent
Russell River NP	0	0	17.2	29/4	Absent
Bellenden Ker NP	>1000	3	17.3	29/4	Absent
Kurrimine NP	>1000	2	17.7	1/5	Absent
Clump Mountain NP	~100	3	17.8	2/5	Absent
Edmund Kennedy NP	~40	1	18.2	2/5	Absent
Lumholtz NP	~25	1	18.5	3/5	Rare
Jourama Falls NP	~15	1	19.0	3/5	Rare
Mt Spec NP	~50	2	19.1	3/5	Rare
Magnetic Island NP	~100	2	19.2	5/5	Abundant
Bowling Green NP	>1000	4	19.4	6/5	Abundant
Dryander NP	>1000	6	20.2	7/5	Moderately common
South Molle Island NP	~50	3	20.3	21/4, 22/4	Rare
Conway NP	>1000	5	20.3	7/5	Moderately common
Eungella NP	>1000	1	21.1	9/5	Rare
West Hill NP	~100	2	21.9	9/5	Abundant
Mt Etna Caves NP	>1000	2	23.2	10/5	Abundant
Mt Colloseum NP	~50	1	24.4	10/5	Abundant
Burrum Coast NP	0	0	25.2	11/5	Abundant
Poona NP	~50	1	25.6	11/5	Abundant
Great Sandy NP	~50	1	25.9	11/5	Abundant
Noosa Heads NP	>1000	1	26.4	11/5	Abundant
Glasshouse Mountains NP	~100	2	27.0	16/5	Abundant
Bribie Island NP	0	0	27.1	16/5	Abundant
Brisbane Forest Park NP	>1000	10	27.4	28/3, 11/4, 15/4	Abundant
Vennman's Bushland NP	>1000	1	27.6	14/5	Abundant

NP, National Park; WHA, World Heritage Area.

scale of the study it was not possible to randomize the order in which National Parks were visited. We might reasonably expect fruit set to vary with both latitude and season, and it would be impossible to distinguish between these effects if sites were visited in sequence. Hence the transect was traversed twice, going northwards and then southwards. Different parks were visited when travelling in each direction.

Once a patch of *L. camara* was located, a near-instantaneous count was made of the numbers and species of insects visiting the first 400 inflorescences that were found. Counts of insects were made between 10:00 and 16:00 hours, and only during warm weather favourable to insect activity. At two sites there were less than 400 inflorescences present; for these sites the number of insects recorded on the inflorescences that were present was scaled up to give an estimated value per 400.

In *L. camara*, each inflorescence is composed of *c.* 20–40 tightly packed florets. After flowering the corollas wilt and drop off. If pollination has occurred the ovule swells to form a green fruit, or if not, it falls off leaving a scar. Approximately 3–4 weeks after flowering, it is possible to record the number of florets per inflorescence, and the number, which set fruit. This was carried out for 10 inflorescences selected at random from separate plants (using random number tables, counting downwards from the highest inflorescence on the plant). All fruits were counted, including those damaged by insects such as the seed fly *Ophiomyia lantanae* (Broughton, 1999b), as many were. In addition, at each site the approximate population size was recorded (the number of plants that had been found). Habitat type was crudely classified as rainforest, eucalypt forest, heathland or swamp. The percentage shade falling on the plants that were sampled for fruit set and insect visitation was also estimated.

The proportion of florets setting fruit of the total number of florets present was calculated for each inflorescence, and a mean calculated from the 10 inflorescences sampled at each site. Only these means were used in analysis, to avoid pseudoreplication (thus each site was treated as a single replicate). A multiple

factor analysis of variance was used to investigate whether the mean proportion of florets setting fruit varied according to the number of honeybees and of butterflies observed visiting inflorescences at each site, and also according to latitude, date of sampling, habitat, percentage shade and population size. Factors that did not contribute significantly to the model were removed. Proportions do not generally satisfy the conditions of analysis of variance. However, here we were using means of 10 proportional values, and these means did not differ significantly from a normal distribution. A linear regression was used to examine the relationships between honeybee and butterfly abundance (as measured by numbers recorded on inflorescences) and latitude.

Results

Pollination requirements of L. camara

Fruit set differed significantly between unpollinated, selfed, and cross-pollinated inflorescences (Kruskal–Wallis test, $\chi^2_2 = 25.4$, $P < 0.001$). When inflorescences were enclosed within bags and not hand-pollinated, few florets set fruit (mean ± SE; 1.0% ± 0.48). When flowers were hand-pollinated with pollen from the same plant, fruit set was higher (2.2 ± 0.56%), but fruit set was greatest following cross-pollination (8.1 ± 1.41%). Pairwise Kruskal–Wallis tests reveal that the difference between unpollinated and selfed plants was not significant ($\chi^2_1 = 3.49$, $P = 0.062$), but that cross-pollinated inflorescences set significantly more fruit than those that were self-pollinated ($\chi^2_1 = 11.7$, $P = 0.001$).

Effectiveness of honeybees as pollinators

Fruit set differed significantly between inflorescences visited by honeybees, and those not visited by any insects ($\chi^2_1 = 20.3$, $P < 0.001$). In the absence of pollination, fruit set was low (1.8% ± 0.46), and similar to the control plants described above. Following visitation by a single honeybee that had previously foraged on another plant, seed set was greatly increased (10.8 ± 1.31%), and was higher than following hand pollination.

Insect visitation and fruit set in wild populations

Overall, by far the most abundant insect visiting *L. camara* was the honeybee, which accounted for 62.9% of all visits. At 18 of the 63 sample sites honeybees were the only insects observed visiting *L. camara*. The only native bees recorded belonged to the genus *Amegilla* (Anthophoridae), which accounted for only 4.0% of visits. Most of the remaining insects were butterflies, which comprised 30.5% of visits. Twenty-seven butterfly species from five different families were recorded (Table 2). The only other insects observed were two individual moths (Lepidoptera) and seven Syrphids (Diptera), which were not identified. All of the insects observed were gathering nectar, although some honeybees were also observed to gather pollen from their tongues after collecting nectar. Florets of *L. camara* are narrow and tubular so that nectar can only be reached by insects with long tongues. The stamens are contained within the narrow tube, preventing easy collection of pollen.

The proportion of florets setting fruit did not vary significantly according to latitude, percentage shade falling on the plants, or according to the type of habitat that the plants were growing in (Table 3). The only factors to contribute significantly towards explaining variation in fruit set were numbers of honeybees, numbers of Lepidoptera, the date on which fruit set was measured, and the size of the population of *L. camara* (Table 3). Fruit set declined markedly as the season progressed. Fruit set was significantly higher at sites where honeybees were abundant (Fig. 1A). At the five sites with highest fruit set, the only recorded visitors were honeybees. However, fruit set was also positively correlated with abundance of butterflies (Fig. 1B). Finally, fruit set tended to be higher in small populations (the mean proportion of florets setting fruit was 0.161 for populations of <20 plants, 0.114 for populations of 20–100, and 0.116 for populations of >100). It is important to note that although latitude did not contribute significantly to the model, fruit set was lower at more northerly sites, and if considered in isolation from other explanatory factors, this relationship is significant (linear regression, $r^2 = 0.09$, $F_{1,62} = 6.14$, $P = 0.016$).

Honeybees exhibited a clear decline in abundance with declining latitude, being common at most southerly sites and scarce or absent in the north (linear regression, $r^2 = 0.37$, $F_{1,62} = 36.0$, $P < 0.001$) (Fig. 2A). Lepidoptera exhibited the opposite trend, being more abundant at northerly sites (linear regression, $r^2 = 0.08$, $F_{1,62} = 5.46$, $P < 0.05$) (Fig. 2B).

Discussion

Lantana camara showed no clear association with habitat types, being common in areas dominated by rainforest (e.g. Eungella National Park), eucalypt forests (e.g. Brisbane Forest Park), and also occurring on sand dunes (Great Sandy National Park) and in swamps dominated by *Melaleuca* spp. scrub (Edmund Kennedy National Park). However, it was noticeably more

Table 2 Identity, species and numbers of insects observed visiting *Lantana camara*, based on near-instantaneous assessment of the insects on 24 789 inflorescences at 63 sites throughout coastal Queensland

Family	Species	No. recorded
Apidae	*Apis mellifera* (L.)	171
Anthophoridae	*Amegilla* spp.	11
Papilionidae	*Graphium macleayanum* (Leach)	1
	Graphium sarpedon choredon (C. and R. Felder)	2
	Papilio ulysses joesa Butler	3
	Papilio aegeus aegeus Donovan	6
	Ornithoptera priamus euphorion (Gray)	1
	Cressida cressida cressida (Fabricius)	1
Nymphalidae	*Cethosia cydippe chrysippe* (Fabricius)	4
	Hypolimnas bolina nerina (Fabricius)	1
	Pantoporia consimilis consimilis (Boisduval)	2
	Euploea sp.	1
	Danaus hamatus hamatus (W.S. Macleay)	5
	Danaus affinis affinis (Fabricius)	2
	Danaus plexippus plexippus (L.)	2
	Hypocysta adiante adiante (Hübner)	1
	Junonia orithya albicincta Butler	1
Pieridae	*Eurema brigitta australis* (Wallace)	14
	Delias mysis mysis (Fabricius)	5
	Catopsilia pyranthe crokera (W.S. Macleay)	1
	Appias paulina ega Boisduval	1
	Elodina perdita perdita Miskin	2
Lycaenidae	*Hypochrysops digglesii* (Hewitson)	1
	Lampides boeticus (L.)	3
Hesperiidae	*Pelopidas agna dingo* Evans	8
	Notocrypta waigensis proserpina (Butler)	7
	Parnara naso sida (Waterhouse)	1
	Telicota mesoptis mesoptis Lower	2
	Ocybadistes sp.	1

Table 3 Multiple factor analysis of variance in the proportion of florets setting seed at 63 sample sites. At each site 10 inflorescences were sampled, each from a separate plant, and the mean proportion of florets that had set fruit used in the analysis. Factors that did not contribute significantly to the model were removed, and the analysis repeated (hence the variation in residual degrees of freedom)

Factor	d.f.	*F*	*P*
Sample date	1,58	34.7	<0.001
Population size	1,58	4.57	<0.05
Latitude	1,49	0.52	NS
Shade	1,49	0.01	NS
Habitat type	2,49	0.32	NS
No. of honeybees	1,58	29.6	<0.001
No. of butterflies	1,58	11.8	<0.005

NS, not significant.

abundant in disturbed areas such as along roads passing through parks, and was generally rare within dense forests (although we did not gather quantitative data on this). This accords with previous work which has found that *L. camara* is unable to tolerate the shade cast by intact forest, but can rapidly invade when forests are damaged by fire, felling or grazing (Gentle & Duggin, 1997; Duggin & Gentle, 1998).

Lantana camara spreads primarily through production of seeds that are dispersed by birds (Anon., 2000). Thus improving our understanding of the factors that influence fruit set could be of great value in designing control programmes for this weed. In accordance with Barrows (1976), we found that *L. camara* set few or no fruits without cross-pollination. Hand pollination or visitation by a honeybee (each on a single occasion) gave *c.* 10% fruit set. This is notably lower than fruit set in some natural populations. This is presumably because at any one time many of the florets on an inflorescence are not open, and so could not be pollinated either by hand or by a bee visiting on just one occasion. In contrast, in natural situations inflorescences can be visited by a succession of insects over several days as each floret opens.

We found that fruit set in the wild declined markedly as the season progressed, perhaps the result of declining temperatures from March to May. There was also a weak effect of population size, with smaller populations tending to set more fruit. This is likely to be the result of greater intraspecific competition for resources (such as light, moisture, etc.) in large populations. However, neither of these factors offers much scope for manipulation. More interestingly, we found that fruit set was strongly influenced by abundance of pollinators. As we have shown that *L. camara* exhibits low self-fertility, fruit set depends on adequate pollinator services.

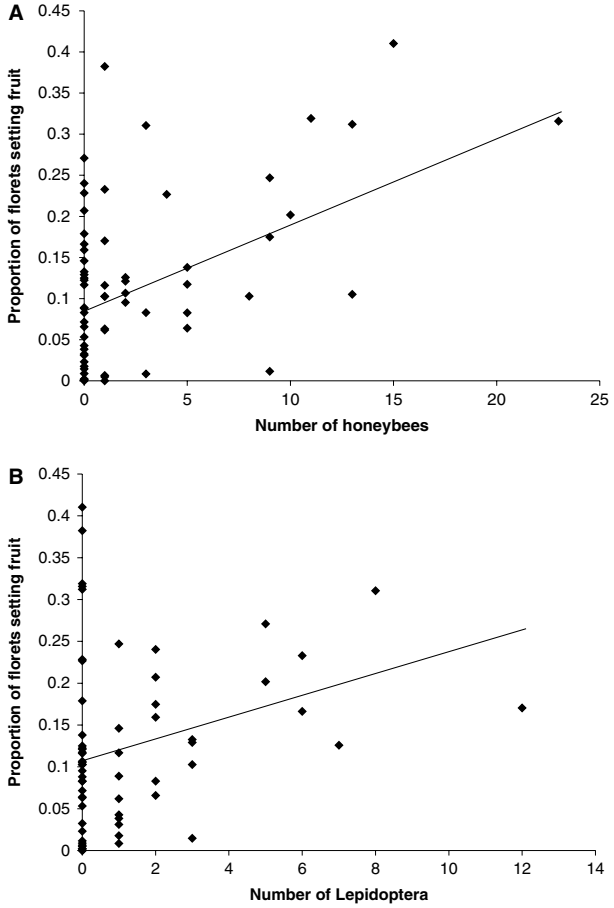

Fig. 1 Proportion of florets setting fruit at 63 sites, according to the abundance of (A) honeybees (linear regression, $r^2 = 0.24$, $F_{1,61} = 19.1$, $P < 0.001$) and (B) Lepidoptera (linear regression, $r^2 = 0.063$, $F_{1,61} = 4.13$, $P = 0.046$) recorded foraging on 400 inflorescences. Proportions of florets setting fruit are means of 10 inflorescences sampled from different plants.

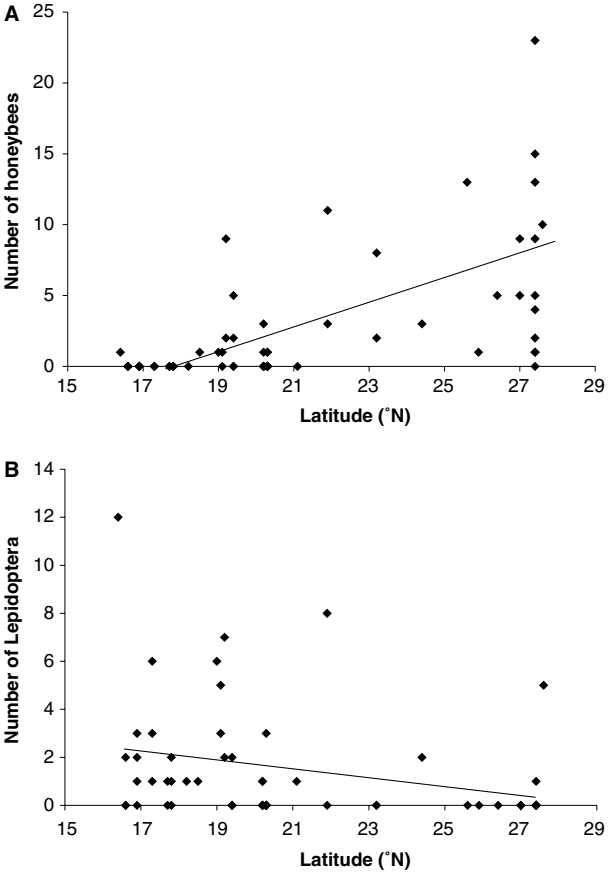

Fig. 2 Variation in abundance of (A) honeybees and (B) Lepidoptera feeding on *Lantana camara* with latitude. Numbers recorded are bees per 400 inflorescences of *L. camara*.

We did not examine nocturnal visits to *L. camara*, and it is probable that the plant is visited by moths at night. Nonetheless, our data strongly suggest that the main pollinator of *L. camara* in National Parks throughout much of Queensland is the honeybee. In glasshouse studies, we demonstrated that visits by honeybees do result in pollination, giving fruit set similar to that achieved by hand pollination. Honeybees were by far the most abundant daytime visitors in Queensland, and the abundance of honeybee visitors strongly correlated with fruit set. At 18 of the 63 sites examined, honeybees were the only visitors to *L. camara* that we recorded. At the five sites with highest fruit set, the only recorded flower visitors were honeybees. The correlations between honeybee (and butterfly) abundance and fruit set strongly suggests that pollinator services are a limiting factor in seed production in *L. camara* in Queensland. Furthermore, it seems certain that the most important pollinator at many sites is the honeybee.

Honeybees exhibited a marked decline with decreasing latitude, being scarce or absent in the most northerly sites examined. This is to be expected as these bees originate from Europe and are not adapted to the wet tropical conditions of northern Queensland. At the more northerly sites butterflies were more abundant, and were probably the main pollinators.

The structure of florets of *L. camara* preclude short-tongued insects from reaching the nectar, yet most native Australian bees have very short tongues (Armstrong, 1979). This presumably explains why they were generally not recorded as visitors to *L. camara* (the rare exception being *Amegilla* sp. which have long tongues of approximate length 9–12 mm; D. Goulson, unpubl. obs.). Honeybees have longer tongues than most Australian bees, at 6.5–6.7 mm (Alpatov, 1929). They are just able to reach the nectaries in *L. camara* by pushing their head into the opening of the flower (D. Goulson, unpubl. obs.).

Lantana camara is regarded as one of the worst exotic weeds of both nature reserves and pasture in Australia and throughout the old world tropical and subtropical zone (Fensham *et al.*, 1994; Anon., 2000). It was readily

located in or close to the majority of National Parks visited (25 of 29), and was abundant in many. Apiarists routinely station hives next to and sometimes within National Parks. There is a clear conflict of interest. It seems certain that the presence of hives will enhance seed set of nearby populations of *L. camara*. It is not known whether seed-set limits population growth in *L. camara*, but common sense suggests that increasing seed set is likely to make the plant more invasive. Vast expense is incurred attempting to control this weed, generally with limited success. Our data suggest that a simple and effective means of improving control of *L. camara* may be to remove honeybee hives from the vicinity of infestations, particularly in areas such as southern Queensland where other pollinators are rare or absent. Controlled experiments involving removal of hives and, if present, removal of wild nests are required to test how effective this strategy might be.

Possible impacts of introduced honeybees on native ecosystems have attracted considerable attention in recent years. Much of this research has focused on competition with native flower visitors. Although many researchers have concluded that competitive effects are inevitable, this is disputed and conclusive evidence of major impacts on native pollinators has yet to be found (for reviews of the impacts of honeybees which draw different conclusions compare Robertson *et al*., 1989; Buchmann & Nabhan, 1996; Roubik, 1996; Sugden *et al*., 1996; Goulson, 2003 with Butz Huryn, 1997). Rather less attention has been paid to discerning what effects honeybees may have through pollination of weeds. In general rather little is known of the pollination biology of non-native plants, and it is unclear whether inadequate pollination is commonly a limiting factor (Richardson *et al*., 2000). Some instances are known where seed set of non-native plants has been severely limited by the absence of suitable pollinators: notably *Trifolium repens* L. in New Zealand before the introduction of bumblebees (Hopkins, 1914) and *Melilotus* spp. in North America (Faegri & van der Pijl, 1966). Similarly, seed set of Scotch broom, *Cytisus scoparius* L. Link (Parker 1997) in USA was strongly limited by lack of pollinators at some sites, but not at others, depending on the local abundance of bee species. In North America, honeybees increase seed set of the yellow star thistle, *Centaurea solstitialis* L. (Barthell *et al*., 1994) and are the main pollinators of two important weeds, purple loosestrife, *Lythrum salicaria* L. (Mal *et al*., 1992) and *Raphanus sativus* L. (Stanton, 1987). Given that honeybees have been spread around the globe at the hands of man, and that many of the countries to which they have been introduced suffer from substantial exotic weed problems, it seems likely that there are many other examples of important weeds that benefit from the pollination services of honeybees. In turn, honeybees no doubt benefit from rewards provided by nectar or pollen-rich weeds such as *L. camara*. Although suppression of honeybee numbers may not always be practical or desirable, it is a tool for weed management which has been largely overlooked and which should be considered when devising weed control programmes.

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