

CORRECTION

Visual acuity trade-offs and microhabitat-driven adaptation of searching behaviour in psyllids (Hemiptera: Psylloidea: Aphalaridae)

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There was an error published in *J. Exp. Biol.* **218**, 1564-1571.

The images in Fig. 5 were mislabelled. The correct version is given below.

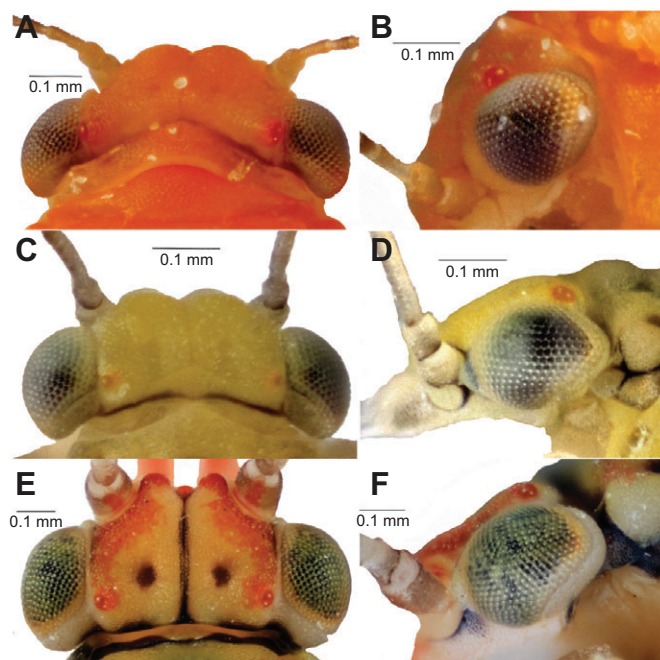


Fig. 5. Images of psyllid eyes in dorsal and lateral views. (A,B) *Ctenarytaina bipartita*, (C,D) *A. bundoorensis* and (E,F) *G. brimblecombei*.

The authors apologise for any inconvenience this may have caused.

Table 1. Searching behaviours of four psyllid species tested in the presence of colour stimuli

Species	Distance traversed (cm)		Number of turns		Searching duration (s)	
	Mean±s.e.	Median	Mean±s.e.	Median	Mean±s.e.	Median
<i>C. bipartita</i>	9.8±0.6 ^a	7.9	4.6±0.4 ^a	4.0	104.2±10.2 ^a	75.8
<i>C. eucalypti</i>	10.9±0.6 ^{a,b}	9.4	4.3±0.3 ^a	4.0	103.5±8.3 ^a	91.2
<i>A. bundoorensis</i>	12.6±1.1 ^b	9.3	7.2±0.8 ^b	5.0	242.8±31.8 ^b	179.6
<i>G. brimblecombei</i>	42.2±3.9 ^c	33.7	36.0±4.0 ^c	25.0	424.9±62.3 ^b	181.3
Kruskal–Wallis	$H_{3,245}=91.38, P<0.001$		$H_{3,255}=101.22, P<0.001$		$H_{3,252}=23.45, P<0.001$	

Different letters indicate different levels of statistical significance from Mann–Whitney pair-wise comparisons.

Y-maze experiments was not influenced by the size of the stimuli. This concurs with previous work that demonstrated a pronounced preference for the ‘red’ stimulus over achromatic stimuli of higher intensity contrast with the background and suggests that psyllid innate colour responses are consistent independent of stimulus size (Farnier et al., 2014).

Morphological measurements of psyllid eyes also revealed prominent differences. Predictably, *G. brimblecombei*, the largest species (2.5–3.1 mm body length), has the greatest number of ommatidia and the largest ommatidial diameter of the four species. Likewise, *C. eucalypti*, the larger of the two *Ctenarytaina* species (2.5–2.8 mm), has more and larger ommatidia than *C. bipartita* (1.2–1.8 mm). However, the absence of significant differences in the eye parameter of *C. eucalypti*, *C. bipartita* and *G. brimblecombei* suggests that inter-specific differences in eye morphology are primarily size related. This is consistent with positive correlations between body size, number of ommatidia and inter-ommatidial angle as well as conserved eye parameters between species of bees of varying size, i.e. isometric scaling (Jander and Jander, 2002). Interestingly, our results seem to differ from previous studies conducted on aphids. Döring and Spaethe (2009) found no correlation between the number of ommatidia, inter-ommatidial angle and body length in aphids, i.e. allometric scaling. They concluded that light sensitivity might be a limiting factor for aphids, which therefore prioritize facet diameter to the detriment of spatial resolution (Döring and Spaethe, 2009). Although our study focused on a limited number of species, there is no indication of a similar compromise between light sensitivity and visual acuity in psyllids. On the contrary, measurements of the eyes of *A. bundoorensis* provide an example of a trade-off where light sensitivity is sacrificed in favour of visual acuity. Despite its small body length (1.7–2.4 mm), *A. bundoorensis* possesses a relatively large number of ommatidia; it has more ommatidia than either *C. eucalypti* or *C. bipartita*. The large number of ommatidia in this species is associated with small facet diameter. The existence of such a trade-off is further supported by a significantly smaller eye parameter than that found in the other species. Similar trade-offs were also observed in a limited number of aphid species by Döring and Spaethe (2009), who attributed such adaptation to the greater mobility of these species in response to predation (e.g. insectivorous birds) and the subsequent necessity to return to the host. Escape response is unlikely to explain this trade-off in psyllids as *G. brimblecombei* is arguably the species most exposed to predation as a consequence of its larger size and the sugary lerps the nymphs build, which birds consume (Paton, 1980; Pereira et al., 2012; Steinbauer et al., 2015). However, *A. bundoorensis* is unique because it oviposits and feeds on different plant modules, i.e. feeding occurs on leaves and oviposition occurs in crevices on stems. Such resource preferences are associated with higher mobility than evident in the other species.

Our observations of psyllid searching behaviours revealed significant differences between species, which appear to be

influenced by their microhabitat preferences. For instance, the sedentary bud-dwelling species *C. eucalypti* and *C. bipartita* (Steinbauer, 2013) exhibit similar patterns characterized by short unidirectional paths, consistent with searching acropetally along stems towards apical buds. Likewise, *A. bundoorensis*, which does not occupy protected microhabitats (Taylor et al., 2013), exhibits similar unidirectional movements. However, longer distances traversed and prolonged searching durations seem to reflect differences in the utilization of host ‘architecture’ of this species, which, unlike the bud-dwelling species, frequently moves between growing branches and young leaves to find either feeding or oviposition sites. The searching behaviour of *G. brimblecombei* differed markedly from that of the three other species, with intense and protracted sinuous movements possibly in accordance with the utilization by this species of the surface of flat leaves for feeding and oviposition.

In the light of these findings and of the apparent linkage of psyllid colour preference and leaf spectral characteristics, we suggest psyllids have sufficient visual acuity to locate different modules within the canopies of their hosts. Generally, our results suggest that greater acuity is associated with a greater need for higher mobility. The fact that *A. bundoorensis*, for which morphological trade-offs favouring acuity over light sensitivity were found, spends a substantial amount of time searching branches and stems for oviposition sites supports such an hypothesis. In contrast, more sedentary bud-dwelling species seem to be attracted to brighter stimuli, suggesting constant intensity-dependent responses to visual stimuli. In the latter instance, simple phototactic responses appear ideal for these species to orientate toward the sun-lit apical ends of branches.

MATERIALS AND METHODS

Psyllids

Glycaspis brimblecombei Moore (from *Eucalyptus camaldulensis* Dehnh.) and *Ctenarytaina bipartita* (Burckhardt et al., 2013) (from *E. kitsoniana* Maiden) were collected from populations on the Bundoora Campus of La Trobe University and at Hoddle Range (State of Victoria, Australia), respectively. *Ctenarytaina eucalypti* (Maskell) were collected from a *Eucalyptus globulus* Labill. plantation at Clonbinane. *Anoeconeossa bundoorensis* Taylor and Burckhardt were taken from a glasshouse colony maintained on potted *E. camaldulensis*. Experiments were conducted between May 2012 and October 2014 during the austral spring–summer, which corresponds to the peak of psyllid activity in the field. Important aspects of the feeding and oviposition behaviours of our model species are available in Moore (1961), Morgan (1984), Burckhardt et al. (2013) and Taylor et al. (2013).

Y-maze bioassay

The object detection threshold of different psyllid species was tested in a V-shaped maze, which was adapted from a conventional Y-shaped maze previously used to test free-flying insects (Giurfa et al., 1996, 1997; Reisenman and Giurfa, 2008) and, more recently, walking insects (Yilmaz et al., 2014; de Brito Sanchez et al., 2015). Experiments were conducted in a controlled laboratory chamber surrounded by white fabric curtains and illuminated from the top by four Philips Master TLSHE slimline 28W/865UV+ daylight

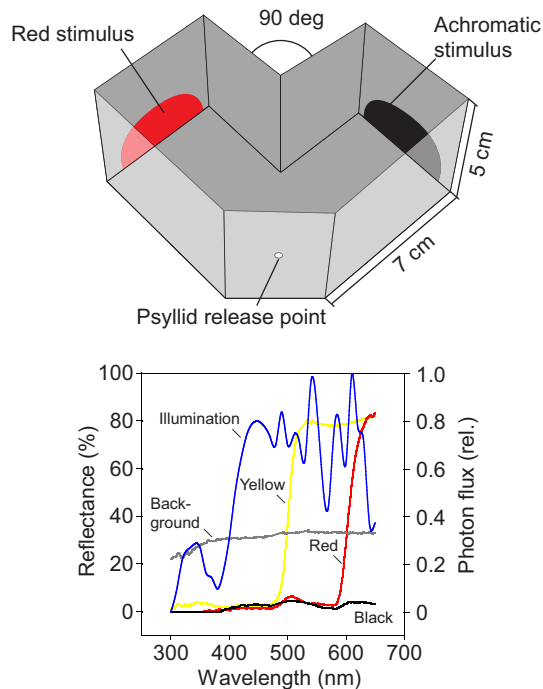


Fig. 4. Schematic description of the Y-maze. The maze was composed of two arms at the end of which pre-printed colour stimuli of varying size were applied. One psyllid at a time was released at the white dot in the middle part of the maze located 7 cm from the end of each arm, and was allowed 10 min to orient and climb on one of the targets. Only the first choice was recorded. The number of 'successful' insects for each visual angle subtended by the stimuli tested was used to estimate the probability of an insect detecting the stimulus according to its size. Illumination and reflectance spectra of the background and the different stimuli used in the bioassay are represented in the inset.

fluorescent tubes (Philips, The Netherlands) with specially fitted high-frequency (1200 Hz) ATEC Jupiter EGF PMD2614–35 electronic dimmable ballasts. A sheet of UV-permitting Rosco216 white diffusion screen (Rosco, Munich, Germany) was used to diffuse the light in the chamber, providing a controlled illumination close to the spectral quality of natural illumination for insects (Dyer, 2006). The intensity of light in the arena was measured with a Fieldscout Quantum lightmeter (Spectrum Technologies, Inc., USA) and kept constant at $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($\sim 5180 \text{ lx}$). The illumination under the screen to which psyllids were exposed is shown in Fig. 4. The maze was assembled on a glass pane, allowing its surface to be cleaned with a 70% ethanol solution after every insect tested, to eliminate any possible olfactory cue left behind. A sheet of non-fluorescent cardboard (160 gsm; K. W. Doggett, Melbourne, Australia) coloured in grey using a Xerox 4350 printer (colour edited using Microsoft Powerpoint custom RGB settings; R: 166, G: 166, B: 166; $\sim 35\%$ reflectance) was placed under the glass pane and used to construct the maze walls (see Fig. 4). Coloured semi-circles, positioned at the end of the arms, were used as stimuli. Four stimulus sizes (semi-circles of different diameter) determined using Eqn 1 were tested to assess the psyllids' ability to perceive and orientate to the stimuli for horizontal visual angles of 35, 15, 10 and 5 deg:

$$D = 2(\tan \alpha \times l), \quad (1)$$

in which D is the horizontal diameter of the stimulus, α is the subtended visual angle tested and l is the distance between the release point and the target.

The horizontal directionality of the field of vision appears to be the most relevant to the psyllid's line of approach from a linear shape such as a stem or leaf pedicel as it attempts to climb onto a given plain coloured surface like a leaf. In practice, psyllids did not climb onto colour stimuli unless they intersect with the horizontal plane of the bioassay arena. Stimulus sizes were chosen based on the visual angles of stimuli used in previous experiments (for the largest stimuli) and arbitrarily decreased to sizes at which limits of psyllid

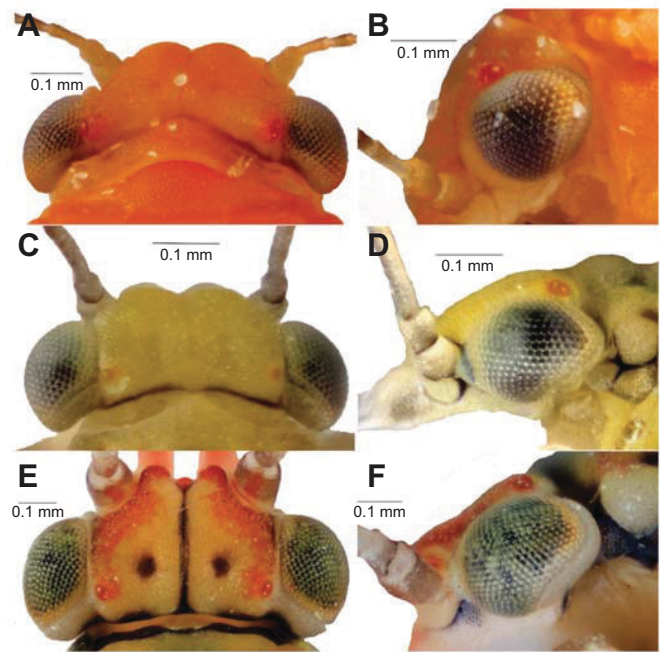


Fig. 5. Images of psyllid eyes in dorsal and lateral views. (A,B) *Anoeconeossa bundoorensis*, (C,D) *G. brimblecombei* and (E,F) *C. bipartita*.

visual performance could be observed. The selection of stimulus colours was based on the innate preferences reported in Farnier et al. (2014). Red stimuli (Microsoft RGB settings: R: 255, G: 0, B: 0, see Fig. 4 for reflectance spectra) were presented to *G. brimblecombei* and *A. bundoorensis* whereas yellow stimuli (R: 255, G: 255, B: 0) were presented to *C. eucalypti*. In addition to the preferred coloured stimulus, a dark (black), achromatic stimulus (i.e. G45; R: 45, G: 45, B: 45), which was previously shown to attract *A. bundoorensis* and *G. brimblecombei* in the absence of coloured stimuli, of the same size was presented in the other arm as an alternative choice.

Bioassays were conducted as follows: 50 insects (25 males and 25 females) of each of *C. eucalypti*, *A. bundoorensis* and *G. brimblecombei* were tested individually and only once. Psyllids were anaesthetized at -18°C for 3 min and then placed on the white dot in the maze, which was positioned equidistant (i.e. 7 cm) from the ends of the arms of the maze. Psyllids were allowed to orientate in the maze for 10 min and any individual that did not make a choice in that time was excluded. Only insects orientating and subsequently climbing onto a target were recorded as having perceived a stimulus. Psyllids choosing to climb onto any other part of the maze or on the background (including background areas located next to the stimuli) were considered as not having completed the task. Whilst this is a conservative criterion for determining visual angle, it is most ecologically relevant, as the insect must use its vision to correctly find the target. In order to compensate for the absence of training, data were normalized to account for the noise caused by between-species differences at cooperating with the task. Normalization consisted of the calculation of a response score ranging between 0 and 1 relative to the highest number of 'finders' of each species at any visual angle tested. Our normalization allows us to take into consideration differences in the magnitude of responses exhibited by different psyllid species and to estimate detection thresholds in a way comparable to that for other model insects such as bees and butterflies. The orientation of stimuli was changed after every four insects to preclude position effects. Different species and sexes were tested in separate mazes. Nominal logistic regressions revealed no influence of sex on psyllid responses for all species. Therefore, male and female responses were pooled for statistical analyses. Fisher's exact tests were used to determine the influence of stimulus size on psyllid detection performance and to compare the choice of the red or dark stimulus for different stimulus sizes.

Morphometric measurements

Psyllids that had been preserved in 70% ethanol were point-mounted on card using entomological glue (Australian Entomological Supplies,

Bangalow, NSW, Australia) before being photographed using a Canon EOS 7D digital camera fitted with a LU Plan Fluor 10×/0.30A lens (Nikon, Japan) on a Visionary Digital BK Imaging System (Visionary Digital, USA). Individual images were collated with Zerene automontage software version 4.02 (Synchroscope, Cambridge, UK). The eyes of eight individuals were photographed for each of the four species in both dorsal and lateral views (Fig. 5). Contrast and sharpness were adjusted using Adobe Photoshop to optimize the definition of the structure of the eyes. Measurements were taken using ImageJ software. The inter-ommatidial angle and the angle subtended by the eye were measured using the dorsal view following the same procedure as in Döring and Spaethe (2009) and Yilmaz et al. (2014). The number of ommatidia on each eye was counted directly using the lateral view. The same view was used to measure the surface area of both eyes. The ommatidial diameter was calculated by drawing a segment across 'in-focus' ommatidia in the lateral view and dividing the length of the segment by the number of ommatidia crossed. The measurement of the ommatidial diameter was performed on both eyes and repeated three times. The eye parameter was calculated by multiplying the inter-ommatidial angle by the mean ommatidial diameter (Snyder, 1979). Data for each measurement were tested for normality and analysed using ANOVA test of variance followed by Tukey's *post hoc* tests (95%) for pairwise comparisons. The number of ommatidia and surface area of the ommatidia were analysed using non-parametric Kruskal–Wallis tests followed by Mann–Whitney tests for pair-wise comparisons.

Psyllid movement tracking

Psyllid movement was recorded in different experiments conducted under similar environment and illumination conditions as those described for the Y-maze experiments. Psyllids were placed in arenas formed by a 15.5 cm diameter glass Petri dish positioned above a grey coloured cardboard sheet. The inner walls of the dish were encircled with a 5 cm wide strip of the same grey cardboard (160 gsm; K. W. Dogget; colour edited, R: 166, G: 166, B: 166; ~35% reflectance) on which four 4×4 cm colour stimuli were preprinted (no use of glue) and arranged opposite one another. Psyllids were placed in the centre of the arena and allowed to search until they eventually climbed onto one of the stimuli. Psyllid movements were recorded (at 30 frames s⁻¹) with a video camera (540TVL high resolution, EVO series, Pacific Communications, Australia) positioned approximately 60 cm above the arena and connected to a digital video recorder (PDRH-800e, Pacific Communications). Footage length for each insect was reduced using Windows Movie Maker (Microsoft) to only include sequences where active searching characterized by steady and continuous motion was evident. Psyllid positions were digitized using digitizing software (Hedrick, 2008) in MATLAB R2013a (MathWorks Inc.). The *x–y* coordinate data were then used to summarize searching behaviour, including search duration, distance traversed and number of turns defined by deviations exceeding a 30 deg angle from the initial trajectory, using custom-written functions in Matlab R2013a (R. Peters, La Trobe University). Psyllid searching behaviour was compared in the presence of three colour stimuli as described in Farnier et al. (2014). As data for distance traversed, duration searching and number of turns failed normality tests, non-parametric Kruskal–Wallis tests followed by multiple Mann–Whitney tests for pairwise comparisons were used to compare species' responses.

Acknowledgements

We thank Ms Renae Forbes for helping with the acquisition of searching behaviour data and Mr Rob Evans for helping to maintain plants supporting our psyllid colonies.

Competing interests

The authors declare no competing or financial interests.

Author contributions

K.F. designed, conducted the experiments, analysed the data and wrote the manuscript. A.G.D. provided equipment for the behavioural assays and contributed to data interpretation and analyses and the writing of the manuscript. G.S.T. provided the equipment and guidance for the acquisition of close-up high-resolution photographs of psyllid eyes. R.A.P. supplied equipment, wrote the program for the tracking of insect movement and contributed to writing the

manuscript. M.J.S. provided funding and guidance, and contributed to the writing of the article.

Funding

The research was funded by an Australian Research Council (ARC) Future Fellowship [FT100100199] to M.J.S. with associated Australian Postgraduate Award (APA) scholarship with top-up from La Trobe University to Kevin Farnier and an ARC Queen Elizabeth II (QEII) Research Fellowship [DP0878968] to A.G.D.

References

- Austin, A. D., Yeates, D. K., Cassis, G., Fletcher, M. J., La Salle, J., Lawrence, J. F., McQuillan, P. B., Mound, L. A., Bickel, D. J. and Gullan, P. J. (2004). Insects 'down under'—diversity, endemism and evolution of the Australian insect fauna: examples from select orders. *Aust. J. Entomol.* **43**, 216–234.
- Avarguès-Weber, A., d'Amaro, D., Metzler, M. and Dyer, A. G. (2014). Conceptualization of relative size by honeybees. *Front. Behav. Neurosci.* **8**, 80.
- Brennan, E. B. and Weinbaum, S. A. (2001). Psyllid responses to colored sticky traps and the colors of juvenile and adult leaves of the heteroblastic host plant *Eucalyptus globulus*. *Environ. Entomol.* **30**, 365–370.
- Briscoe, A. D. and Chittka, L. (2001). The evolution of color vision in insects. *Annu. Rev. Entomol.* **46**, 471–510.
- Bukovac, Z., Dorin, A. and Dyer, A. (2013). A-bees see: a simulation to assess social bee visual attention during complex search tasks. In *Advances in Artificial Life, ECAL*, vol. 12, pp. 276–283.
- Burckhardt, D., Farnier, K., Queiroz, D. L., Taylor, G. S. and Steinbauer, M. J. (2013). *Ctenarytaina bipartita* sp. n. (Hemiptera, Psylloidea), a new eucalypt psyllid from Southeast Australia. *Zootaxa* **3613**, 589–596.
- Chittka, L. and Tautz, J. (2003). The spectral input to honeybee visual odometry. *J. Exp. Biol.* **206**, 2393–2397.
- de Brito Sanchez, M. G., Serre, M., Avarguès-Weber, A., Dyer, A. G. and Giurfa, M. (2015). Learning context modulates aversive taste strength in honey bees. *J. Exp. Biol.* **218**, 949–959.
- de Ibarra, N. H., Vorobyev, M. and Menzel, R. (2014). Mechanisms, functions and ecology of colour vision in the honeybee. *J. Comp. Physiol. A* **200**, 411–433.
- de Queiroz, D. L., Burckhardt, D. and Majer, J. (2012). Integrated pest management of eucalypt psyllids (insecta, hemiptera, psylloidea). In *Integrated Pest Management and Pest Control – Current and Future Tactics* (ed. M. L. Larramendy and S. Soloneski), pp. 385–412. INTECH Open Access Publisher.
- Döring, T. F. and Chittka, L. (2007). Visual ecology of aphids—a critical review on the role of colours in host finding. *Arthropod Plant Interact.* **1**, 3–16.
- Döring, T. F. and Spaethe, J. (2009). Measurements of eye size and acuity in aphids (Hemiptera: Aphididae). *Entomol. Gen.* **32**, 77–84.
- Döring, T. F., Kirchner, S. M., Skorupski, P. and Hardie, J. (2011). Spectral sensitivity of the green photoreceptor of winged pea aphids. *Physiol. Entomol.* **36**, 392–396.
- Dyer, A. G. (2006). Bumblebees directly perceive variations in the spectral quality of illumination. *J. Comp. Physiol. A* **192**, 333–338.
- Dyer, A. G., Spaethe, J. and Prack, S. (2008). Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *J. Comp. Physiol. A* **194**, 617–627.
- Dyer, A. G., Paulk, A. C. and Reser, D. H. (2011). Colour processing in complex environments: insights from the visual system of bees. *Proc. R. Soc. B Biol. Sci.* **278**, 952–959.
- Farnier, K., Dyer, A. G. and Steinbauer, M. J. (2014). Related but not alike: not all Hemiptera are attracted to yellow. *Front. Ecol. Evol.* **2**, 67.
- Galizia, G., Eisenhardt, D. and Giurfa, M. (2011). *Honeybee Neurobiology and Behavior: A Tribute to Randolph Menzel*. Heidelberg: Springer Science & Business Media.
- Giurfa, M., Vorobyev, M., Kevan, P. and Menzel, R. (1996). Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *J. Comp. Physiol. A* **178**, 699–709.
- Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. and Menzel, R. (1997). Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *J. Comp. Physiol. A* **180**, 235–243.
- Grafton-Cardwell, E. E., Stelinski, L. L. and Stansly, P. A. (2013). Biology and management of Asian citrus psyllid, vector of the Huanglongbing pathogens. *Annu. Rev. Entomol.* **58**, 413–432.
- Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.
- Hodkinson, I. D. (2009). Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): a global synthesis. *J. Nat. Hist.* **43**, 65–179.
- Hollis, D. (2004). *Australian Psylloidea Jumping Plantlice and Lerp Insects*. Canberra: Australian Biological Resources Study (ABRS).
- Jander, U. and Jander, R. (2002). Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct. Dev.* **30**, 179–193.
- Kelber, A. (2005). Alternative use of chromatic and achromatic cues in a hawkmoth. *Proc. R. Soc. B Biol. Sci.* **272**, 2143–2147.

- Kelber, A. and Osorio, D.** (2010). From spectral information to animal colour vision: experiments and concepts. *Proc. R. Soc. B Biol. Sci.* **277**, 1617-1625.
- Kemp, D. J., Herberstein, M. E., Fleishman, L. J., Endler, J. A., Bennett, A. T. D., Dyer, A. G., Hart, N. S., Marshall, J. and Whiting, M. J.** (2015). An integrative framework for the appraisal of coloration in nature. *Am. Nat.* **185**.
- Kinoshita, M., Shimada, N. and Arikawa, K.** (1999). Colour vision of the foraging swallowtail butterfly *Papilio xuthus*. *J. Exp. Biol.* **202**, 95-102.
- Kirchner, S. M., Döring, T. F. and Saucke, H.** (2005). Evidence for trichromacy in the green peach aphid, *Myzus persicae* (Sulz.) (Hemiptera: Aphididae). *J. Insect Physiol.* **51**, 1255-1260.
- Kirschfeld, K.** (1976). The resolution of lens and compound eyes. In *Neural Principles in Vision* (ed. F. Zettler and R. Weiler), pp. 354-370. Berlin: Springer.
- Land, M. F.** (1997). Visual acuity in insects. *Annu. Rev. Entomol.* **42**, 147-177.
- Land, M. F. and Chittka, L.** (2013). Vision. In *The Insects: Structure and Function* (ed. S. J. Simpson and A. E. Douglas), pp. 708-737. Cambridge: Cambridge University Press.
- Lehrer, M.** (1994). Spatial vision in the honeybee: the use of different cues in different tasks. *Vision Res.* **34**, 2363-2385.
- Lehrer, M. and Bischof, S.** (1995). Detection of model flowers by honeybees: the role of chromatic and achromatic contrast. *Naturwissenschaften* **82**, 145-147.
- Lehrer, M. and Srinivasan, M. V.** (1993). Object detection by honeybees: why do they land on edges? *J. Comp. Physiol. A* **173**, 23-32.
- Mellor, H. E., Bellingham, J. and Anderson, M.** (1997). Spectral efficiency of the glasshouse whitefly *Trialeurodes vaporariorum* and *Encarsia formosa* its hymenopteran parasitoid. *Entomol. Exp. Appl.* **83**, 11-20.
- Moericke, V.** (1955). Über die Lebensgewohnheiten der geflügelten Blattläuse (Aphidina) unter besonderer Berücksichtigung des Verhaltens beim Landen. *Z. Angew. Entomol.* **37**, 29-91.
- Moore, K.** (1961). Observations on some Australian forest insects. 6. Insects associated with *Eucalyptus saligna*, *E. acmenioides* and *Angophora intermedia*. In *Proceedings of the Royal Zoological Society of New South Wales*, pp. 87-95. Sydney.
- Morgan, F. D.** (1984). *Psylloidea of South Australia*. Adelaide: Govt. Printer.
- Nissinen, A. I., Haapalainen, M., Jauhainen, L., Lindman, M. and Pirhonen, M.** (2014). Different symptoms in carrots caused by male and female carrot psyllid feeding and infection by 'Candidatus Liberibacter solanacearum'. *Plant Pathol.* **63**, 812-820.
- Niven, J. E., Anderson, J. C. and Laughlin, S. B.** (2007). Fly photoreceptors demonstrate energy-information trade-offs in neural coding. *PLoS Biol.* **5**, e116.
- Paton, D.** (1980). The importance of manna, honeydew and lerp in the diets of honeyeaters. *Emu* **80**, 213-226.
- Pereira, J. M., Baldin, E. L. L., Soliman, E. P. and Wilcken, C. E.** (2012). Attractiveness and oviposition preference of *Glycaspis brimblecombei* Moore in *Eucalyptus* spp. *Phytoparasitica* **41**, 117-124.
- Reisenman, C. E. and Giurfa, M.** (2008). Chromatic and achromatic stimulus discrimination of long wavelength (red) visual stimuli by the honeybee *Apis mellifera*. *Arthropod Plant Interact.* **2**, 137-146.
- Snyder, A. W.** (1979). The physics of vision in compound eyes. In *Comparative Physiology and Evolution of Vision in Invertebrates* (H. Autrum), pp. 225-313. Berlin: Springer.
- Spaethe, J. and Chittka, L.** (2003). Interindividual variation of eye optics and single object resolution in bumblebees. *J. Exp. Biol.* **206**, 3447-3453.
- Srinivasan, M. V.** (2014). Going with the flow: a brief history of the study of the honeybee's navigational 'odometer'. *J. Comp. Physiol. A* **200**, 563-573.
- Srinivasan, M. V. and Lehrer, M.** (1988). Spatial acuity of honeybee vision and its spectral properties. *J. Comp. Physiol. A* **162**, 159-172.
- Stach, S., Benard, J. and Giurfa, M.** (2004). Local-feature assembling in visual pattern recognition and generalization in honeybees. *Nature* **429**, 758-761.
- Steinbauer, M. J.** (2013). Shoot feeding as a nutrient acquisition strategy in free-living Psylloids. *PLoS ONE* **8**, e77990.
- Steinbauer, M. J., Sinai, K. M. J., Anderson, A., Taylor, G. S. and Horton, B. M.** (2015). Trophic cascades in bell miner-associated dieback forests: quantifying relationships between leaf quality, psyllids and *Psyllaephagus* parasitoids. *Austral Ecol.* **40**, 77-89.
- Takeuchi, Y., Arikawa, K. and Kinoshita, M.** (2006). Color discrimination at the spatial resolution limit in a swallowtail butterfly, *Papilio xuthus*. *J. Exp. Biol.* **209**, 2873-2879.
- Taylor, G. S., Farnier, K., Burckhardt, D. and Steinbauer, M. J.** (2013). *Anoeconeossa bundoorensis* sp. n., a new psyllid (Hemiptera: Psylloidea) from *Eucalyptus camaldulensis* (Myrtaceae) from Southeast Australia. *Zootaxa* **3609**, 351-359.
- Telles, F. J., Lind, O., Henze, M. J., Rodríguez-Gironés, M. A., Goyret, J. and Kelber, A.** (2014). Out of the blue: the spectral sensitivity of hummingbird hawkmoths. *J. Comp. Physiol. A* **200**, 537-546.
- von Frisch, K.** (1967). *The Dance Language and Orientation of Bees*. Cambridge: Harvard University Press.
- Walker, P. W., Allen, G. R., Tegg, R. S., White, L. R. and Wilson, C. R.** (2014). The tomato potato psyllid, *Bactericera cockerelli* (Šulc, 1909) (Hemiptera: Trioziidae): a review of the threat of the psyllid to Australian solanaceous crop industries and surveillance for incursions in potato crops. *Aust. Entomol.*
- Wertlen, A. M., Niggebrügge, C., Vorobyev, M. and de Ibarra, N. H.** (2008). Detection of patches of coloured discs by bees. *J. Exp. Biol.* **211**, 2101-2104.
- Yen, A. L.** (2002). Short-range endemism and Australian Psylloidea (Insecta: Hemiptera) in the genera *Glycaspis* and *Acizzia* (Psyllidae). *Invertebr. Syst.* **16**, 631-639.
- Yilmaz, A., Aksoy, V., Camlitepe, Y. and Giurfa, M.** (2014). Eye structure, activity rhythms, and visually-driven behavior are tuned to visual niche in ants. *Front. Behav. Neurosci.* **8**, 205.