Reduction of Visitation Rates by Honeybees (Apis mellifera) to Individual Inflorescences of Lavender (Lavandula stoechas) upon Removal of Coloured Accessory Bracts (Hymenoptera: Apidae)

ANDREW D HUGGINS, FRANCIS S GILBERT, TOM READER & CHRISTOPHER J BARNARD

Received: 2006-06-02/2006-06-30
Accepted: 2006-09-09


Honeybees (Apis mellifera Linnaeus 1758) choosing between inflorescences of Lavandula stoechas appear to use a two-stage decision process based on different morphological criteria at each stage. The first stage, whether to closely inspect inflorescences, is based on display size. Lavandula inflorescences have large showy terminal bracts at the apex which increase the apparent display size. However, crab spiders often conceal themselves by closing the bracts around themselves using silk. Two manipulation experiments were carried out on the effects of the bracts on visitation rates to individual inflorescences. In the first, inflorescences from which bracts were removed received a reduced rate of inspection. In the second, inflorescences in which bracts were stuck together, mimicking the spider behaviour, experienced the same number of inspections as controls. Hence, the bracts did play a role in attracting honeybees to inflorescences, because a lack of bracts is usually only seen in very young or very old inflorescences, neither of which produce any nectar. However, honeybees did not avoid the closed bracts (assumed to provide an indirect cue of spider presence), probably because spiders often move between inflorescences, thus making closed bracts unreliable as a cue to predation risk.

Key words: Apis mellifera (Linnaeus 1758) – crab spider – display size – pollination – predation risk – smelling
Im zweiten Versuch wurden Blütenstände, deren Tragblätter zusammengeklebt worden waren, um das Verhalten der Spinnen nachzuahmen, nicht selten inspiziert als die Konsollblätter. Daraus ergibt sich, daß die Tragblätter eine Rolle bei der Anziehung der Honigbienen spielen, vielleicht weil Tragblätter in der Regel nur bei sehr jungen oder sehr alten Blütenständen fehlen, die beide keinen Nektar produzieren. Honigbienen sahen die ungestörten Tragblätter von denen angezogen worden war, sie würden als indirekter Hinweis auf die Anwesenheit von Kranzspinnen dienen jedoch nicht vermögend, vermutlich weil Spinnen sich oft hin und her bewegen unter Blütenständen, so daß die geschlossenen Tragblätter nur unauffällige Hinweise auf das Prädationsrisiko darstellen.

Schlüsselbegriffe: Apis mellifera (Linnaeus 1758) – Bestäubung – Blütengröße – Dauerstörfung – Kranzspinnen – Prädationsrisiko

1 Introduction

Models of optimal foraging which seek to explain patterns of behaviour in insects foraging for nectar and pollen often ignore the effects of predators [Mosse 1984; Lima 1998, Doogan 20001], largely on the assumption that predation is too rare to exert strong selection [Pra 1979, Skov-Hansen 1991, Schmitt 2001]. However, if honeybees are adapted to maximise their total lifetime energy input to the hive, we might expect them to take some steps towards prolonging their foraging lifespan. One predation pressure is exerted by crab spiders (Araneida: Thomisidae) which are ambush predators, that pose on flower visitors that land on nectar sources [Mosse 1986b]. Crab spiders can camouflage themselves on flowers [Chittka 2001] and can make flowers or inflorescences they are in more attractive to foragers [Hillman, Herbst and Chittka 2003]. There is also some evidence that bees avoid foraging in areas of high spider density [Doogan and Morris 2003], and avoid signs of spider presence [Doogan 2001, Reaka, Hodgson, Gilbert et al. 2006], indicating that they take some measures to safeguard their future survival.

Recent work by the authors has concentrated on honeybee foraging on the Mediterranean shrub lavender (Lavandula stoechas) [Hegelson & Barnard 2004, Hegelson, Gilbert & Barnard 2006, Reaka et al. 2006]. Lavandula flowers grow as inflorescences, which usually have a set of 1-6 colourful sterile bracts at the apex. Previous work on choice of Lavandula inflorescences by honeybees has produced a contradictory picture of the effects of the terminal bracts. In previous work, inflorescences have been categorized according to observed bee responses to them. Inflorescences that bees alighted on were categorized as accepted. Before alighting, bees orientated towards and hovered close to inflorescences, appearing to inspect them closely, probably to assess whether to alight. Inflorescences that bees inspected but on which they did not alight were called rejected. Bees passed close (< 3 cm) to many other inflorescences that they were assumed to have detected but did not pause to inspect; these inflorescences were categorised as ignored. Of course, it is possible that ignored inflorescences were, in some cases, simply not detected. While bees are initially attracted to inspect inflorescences with larger, more numerous bracts, they appear to inspect inflorescences with smaller bracts [Dufour, Gibson, Gillooly et al. 1993, Gonzalez, Reaka, Vazquez et al. 1995], and at this stage the decision appears to be based on the number of flowers and inflorescence age [Hegelson et al. 2006]. It may be that bees do not use the spatial distribution of flowers on the inflorescence, or absolute number of flowers, but they appear to use some correlate of age and number of flowers, which could also be colour or patterns of colour [Coles & Vorobyev 1997, Spatt, Tait and Chittka 2001, Peck and Chittka 2004] to choose the most productive inflorescences. The bracts grow as the inflorescence ages, but stop growing by the time the number of flowers begins to decline [Hegelson et al. 2006]. This bract length is not related in a simple way to the number of flowers, but to the nectar secretion rate, which may confound the bees learned responses to bract size and number. [Herrera 1987] experimentally removed all the bracts from L. stoechas tusches and observed a clear reduction in visitation rate by bees. When a bush was spatially split in half, and all the bracts were removed from one half, that half experienced 41% fewer visits than the control half.
Honeybees are more likely to reject *Lavandula* inflorescences that contain spiders [Rücker et al. 2006] and several cues could potentially indicate the presence of a spider. The bee may be able to detect the spider directly by smell or sight. The latter is unlikely since the spiders are usually not visible except from directly above the inflorescence, and even then not always because the bracts are often joined together at the top by the spider. Alternatively, the bee may simply avoid inflorescences where there is a high probability of spider occupancy, i.e. those with at least four large bracts. Spiders usually conceal themselves within the terminal bracts, tying them together with silk (A D Hopper, pers. obs.). Spiders also select among inflorescences based on the number and size of bracts because they require a certain amount of bract material in which to conceal themselves [Rücker et al. 2006]. Therefore, bees may learn that inflorescences that have at least four large bracts may be particularly likely to contain spiders, especially if the bracts are closed.

In order to investigate the role of bracts in bee choice, two experiments were carried out where visits by bees to marked inflorescences were recorded before and after manipulation of the bracts. In the first experiment, the treatment was removal of the bracts. As Hopper [1987] showed that removal of bracts reduces visitation rates to bushes or half-bushes, the aim of the first experiment was to assess whether such an effect was detectable at the level of visitation rates to individual inflorescences, and whether bees were less likely to inspect or accept manipulated inflorescences. It was predicted that removal of bracts should reduce the number of bees inspecting inflorescences. However, if the bracts that were removed were closed and large enough to conceal a spider, bees may be more likely to accept these inflorescences when the bracts were removed. In the second experiment, the aim was to assess whether bees avoid inflorescences with closed bracts. Therefore, the bracts of some inflorescences were stuck together as though by a spider and it was predicted that bees would be less likely to accept these inflorescences.

Honeybees sometimes use scent marks in order to avoid visiting inflorescences that have recently been depleted of nectar [Gómez & Ninéz 1992, William 1998, Goulson, Chapman & Hughes 2001]. The role of scent marks has not been studied in the current system, and it is possible that scent marks of previous visiting bees affect the decision whether to visit a *Lavandula* inflorescence. If bees were using scent marking, the probability that a bee visits an inflorescence should be lower if it has recently been visited.

### 2 Material and methods

Experiment I was carried out at the Quinta de São Pedro research station near Lisbon in Portugal (24°34'33.67"N 9°00'11.341"W) in April 2004. Experiment II was conducted in the nearby Parque da Arroio Fossil da Costa Caparica in April 2005. At both sites large numbers of lavender shrubs containing many thousands of inflorescences were heavily exploited by honeybees.

All selected inflorescences were measured with a small piece of marking tape, the day before the observations started, so that if the labels affected visitation, the foragers would have become habituated to them by the time of the experiment. On the days of manipulations, all inflorescences were measured for morphological characteristics previously shown to affect bee's decisions: length of inflorescence, length of longest bract, number of bracts, number of flowers and age of inflorescence. The age of inflorescence was recorded as the generation of the flowers (1st, 2nd, 3rd) assessed by the spatial arrangement of the flowers, since the flowers of each generation are distinctively distributed around the inflorescence [Hopper et al. 2006]. The position of the bracts relative to one another was also noted. If they were together and enclosed a space large enough to conceal a spider they were classified as closed, otherwise they were open.
All decisions made by observed bees were classified into three groups following earlier work [Dobson et al. 1995; Goulas et al. 1995; Heyenow & Barnard 2004] based on the bees’ responses to inflorescences:

Accepted inflorescences were those on which a bee alighted and probed one or more flowers.

Rejected inflorescences were those that appeared to be inspected by a bee (and sometimes touched by the antenna or legs) in a brief hovering flight, but on which the bee did not alight.

Ignored inflorescences were those that a bee approached (within 3 cm) but at which it did not visibly pause or make any physical contact. Such inflorescences may have been detected but ignored, or not detected, by the bee.

Accepted and rejected inflorescences will be referred to collectively as inspected inflorescences.

Bee decisions were recorded by a single observer in Experiment I, but two observers in Experiment II. Before behavioural recordings started, trial observations were carried out where both observers independently recorded decisions made by bees to check that classification of decisions were consistent across observers. The inspection behaviour is so distinctive that all decisions were categorized the same by both observers.

2.1 Experiment I: Removal of bracts

Four patches each of 100 inflorescences were chosen arbitrarily in a large stand of Lavandula of many thousands of inflorescences. Each patch was a section of a bush that was at least one metre from the bushes containing other designated patches. All 400 inflorescences were labelled with a small piece of numbered masking tape around the stem. For three days before and three days after manipulation, bees were observed between 1000 and 1800 h (GMT) foraging in the patches. Patches were observed in rotation for 20 minutes at a time, so approximately one quarter (2 hours per patch per day) of the activity at each patch was recorded. Most of the time there was only one bee in the patch at any one time. However, during busy periods there was more than one bee foraging in a patch, so a few visits may have been unrecorded some of the time. On the day of manipulation, 50 inflorescences were selected randomly on each patch and their bracts were removed; the other 50 inflorescences per patch were left as controls. It was expected that manipulated inflorescences, but not control inflorescences, would experience a reduction in the number of inspections.

2.2 Experiment II: Closure of bracts

Three patches were chosen arbitrarily in a large stand of Lavandula of, again, many thousands of inflorescences. Each patch was a section of a bush that was at least one metre from the bushes containing other designated patches. Within each patch, 40 inflorescences that had four or more bracts were marked with numbered masking tape. For four days before and two days after manipulation, bees were observed between 1000 and 1600 h (GMT) foraging in the patches. Patches were observed in rotation for 20 min at a time, so approximately one third (2 hours per patch per day) of the activity was recorded. The experimental manipulation in this case involved gluing (Gripfilltachen, E. H. Thorne [Beehives] Ltd, U.K.) the bracts together at the top (so they were closed) to initiate the spiders’ behaviour. It was possible that the bees would respond to the glue, so controls for the presence of glue per se were included.

As Experiment II was carried out in a different year and location, it was important to replicate the results of Experiment I, along with a control where bracts were removed and glue was added. Since closure of bracts may reduce the visible surface area of bracts, a control was also needed that reduced the area without closing the bracts. Hence, there were four treatments of 30 randomly selected inflorescences each that were randomly distributed among the three patches: (a) Control, otherwise unmanipulated bracts with glue added, (b) All bracts removed, glue added to stem below inflorescence to replicate the results of experiment one with glue, (c) Half bract material removed to reduce the visible surface area, glue added to other half, (d) Bracts stuck together at the top to close them.
It was expected that, if bracts attract bees to inflorescences, Treatment 1 inflorescences would experience a reduction in the number of inspections. Furthermore, it was expected that, if bees avoid closed bracts, there would be a difference between Treatments e and d in the change of the number of inspections or the probability of acceptance.

2.3 Data processing and analysis

The data consisted of morphological data for all marked inflorescences, and the decisions by bees at numbered inflorescences. In Experiment 1, 2,333 decisions were recorded (5.3 per inflorescence) and, in Experiment 2, 1,147 decisions were recorded (9.6 per inflorescence). The spiderwebness, which were cross-referenced in Microsoft Excel by a Visual Basic macro, resulted in the total numbers of inspections, rejections and ignores before and after the manipulations for each inflorescence. In addition, in Experiment 2, the total number of acceptances, rejections and ignores prior to each decision within each 20-min period were summed in order to see whether there was any effect of recent visitation on the probability of accepting a given inflorescence.

Morphological data were analyzed in SPSS (SPSS, Inc.), but all analyses of the number of visits to inflorescences were carried out in R (Free Software Foundation) using Poison errors. Other data were non-normal and non-Poisson so non-parametric tests were used: in the text, ‘KW’ implies the test statistic of the Kruskal-Wallis test (distributed as a chi-squared with k degrees of freedom, and ‘U’ implies the large-sample statistic of a Mann-Whitney U test.

3 Results

3.1 Experiment I

Patches did not differ in the number of flowers on inflorescences (KW₁ = 2.21, P = 0.15), or age of inflorescences (KW₁ = 1.96, P = 0.38), but did differ in the length (KW₁ = 25.6, P < 0.001) and number of bracts (KW₁ = 28.4, P < 0.001) and inflorescence length (KW₁ = 19.29, P < 0.001). Inflorescences in patch one had fewer smaller bracts, and patch four inflorescences were shorter than those in other patches. There was no significant difference in any of the morphological measures between the control and experimental inflorescences (U tests, P > 0.37 in all cases).

Day number (starting with the first day of observation as Day 1) was entered into the analysis to check that there was not an overall decrease in visitation rate over the course of the experiment. While there were differences between patches, the visitation rate to each did not decline over the course of the experiment (F₁,₂₃₉ = 0.966, P = 0.409), as may have been expected to happen due to the removal of some the bracts in the patches.

Principal component analysis (PCA) was performed on the morphological measures of all inflorescences to derive independent axes of variation among inflorescences. The PCA yielded five components of which the first two together accounted for 70% of the variance and reflected loadings similar to the PCs used in previous studies (Duffield et al 1993, González et al 1995, Hoggisson & Baskart 2004). The first (explaining 38.97% of the variance) mainly reflected the length of the inflorescence and the number and length of the bracts, and the second (explaining 7.29%) contrasted the number of flowers (positive) and the age of the inflorescence (negative). The first therefore reflected overall size (hereafter Size), and the second reflected morphological characteristics that closely predict the amount of nectar available (hereafter Quality) (Hoggisson et al 2006).
Using multiple regression analysis, it was found that the number of acceptances per inflorescence before the manipulation was positively related to Quality of inflorescences (G1,395 = 5.626, P < 0.001) but not their Size (G1,395 = 1.118, P = 0.264). However, the total number of inspections (acceptances + rejections) was related to both Size (G1,395 = 2.315, P = 0.023) and Quality (G1,395 = 4.225, P = 0.001), supporting the hypothesis that bees inspect inflorescences on the basis of display size but accept based on number of flowers and age (Heggs, Fairly & Barnard 2004, Heggs et al. 2006). After the manipulation, the number of inspections of manipulated inflorescences was not related to the Size (G1,395 = 1.228, P = 0.221), but only to the Quality (G1,395 = 4.404, P = 0.001), since the bees had been removed so the size had been reduced.

Two-way ANOVA with treatment and patch as factors showed that the change in the number of inspections was affected by the removal of bees (F1,392 = 11.649, P = 0.001); inflorescences that had their bracts removed were inspected less (a 25% decrease), and there was either no change or a slight increase for the controls. There was a significant difference between patches (F1,392 = 3.047, P = 0.022), but no interaction between patch and treatment (F1,392 = 1.538, P = 0.204), despite there being an increase of inspections of manipulated inflorescences on patch one (Fig. 1). The same analysis on each treatment showed that the change in number of acceptances was different between control and manipulated inflorescences (F1,392 = 4.853, P = 0.028), as was the change in the number of rejections (F1,392 = 7.668, P = 0.006), in that manipulated inflorescences experienced a fall in the number of acceptances and rejections (19%, 34% respectively) but controls did not.

Almost all spiders (91.9%) were found on inflorescences that had four or more bracts (Heggs, 2005, Reader et al. 2006), and pulled the bracts closed when they were waiting in ambush.

![Fig 1: The mean (+1 SE) change in the number of inspections by honeybee workers (Apis mellifera Linnaeus 1758 [Hymenoptera: Apidae]) per inflorescence (lavandula stoechas L) for each patch. Removal of the bracts caused a decrease in the number of inspections.](image-url)
To test whether the position of the bracts (open or closed) had an effect on bee behaviour, an inflorescence was said to be dangerous if it had more than four bracts and they were closed. After manipulation the number of inspections of inflorescences with closed bracts which were removed did not decrease, unlike the number of inspections of all other manipulated inflorescences (Fig 2). Two-way ANOVA of the change in the number of inspections against the two factors of danger and treatment showed that this interaction was not significant ($F_{1,35} = 0.366, P = 0.546$), which was perhaps because there were only 39 dangerous inflorescences (compared to 35 others).

![Diagram showing change in the number of inspections](image)

**Fig 2:** The mean (+1 SE) change in the number of inspections by honeybee workers (*Apis mellifera* Linnaeus 1758 [Hymenoptera: Apidae]) for lavender (*Lavandula angustifolia* L.) inflorescences that were (dangerous) or were not (as dangerous) able to conceal a spider for control (open bars) and treated (hatched bars) inflorescences.

Since the inspection process may involve an attempt to detect spiders, the risk of predation may affect the probability of acceptance once the inflorescence had been inspected, rather than the number of inspections. The change in the probability of acceptance was calculated as the difference between before and after the manipulation in the proportion of inspections that were acceptances. The change in the probability of acceptance suggested an interaction between predation risk and treatment, as only dangerous inflorescences whose bracts were removed experienced an increase after the manipulation (Fig 3). Hence, whilst there was no difference between non-dangerous control and manipulated inflorescences in the change in the probability of acceptance ($U = 6687.5, N_1 = 125, N_2 = 111, P = 0.631$), there was a difference between control and manipulated dangerous inflorescences, which was significant at the 1% level despite the small sample sizes ($U = 75, N_1 = 14, N_2 = 17, P = 0.077$). The probability of acceptance of inflorescences that were likely to contain a spider increased after the removal of bracts.
3.2 Experiment 2

Inflorescences in each treatment group did not differ in any of the morphological measures taken (KW, χ², p > 0.14). There were no differences between treatment groups before the application of treatments in the number of acceptances, rejections and ignoresses per inflorescence (KW, χ², p > 0.14).

In order to investigate whether the number of previous decisions affected whether an inflorescence was inspected, or whether it was accepted after inspection (binary variables), binary logistic regression was performed entering the total number of acceptances, rejections and ignoresses to each decision in a twenty-minute period and all morphological measures of inflorescences. Only the second half of decisions within the twenty-minute period before the application of treatments were used as the response variables so there would be no effect of treatments and to reduce inaccuracy in visiting observations due to the time since the start of the observation period. The probability of inspecting an inflorescence was not affected by the previous number of acceptances (G₁, 11 = 1.288, P = 0.264), rejections (G₁, 11 = 1.733, P = 0.194), or ignoresses (G₁, 11 = 0.244, P = 0.807), but only by the number of flowers (G₁, 11 = 3.467, P = 0.001). Similarly, the probability of accepting an inflorescence (once it had been inspected) was not affected by the previous number of acceptances (G₁, 11 = 0.164, P = 0.657, Fig 4), rejections (G₁, 11 = 0.037, P = 0.972), or ignoresses (G₁, 11 = 0.426, P = 0.657), but only by the number of flowers (G₁, 11 = 4.752, P = 0.001), suggesting that previous acceptances, and hence scent marks, play little role in foraging on Lavandula.

The total number of inspections and ignoresses was much lower after the manipulation (inspected before: 666, inspected after: 697, ignored before: 106, ignored after: 68), probably as the nectar production of inflorescences deteriorated overall.
The decrease in the number of inspections for each treatment tended to be greater (though not significantly) for Treatments 2 and 3, where bracts were removed ($F_{1,15} = 1.04$, $P = 0.378$). There was, however, a significant difference between treatments in the change in the number of ignores ($KW_{1} = 9.373$, $P = 0.025$): only Treatment 2 increased. The change in the proportion of the number of inspections to ignores was strongly significant ($KW_{1} = 14.017$, $P = 0.003$): inflorescences whose bracts were removed were ignored proportionally more (as found in experiment one), but there was no effect of closing the bracts (Fig 5). However, not all inflorescences had four bracts of equal size, and many that had four bracts had a large pair and smaller pair. Such asymmetrical bracts would be unable to conceal a spider, even when closed, so bees may not avoid them. Inflorescences that had four large bracts were separated from the others in analysis, but there was still no significant interaction with treatment in the change in the number of inspections ($F_{1,15} = 1.203$, $P = 0.312$), and no difference for the closed treatment alone in the change in proportion of inspections ($KW_{1} = 1.192$, $P = 0.273$): if anything, bees were more likely to inspect inflorescences with four equal-sized bracts when they were closed (Fig 6).

There was no difference between groups in the change in the number of acceptances ($KW_{1} = 1.733$, $P = 0.62$) or rejections ($KW_{1} = 2.273$, $P = 0.518$). There was no difference in the change in the probability of acceptance between groups ($KW_{1} = 0.815$, $P = 0.846$); all inflorescences were rejected more frequently after the treatment (Fig 7).
Fig 5: The mean (± 1 SE) change in the proportion of inspections by honeybee workers, *Apis mellifera* Linnæus 1758 [Hymenoptera: Apidae] for the four treatment groups of experiment two. Lavender (*Lavandula stoechas* L.) inflorescences whose bracts were removed were inspected less, but closure of the bracts had no effect.

Fig 6: The mean (± 1 SE) change in the proportion of inspections by honeybee workers, *Apis mellifera* Linnæus 1758 [Hymenoptera: Apidae] for the four treatment groups of experiment two. Lavender (*Lavandula stoechas* L.) inflorescences with four large bracts (hatched bars) from the others (open bars). The size of the bracts had no effect.
Fig 7: The mean (± 1 SE) change in the probability of acceptance by honeybee workers, *Apis mellifera* (Hymenoptera: Apidae) for the four treatment groups in experiment two. All lavender (*Lavandula stoechas L.* ) inflorescences were rejected more but there were no differences between groups.

4 Discussion

The results suggest that, as expected from other studies [DUFTFIELD et al 1993, HERRERA 1997, HOGGISON & BARNARD 2004, HOGGISON et al 2006], the removal of bracts did have an effect on visitation rate. The present study shows that the effect on visitation rate to bushes or half-bushes observed previously [HERRERA 1997] is also observed when bracts are removed from inflorescences randomly within bushes. That is, the effect on the attractiveness of inflorescences acts even at short distances between inflorescences on the same plant. One possibility that could have affected the results was that damaged inflorescences smell differently to others, and if the damage released some repellent chemicall this could have influenced the bees’ behaviour in the observed direction. This possibility should be tested in future work.

The use of a tree decision classification (accept, reject, ignore) enabled the novel finding that this decrease was the same for both the number of acceptances and the number of rejections, suggesting that the removal of bracts means that the bee will be less likely to inspect the inflorescence. This finding ties in well with earlier work [HOGGISON et al 2006] suggesting that display size does not affect whether the bees accept after inspecting, but does strongly influence which inflorescences bees inspect, either because bees avoid small inflorescences or detect them less frequently. The bracts are an advertisement, but do not necessarily provide an honest indication of nectar content [HOGGISON et al 2006], so, when closer, the bee uses the morphotypical characters that are good predictors of nectar production: age and number of flowers, or some correlate thereof (such as colour). This hypothesis is supported by the fact that the size of inflorescences before manipulation was correlated with the number of inspections, but not the number of acceptances.
Work on the visual spatial perception of bees has shown that their colour vision resolu-
tion is poor [Gurara, VOORWEBER, KEVIN et al. 1993]; bees have only been shown to be capable of
detecting an 83mm circle from a distance of 120mm [Land 1997]. Since inflorescences
are densely clustered in this study system, bees are rarely further than a few centimetres
from several inflorescences, so they are likely to be capable of judging the size of
inflorescences. However, since the judgement of age and number of flowers probably requires comparison
of the amount of flower colour to bract colour, bees probably need to be closer (inspect) to
the inflorescence in order to make a final decision.

Removal of the bracts does not necessarily make the inflorescence less attractive, but
the removal of the bracts could have caused the inflorescence merely to be less conspicuous
to searching bees so they were less likely to detect it. An alternative, but not mutually exclu-
sive, explanation is that the bees actively ignored inflorescences with no terminal bracts. A
lack of bracts is only usually seen in immature or very old inflorescences, neither of which
produces much nectar [Hossono et al. 2006]. Hence bees could learn by negative associa-
tion that a lack of bracts indicates low reward and therefore ignore those inflorescences.
It is interesting to note that the visitation rate to inflorescences with closed bracts did not
fall as much as that to inflorescences with half their bracts removed, despite the fact that
the reduction in visible bract area would be similar. This suggests that it is not only display
size that affects inspection rate, and other factors affect the attractiveness of inflorescences,
which may include colour and flower scent.

The finding that bees did not avoid visiting inflorescences that had recently been visited
by a honeybee suggests that scent marking, if it occurs in Lavandula, does not significantly
affect foraging decisions. Scent marking may be inefficient on an inflorescence bearing plant
that has many bees foraging on it simultaneously, because not all flowers on a particular
inflorescence are probed by bees, so a scent mark may not provide an accurate cue to the
total nectar content of the inflorescence.

The results suggest that honeybees do not avoid inflorescences that have closed bracts,
Despite the fact that closed bracts are normally an indication that a crab spider is present.
The earlier finding that the probability of accepting an inflorescence is lower if it contains a
spider [Kanoa et al. 2006] is thus unlikely to be due to a closed bract cue. Bees are unlikely
to have the chance to learn the association between closed bracts and the presence of a spider,
because spiders frequently move between inflorescences and leave behind closed bracts.
Therefore a significant proportion of inflorescences with closed bracts would not actually
contain a spider, so it would be non-adaptive to avoid them all. It is likely that bees never
acquire the association, since every acceptance of an inflorescence with closed bracts that
does not contain a spider would weaken the association. However, in Experiment I, bees
appeared to avoid closed bracts. The difference between Experiments I and II was that, in
Experiment I, bracts had been closed by spiders, rather than by glue as in Experiment II.
Bees in this case use some direct mechanism for avoiding spiders, perhaps the detection
of silk, and this is currently the subject of further work.

5 References

Chittka, L. (2001): Camouflage of predatory crab spiders on flowers and the colour perception
Deutschland.
Unravelling the internal world of 'simple' creatures, whose neuron number several orders magnitude fewer than our own, cannot fail to tempt those looking for a suitable starting block for understanding how neural processing brings about complex behavioural phenomena. What this book highlights, however, is that evolution has had millennia to shape seemingly straightforward nervous machinery into complex, multi-level systems. The complex behavioural algorithms, abstraction and decision-making processes, planning behaviours, and integration of unique experiences presented here are a far cry from the traditional but clearly outdated view of invertebrates as simple reflex machines. Studying creatures so far removed from ourselves as a jumping spider, or a crayfish, or a butterfly, hence offers the dual attractions of providing both the opportunity to directly relate behaviour to underlying nervous systems, and an intriguing glimpse into the astounding creativity of evolution.

'Complex worlds from simpler nervous systems' approaches this task through a range of compelling stories of which each aims to explain aspects of how signal processing creates the internal world, or Umwelt, of a 'simple' organism. In doing so, the authors present a tantalising range of material which touches upon refreshingly few standard model systems, instead exploring the behaviour of a diverse range of small creatures which have traditionally achieved rather less of the limelight.

The book's title is somewhat misleading, in that most chapters focus on sensory systems rather than nervous systems as a whole, and furthermore, on visual sensory systems rather than other modalities. This is reflected in the titles of the book's three sections: Creating Visual Worlds: Abstract Representations and Algorithms, introduced by FR PRUTT; Enhancing the Visual Basics: Using Color and Polarization, introduced by COGON; and Out of Sight: Creating Extravisional Worlds, introduced by VAN DER MAAREL. However, several of these contributions provide excellent reviews of their subject area, and would appeal to those with a wider interest than vision alone. Strong chapters on acoustic processing in grasshoppers (van der MAAREL et al.), mechanoreception in cockroaches and crickets (COMER & LEUNG), and honeybee cognition (GUENIN & BONNEMASSER) also go some way towards redressing this imbalance. Of the rest, a particular highlight is a chapter by HAY and JACKSON, which successfully immerses the reader in the perceptual world of the jumping spider gomphids.

Together, these stories will provide an informative read for anyone interested in the boundaries and possibilities of neural systems of 'simple' and 'advanced' creatures alike. As PRUTT points out in his introduction, in these little animals, we can see the beginnings of the complex intellectual processes that define us as human.