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**The eyes have it: dim-light activity is associated with the morphology of eyes but not antennae across insect orders**

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1 **Abstract**

2 The perception of cues and signals in visual, olfactory and auditory modalities underpins all animal  
3 interactions and provides crucial fitness-related information. Sensory organ morphology is under strong  
4 selection to optimise detection of salient cues and signals in a given signalling environment; the most  
5 well studied example being selection on eye design in different photic environments. Many dim-light  
6 active species have larger compound eyes relative to body size, but little is known about differences in  
7 non-visual sensory organ morphology between diurnal and dim-light active insects. Here, we compare  
8 the micromorphology of the compound eyes (visual receptors) and antennae (olfactory and mechanical  
9 receptors) in representative pairs of day- and dim-light- active species spanning multiple taxonomic  
10 orders of insects. We find that dim-light activity is associated with larger compound eye ommatidia  
11 and larger overall eye surface area across taxonomic orders but find no evidence that in dim-light active  
12 insects, morphological adaptations that enhance the sensitivity of the eye are accompanied by  
13 morphological traits of the antennae that may increase sensitivity to olfactory, chemical or physical  
14 stimuli. This suggests that the ecology and natural history of species is a stronger driver of sensory  
15 organ morphology than is selection for complementary investment between sensory modalities.

16 **Keywords:** antenna - compound eye - diurnal - nocturnal - photic environment - sensory ecology

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27 **Introduction**

28 Animals perceive information about their extrinsic environment, including the location and nature of  
 29 potential mates, food sources, shelter, or predators through a variety of modalities (e.g. light, odour,  
 30 sound). As efficiency is essential for biological fitness, the considerable energetic resources required  
 31 to develop and maintain elaborate sensory systems (Niven & Laughlin, 2008) mean that natural  
 32 selection is expected to favour sensory organs with morphology optimised to detect salient cues and  
 33 signals from the background information in the environment (Elgar, Zhang, Wang, Wittwer, Thi Pham,  
 34 Johnson, Freelance & Coquilleau, 2018; Endler, 1992).

35 With millions of years of a stable light/dark cycle, the photic environment is a consistent  
 36 selection pressure shaping the evolution of sensory structures. Indeed, sensory adaptations to the photic  
 37 environment in which an animal is active are well documented. For example, populations of Mexican  
 38 cave fish (*Astyanax mexicanus*) living in lightless caves no longer have functional eyes, while eyes are  
 39 retained in populations that remain on the surface (Dowling, Martasian & Jeffery, 2002). Similarly,  
 40 reduced investment in eyes is observed in arthropod troglotauna (cave-dwelling animals) including  
 41 crustacea (Christiansen, 2012; Hobbs III, 2012), cave-cricket (Lavoie, Helf & Poulson, 2007), leiodid  
 42 beetles (Friedrich, Chen, Daines, Bao, Caravas, Rai, Zagmajster & Peck, 2011; Peck, 1973) and dytiscid  
 43 beetles (Tierney, Langille, Humphreys, Austin & Cooper, 2018).

44 Many crepuscular (active during twilight) or nocturnal (active beyond astronomical twilight) –  
 45 collectively referred to as dim-light active – arthropods frequently have sensory adaptations specific to  
 46 their photic environment (Tierney, Friedrich, Humphreys, Jones, Warrant & Wcislo, 2017; Warrant &  
 47 Dacke, 2011; Warrant, 2006; Wcislo & Tierney, 2009). Arthropod compound eyes are composed of  
 48 ommatidia, each of which is an independent photoreceptive unit that distinguishes brightness and  
 49 colour. For example, compared with their closest diurnal relatives, the average ommatidia diameter is  
 50 greater in the compound eye of obligate dim-light foraging bees (order Hymenoptera, superfamily  
 51 Apoidea) (Jander & Jander, 2002; Wcislo & Tierney, 2009) and wasps (Hymenoptera: Mutillidae,  
 52 Polistinae, Vespinae) (Warrant, 2008), crepuscular or nocturnal *Myrmecia* ants (Hymenoptera:  
 53 Formicidae) (Greiner, Narendra, Reid, Dacke, Ribi & Zeil, 2007; Narendra, Reid, Greiner, Peters,

54 Hemmi, Ribi & Zeil, 2011), night-flying leafcutter ants of the genus *Atta* (Hymenoptera: Formicidae)  
55 (Moser, Reeve, Bento, Della Lucia, Cameron & Heck, 2004) and night-flying onitine dung beetles  
56 (Coleoptera: Scarabaeidae) (McIntyre & Caveney, 1998). Larger ommatidia capture more photons and  
57 can thus detect changes in luminance in dimmer light (Greiner et al., 2007; Jander & Jander, 2002;  
58 Land, 1997; Tierney et al., 2017). Consequently, low levels of ambient light should favour larger  
59 ommatidia diameter to improve visual sensitivity. Larger ommatidia are often accompanied by distinct  
60 arrangement of the internal structure of the compound eye (Land, 1997; Warrant, 2017) as well as  
61 physiological adaptations of the photoreceptors and of the neural circuitry involved in the processing  
62 of spatial and temporal visual information (Stöckl, Ribi & Warrant, 2016; Warrant, 2017).

63         While there appear to be consistent adaptations of insect compound eyes to dim-light activity,  
64 most studies are taxonomically limited to the Hymenoptera, Coleoptera and Lepidoptera. Furthermore,  
65 it is unclear how differences in compound eye morphology compare with differences in the sensory  
66 organs that insects use to detect odours and vibrations: the antennae. Selection pressures associated  
67 with dim-light activity may not only favour adaptations that increase the sensitivity to light but also  
68 adaptations that increase sensitivity to information in complementary modalities, such as odour and  
69 sound (provided that salient information is available in those modalities). For example, the nocturnal  
70 hawkmoth *Deilephila elpenor* (Lepidoptera: Sphingidae) preferentially uses olfactory rather than visual  
71 cues while the diurnal hawkmoth *Macroglossum stellatarum* shows the opposite preference (Balkenius,  
72 Rosén & Kelber, 2006). This behavioural difference is accompanied by differences in the abundance  
73 of types of antennal sensilla (Balkenius et al., 2006), which are the sensory hairs and pores on antennae  
74 that detect odours, vibrations, stretch, temperature, humidity and carbon dioxide (Chapman, 1982; Elgar  
75 et al., 2018). The density (number per unit area) of sensilla is an ecologically-relevant measure of  
76 resource investment in insect antennae, and is positively associated with the strength of both  
77 behavioural (Gill, van Wilgenburg, Macmillan & Elgar, 2013) and physiological (Spaethe, Brockmann,  
78 Halbig & Tautz, 2007) responses to olfactory stimuli. Differences in the abundance of antennal sensilla  
79 between the nocturnal bull ant *Myrmecia pyriformis* and similarly-sized diurnal ant species have also  
80 been documented (Ramirez-Esquivel, Zeil & Narendra, 2014), although the observed differences may

81 not be due solely to differences in the photic environment in which the ants are active (Ramirez-  
 82 Esquivel et al., 2014). Interestingly, the antennae of nocturnal fireflies (Coleoptera: Lampyridae) are  
 83 relatively shorter than those of their diurnal relatives (Stanger-Hall, Sander Lower, Lindberg, Hopkins,  
 84 Pallansch & Hall, 2018), although it is not known if this corresponds to differences in antennal sensilla  
 85 density.

86 In this study, we simultaneously assess differences in the morphology of the compound eyes  
 87 and antennae in representative pairs of diurnal and dim-light active species across multiple taxonomic  
 88 orders of Australian insects. We ask whether there are consistent eye and antennal adaptations to  
 89 behaviours in dim-light environments across taxonomic orders – specifically, is dim-light activity  
 90 consistently associated with greater ommatidia diameter, greater overall size (area) of the compound  
 91 eye and, as seen in moths (Balkenius et al., 2006) and bull ants (Ramirez-Esquivel et al., 2014), a greater  
 92 density of antennal sensilla? Consistent patterns would suggest that changes to information availability  
 93 in one sensory modality (e.g. vision) may not only favour morphological adaptations that increase the  
 94 sensitivity in that modality but also adaptations that increase sensitivity to information in  
 95 complementary modalities (e.g. olfaction). Alternatively, inconsistent investment into different sensory  
 96 modalities would indicate that they are typically independent of each other and primarily driven by the  
 97 ecology and natural history of the species/family rather than by complementary investment.

## 98 **Materials and Methods**

99 Compiling images of the eyes and antennae of a comprehensive sample of insects across taxonomic  
 100 orders and fitting this into a phylogenetic comparative framework is not possible without a complete  
 101 phylogeny of insects. Instead, we provide taxonomic generality by selecting 12 closely related pairs of  
 102 species that vary in the photic environment in which they are active for foraging and reproduction.  
 103 Thus, we compare a day-active (diurnal) and dim-light active (nocturnal and/or crepuscular) species in  
 104 each pair, with each species pair belonging to a different family and spanning six taxonomic orders of  
 105 insects (Table 1). We ensured that species within a pair overlapped in habitat type (e.g. temperate  
 106 forest) and geographic range. Two to six specimens of each species were obtained from Museum  
 107 Victoria (Melbourne, Victoria, Australia) or the Australian National Insect Collection (Commonwealth

108 Scientific and Industrial Research Organisation) for morphological analysis (Table 1); with the  
 109 exception of the velvet ants (Hymenoptera: Mutillidae), our species pairs were confined to Australian  
 110 taxa for sampling convenience and to provide continental consistency. As there are no nocturnal velvet  
 111 ants found in Australia, the nocturnal species used in our analysis is North American with the specimens  
 112 obtained from Utah State University (Utah, USA).

113 To image the sensory organs, each pinned uncoated specimen underwent low-vacuum scanning  
 114 electron microscopy (SEM) using a FEI Quanta 200F scanning electron microscope (10kV acceleration  
 115 voltage, spot size 2.0, 0.5 mBar pressure) at the Bio21 Advanced Microscopy Facility (Bio21 Institute,  
 116 The University of Melbourne, Victoria, Australia) (Halictidae specimens) or a Hitachi TM3030 Plus  
 117 tabletop scanning electron microscope (5kV acceleration voltage) at the Australian National Insect  
 118 Collection. The katydid (Orthoptera: Tettigoniidae) specimens were too large to be imaged using SEM  
 119 without removing the antennae from museum specimens, and instead underwent stereomicroscopy  
 120 (160x magnification) using a Leica M205 A fitted with a Leica DFC 500 camera at the Australian  
 121 National Insect Collection. Using the microscope images, we determined for each specimen: the  
 122 average diameter of the ommatidia of the compound eye (diameter of three ommatidium averaged;  $\mu\text{m}$ );  
 123 the average surface area of the compound eye ( $\text{mm}^2$ ); and the average density of each type of antennal  
 124 sensilla (number of sensilla in a given area of antenna; sensilla per  $\text{mm}^2$ ). Eye ommatidia size provides  
 125 information about sensitivity to visual information (Jander & Jander, 2002; Land, 1997; Warrant, 2017)  
 126 and antennal sensilla density is a behaviourally relevant indicator of sensitivity to olfactory and tactile  
 127 cues (Elgar et al., 2018; Gill et al., 2013; Spaethe et al., 2007).

128 We measured ommatidia from the anteromedial aspect of each compound eye (i.e. the  
 129 ommatidia that face directly in front of the insect), thereby accounting for potential differences in  
 130 ommatidia diameter between regions of the compound eye (Perl & Niven, 2016) and for potential  
 131 differences between taxa related to whether a species spends most of its time looking above (terrestrial  
 132 species) or below (aerial species). Antennal sensilla were identified and classified into three classes:  
 133 olfactory (detects airborne odours), contact chemosensory (detects chemicals on a surface across which  
 134 the antenna is palpated) and mechanosensory (responds to vibrations or mechanical deformation of the

135 sensilla) (Figure 1, Table 2). Pore-like sensilla were not consistently observed on antennae and were  
136 not included in this analysis. This is unlikely to have affected our assessment of olfactory,  
137 chemosensory or mechanosensory sensilla because pore-like sensilla are often predominantly  
138 thermoreceptors or hygrometers. We accounted for differences in sensilla density between antennal  
139 segments/regions for each taxonomic family, by imaging the sensilla on the most populated part of the  
140 antenna that was consistently observable: ventro-lateral side of the proximal antennomer of the antennal  
141 flagellum for Odonata; dorso-lateral surface of the antennal club for Scarabaeidae (Coleoptera); ventro-  
142 lateral side of the 10<sup>th</sup>-most distal antennomer for Sphingidae (Lepidoptera); and the dorso-lateral  
143 surface of the distal antennomer for all other specimens. Focusing on the antennal region for each taxon  
144 that is the most densely populated minimises the potential for underestimating the diversity of sensilla  
145 types possessed by a given taxon and maximises the behavioural relevance of our data, as sensilla  
146 density on the most populated section of antennae can be a behaviourally relevant indicator of olfactory  
147 sensitivity (Elgar et al., 2018; Gill et al., 2013). While the abundance and distribution of types of  
148 sensilla along the length of antennae may vary, it is unlikely to consistently differ between day active  
149 and dim-light active species and to thus introduce a bias in our results. Only undamaged eyes or  
150 antennae were imaged and analysed.

151 As body size is generally larger for dim-light active species compared with closely related  
152 diurnal bee species (Wcislo & Tierney, 2009), we obtained relevant measures of body size to account  
153 for the potential influence of body size allometry on ommatidia size (Jander & Jander, 2002; Schwarz,  
154 Narendra & Zeil, 2011; Smith, Palermo, Theobald & Wells, 2015) and antennal sensilla density  
155 (Spaethe et al., 2007). To obtain measures of body size, we either imaged the relevant body parts of  
156 the specimen under the scanning electron microscope or took digital images of the specimens using a  
157 Canon 6D DSLR with Canon EF-L 100mm f2.8 macro lens (Canon, Tokyo, Japan) with a ruler included  
158 as a scale. Body size was measured as average elytra length for the Coleoptera (Frank, Kehrli &  
159 Germann, 2007; Östman, 2005), as the ratio of average wing length to thorax length for the Diptera  
160 (Barker & Krebs, 1995), as head width just posterior to the compound eyes for the Hymenoptera  
161 (Boudinot & Fisher, 2013; Spaethe et al., 2007; Wild, 2007), as average forewing length for the

162 Lepidoptera (van Hook, Williams, Brower, Borkin & Hein, 2012) and Odonata (Johnson, Mantle,  
 163 Gardner & Backwell, 2013) and as average femur length for the Orthoptera (Whitman, 2008). All  
 164 image analysis was performed using FIJI (Schindelin, Arganda-Carreras, Frise, Kaynig, Longair,  
 165 Pietzsch, Preibisch, Rueden, Saalfeld, Schmid, Tinevez, White, Hartenstein, Eliceiri, Tomancak &  
 166 Cardona, 2012).

167 We used the natural log of each of ommatidia diameter, density of contact chemosensory  
 168 antennal sensilla and density of mechanosensory antennal sensilla to normalise the distributions. For  
 169 each metric, we fitted a linear model including active foraging time (day active, dim-light active) and  
 170 body size as fixed effects and taxonomic family (equivalent to species pair ID) as a random effect, with  
 171 variance partitioned using restricted maximum likelihood. All statistical analyses were performed using  
 172 JMP 13.1.0 for Windows (SAS Institute, Cary, NC, USA).

## 173 **Results**

174 As predicted, the ommatidia diameter (natural log transformed) is larger for dim-light active than for  
 175 day active insects ( $F_{1,94.73} = 8.794$ ,  $p = 0.004$ ; Table 3A; Fig 2A). The relationship between ommatidia  
 176 size and body size was not statistically significant ( $\beta = 0.012$ ,  $F_{1,35.61} = 3.868$ ,  $p = 0.057$ ; Table 3A).  
 177 The natural log of compound eye surface area is also larger for dim-light active than for day active  
 178 insects ( $F_{1,96.35} = 4.423$ ,  $p = 0.038$ ; Table 3B; Fig 2B) and was positively associated with body size ( $\beta$   
 179  $= 0.088$ ,  $F_{1,63.98} = 46.50$ ,  $p = <0.0001$ ; Table 3B).

180 Day active and dim-light active insects do not differ in the density of olfactory, contact  
 181 chemosensory or mechanosensory antennal sensilla (Table 3C–E; Fig 2C–E). There is a significant  
 182 negative correlation between body size and the density of olfactory and contact chemosensory antennal  
 183 sensilla: smaller individuals had higher densities of these antennal sensilla (Table 3C–E).

184 Taxonomic family explained 85.51% ( $p = 0.074$ ), 89.70% ( $p = 0.026$ ), 54.05% ( $p = 0.041$ ),  
 185 64.43% ( $p = 0.052$ ) and 75.97% ( $p = 0.031$ ) of the variation in ommatidia diameter, compound eye  
 186 surface area, olfactory sensilla density, contact chemosensory sensilla density and mechanosensory  
 187 sensilla density respectively (Table 3A–E).

188 For each sensory organ metric, means and standard deviations of day and dim-light active  
 189 groups for each taxonomic order and family are described in Supplementary Table 1.

## 190 **Discussion**

191 Our results show that dim-light activity is associated with larger compound eye ommatidia and larger  
 192 overall compound eye size across taxonomic orders of insects, but there is no corresponding difference  
 193 in antennal sensilla densities. There was evidence of body size allometry related to the distribution of  
 194 some classes of antennal receptors.

195 The predicted and observed association between dim-light activity and larger compound eye  
 196 ommatidia is consistent with results in bees (Jander & Jander, 2002; Wcislo & Tierney, 2009) and ants  
 197 (Greiner et al., 2007). Larger ommatidia enable greater photon capture, and therefore sensitivity, though  
 198 at the expense of spatial resolution (Jander & Jander, 2002; Warrant, 2017); however, rhabdomere size  
 199 and receptor photon-responses are also important considerations when assessing visual sensitivity  
 200 (Horridge, 2005). Spatial (across ommatidia) and temporal (across time) summation of photons during  
 201 visual information processing is also beneficial for vision in dim light for insects (Stöckl, Heinze,  
 202 Charalabidis, El Jundi, Warrant & Kelber, 2016; Warrant, 2017): future studies might explore whether  
 203 the increased ommatidia diameter in dim-light active insects is consistently accompanied by this visual  
 204 processing adaptation. The observation that dim-light activity is associated with larger compound eye  
 205 size is unsurprising, as an increase in ommatidia diameter would result in an increase in overall eye size  
 206 unless the number of ommatidia were reduced, which is unlikely to be favoured by selection as it would  
 207 reduce the visual acuity of the eye (Jander & Jander, 2002).

208 Enhanced sensitivity in other sensory modalities – manifested as elaborated antennae and/or  
 209 more numerous antennal sensilla – in response to dim-light living may be expected, with such  
 210 adaptations thought to compensate for reduced availability of visual information. For example,  
 211 nocturnal hawkmoths (Lepidoptera: Sphingidae) tend to preferentially use olfactory cues over visual  
 212 cues while their diurnal counterparts show the opposite preference (Balkenius et al., 2006), suggesting  
 213 increased reliance on non-visual sensory systems. However, our results do not provide evidence that

214 dim-light activity is associated with increased antennal sensilla density and thus contradict the view that  
215 dim-light activity is associated with increased morphological investment in antennae. This view is also  
216 contradicted by recent findings in fireflies (Coleoptera: Lampyridae) that were in the opposite direction  
217 of the predicted pattern, with nocturnal firefly species having relatively shorter antennae than diurnal  
218 species (Stanger-Hall et al., 2018). Investment in non-visual sensory organs may also depend on  
219 whether species are obligately or facultatively dim-light active, as selection for morphological  
220 specialisation is expected to be stronger for obligately dim-light active species (Wcislo & Tierney,  
221 2009). Indeed, facultatively nocturnal bees do not have the visual morphology adaptations that are  
222 typical of obligately nocturnal species, suggesting that behavioural change precedes structural  
223 adaptations (Wcislo & Tierney, 2009). Sufficiently detailed natural history information is not available  
224 for all species in our analysis to determine whether each dim-light active species was obligately or  
225 facultatively dim-light active, however future studies of this nature would ideally make this distinction.  
226 The availability of information in non-visual sensory modalities is also likely to influence investment  
227 in antennal morphology, as the benefit of increasing sensitivity for a given sensory channel (e.g.  
228 olfaction) would depend on the availability of salient cues and signals in that sensory channel. Indeed,  
229 information in non-visual sensory channels may not be equally available for dim-light active species  
230 across taxonomic orders of insects, and such natural history differences potentially explain why our  
231 results do not support the view that dim-light activity is consistently associated with a higher density of  
232 antennal sensilla.

233 While our results do not provide evidence of increased investment in non-visual sensory organs  
234 in dim-light active insects, they also do not support complementary resource allocation between  
235 ommatidia and antennal sensilla that has been documented in fireflies (diurnal species have smaller  
236 eyes and longer antennae compared with nocturnal species) (Stanger-Hall et al., 2018) and multiple  
237 species of *Drosophila* (Diptera: Drosophilidae) (Keeseey, Grabe, Gruber, Koerte, Obiero, Bolton,  
238 Khallaf, Kunert, Lavista-Llanos, Valenzano, Rybak, Barrett, Knaden & Hansson, 2019), and is  
239 frequently characteristic of the troglomorphy exhibited of cave-dwelling arthropods (Christiansen,  
240 2012; Hobbs III, 2012) including leiodid beetles (Peck, 1973; Peck, 1977; Peck, 1998). Finite energetic

241 resources mean that elaboration of one morphological structure may be at the expense of another  
242 structure (Emlen, 2001; Nijhout & Emlen, 1998), and this might be especially evident across different  
243 sensory modalities, given the energetically expensive nature of complex sensory systems (Keesey et al.,  
244 2019; Niven & Laughlin, 2008). Nonetheless, our findings may be unsurprising in three ways. Firstly,  
245 animals typically use information in multiple sensory modalities (e.g. light and odour) simultaneously  
246 (Partan & Marler, 1999) and so it may be disadvantageous to invest heavily in receptors for one sensory  
247 modality at the expense of receptors for another modality; we note that taxa often differ in their reliance  
248 on information in a given sensory modality. Secondly, predicted negative correlations between  
249 investment in morphological structures are not commonly observed (Nijhout & Emlen, 1998; van  
250 Noordwijk & de Jong, 1986): inverse resource allocation between traits can be context dependent with  
251 variation in the direction of relationships between structures influenced by environmental conditions  
252 (Sgrò & Hoffmann, 2004) and, at least for animals which feed continuously, by changes in resource  
253 acquisition (Nijhout & Emlen, 1998). Thirdly, many instances of negative relationships in investment  
254 between sensory systems involve an absence of information in one sensory modality. For example,  
255 many species of cave-dwelling arthropods exhibit regressed visual systems (e.g. smaller compound eyes  
256 with smaller and/or fewer ommatidia) and enhanced olfactory systems (e.g. longer antennae or higher  
257 densities of antennal sensilla) (Christiansen, 2012; Hobbs III, 2012; Peck, 1973; Peck, 1977; Peck,  
258 1998). In the cavernous environment, characterised by the absence of natural light, natural selection  
259 would likely favour diversion of energetic resources from visual to non-visual sensory systems, as the  
260 energetically expensive visual system can no longer detect information that contributes to an  
261 individual's fitness (Niven & Laughlin, 2008; Stearns, 1989).

262         In conclusion, we show that dim-light active insects, across multiple taxonomic families, have  
263 larger compound eyes and ommatidia but no commensurate increase in the density of antennal  
264 receptors. This association of dim-light activity with comparatively greater ommatidia diameter and  
265 larger overall compound eye size is consistent with the predicted close relationship between sensory  
266 organ morphology, signal perception and the signalling environment (Endler, 1992), excluding radical  
267 departures in natural history among the taxa being compared. Given the potential for the use of insects

268 to enhance restoration of anthropogenically-degraded habitats (Elizalde, Arbetman, Arnan, Eggleton,  
 269 Leal, Lescano, Saez, Werenkraut & Pirk, 2020; Prather & Laws, 2018) and the need to inform  
 270 conservation efforts with sensory ecology in response to the prevalence of anthropogenically-induced  
 271 environmental change (Lim, Sodhi & Endler, 2008), understanding the interaction between sensory  
 272 system adaptation and life history specialisation is of increasing relevance. Knowledge of sensory  
 273 organ morphology has implications for understanding how long-term anthropogenic changes to the  
 274 photic environment – such as the penetration of artificial light at night into the once-dark night-time  
 275 environment (reviewed by Hopkins, Gaston, Visser, Elgar & Jones, 2018; Tierney et al., 2017) or the  
 276 presence of daytime light-reducing smog (White, 1976) – may influence species responses, especially  
 277 since many insect species have relatively short generation times and temporally specific mating  
 278 patterns.. Such influences may have cascading effects upon insect community dynamics through altered  
 279 signalling and communication behaviours. Insects provide important ecosystem services, including  
 280 pollination, nutrient cycling, seed dispersal and bioturbation that are not only of obvious environmental  
 281 importance but also considerable economic value (Elizalde et al., 2020; Losey & Vaughan, 2006):  
 282 effective signalling and communication within insect communities, at least for social insects, is essential  
 283 to the efficiency of the provision of these ecosystem services (Dyer, 2002; Elizalde et al., 2020).

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461 **Table 1.** Sister pairs of day- and dim-light- active species used with species sample size for each sensory morphology metric. Members of a sister pair are  
 462 from the same taxonomic family (or genus). Sample sizes represent the number of individuals of a given species for which an average ommatidia diameter,  
 463 average eye surface area or average density of the specified class of antennal sensilla was calculated.

Taxonomic order	Taxonomic family	Species	Day active					Dim-light active							
			Sample size					Sample size							
			Ommatidia	Eye surface area	Olfactory sensilla	Contact chemosensilla	Mechanosensilla	Ommatidia	Eye surface area	Olfactory sensilla	Contact chemosensilla	Mechanosensilla			
Coleoptera	Carabidae	<i>Cicindela semicincta</i>	5	5	5	5	5	<i>Megacephala cylindrica</i>	4	5	4	4	4		
	Scarabaeidae	<i>Phyllotocus macleayi</i>	6	6	6	6	6	<i>Sericesthis geminata</i>	5	5	5	5	5		
Diptera	Culicidae	<i>Aedes albopictus</i>	3	3	3	3	3	<i>Culex quinquefasciatus</i>	3	3	2	2	2		
Hymenoptera	Halictidae	<i>Mellitidia tomentifera</i>	6	6	6	6	6	<i>Reepenia bituberculata</i>	5	5	5	5	5		
	Formicidae	<i>Myrmecia croslandi</i>	6	6	6	6	6	<i>Myrmecia pyriformis</i>	6	6	6	6	6		
	Mutillidae	<i>Ephutomorpha ferruginata</i>	5	5	5	5	5	<i>Odontophotopsis melicausa</i>	3	3	3	3	3		
Lepidoptera	Hesperiidae	<i>Netrocoryne repanda</i>	5	5	4	4	4	<i>Chaetocneme denitza</i>	4	4	3	3	3		
	Sphingidae	<i>Macroglossum micacea</i>	4	4	4	4	4	<i>Macroglossum vacillans</i>	4	4	4	4	4		
Odonata	Austrocorduliidae	<i>Austrocordulia refracta</i>	4	3	2	0	2	<i>Apocordulia macrops</i>	5	5	3	0	3		
	Telephlebiidae	<i>Austroaeschna atrata</i>	5	5	4	0	4	<i>Telephlebia brevicauda</i>	5	5	2	0	2		
Orthoptera	Gryllidae	<i>Bobilla victoria</i>	4	4	4	4	4	<i>Pteronemobius truncatus</i>	3	3	3	3	3		
	Tettigoniidae	<i>Terpandrus jumbunna</i>	2	2	2	2	2	<i>Terpandrus calperum</i>	2	2	2	2	2		
			55	54	51	45	51				49	50	42	37	42

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465 **Table 2.** Types of antennal sensilla identified and included in the analysis for each taxonomic family pair. While pore-like types of sensilla may have been  
 466 identified, they were not included because they were not consistently observed on the antennae of each individual specimen for a given species pair.

Taxonomic order	Taxonomic family	Antennal sensilla types identified and included for analysis			References for sensilla typing
		Olfactory	Contact chemosensory	Mechanosensory	
Coleoptera	Carabidae	Trichodea, coeloconica	Basiconica	Chaetica	Merivee, Ploomi, Rahi, Bresciani, Ravn, Luik and Sammelseg (2002)
	Scarabaeidae	Trichodea, coeloconica, auricillica	Basiconica	Chaetica	Handique, Bhattacharyya, Baruah and Boruah (2017); Romero-López, Morón and Valdez (2010); Shao, Sun, Wang and Chen (2019)
Diptera	Culicidae	Trichodea, coeloconica	Basiconica	Chaetica	Ibrahim, Sawires and Hamza (2018); Seenivasagan, Sharma, Shrivastava, Parashar, Pant and Prakash (2009)
Hymenoptera	Halictidae	Trichodea, placodea	Basiconica	Chaetica	Carvalho, Fujimura, Bonetti, Goulart, Cloonan, da Silva, Araújo, Ueira-Vieira and Leal (2017); Frasnelli, Anfora, Trona, Tessarolo and Vallortigara (2010); Freelance, Majoe, Tierney and Elgar (2019)
	Formicidae	Trichodea, trichodea curvata	Basiconica	Chaetica	Dumpert (1972); Freelance et al. (2019)
	Mutillidae	Trichodea, placodea	Basiconica	Chaetica	Undescribed; based on sensilla typing for Apiidae
Lepidoptera	Hesperiidae	Trichodea, auricillica	Basiconica	Chaetica	Abu-shall and Tawfeek (2015); Xiangqun, Ke, Feng and Yalin (2014)
	Sphingidae	Trichodea, auricillica, coeloconica	Basiconica	Chaetica	Balkenius et al. (2006)
Odonata	Austrocorduliidae	Coeloconica	N/A	Deeply-sunken	Rebora, Piersanti and Gaino (2008); Rebora, Piersanti and Gaino (2010)
	Telephlebiidae	Coeloconica	N/A	Deeply-sunken	Rebora et al. (2008); Rebora et al. (2010)
Orthoptera	Gryllidae	Trichodea	Basiconica	Chaetica	Kostromytska, Scharf and Buss (2015)
	Tettigoniidae	Trichodea	Basiconica	Chaetica	Schneider and Römer (2016)

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468 **Table 3.** Mixed effects models explaining variation in the compound eye ommatidia diameter,  
 469 compound eye surface area and the densities of antennal sensilla between day active and dim-light  
 470 active insects.

Model/parameter		Statistics		
<b>A. Ln (ommatidia diameter)</b>				
Model fit		R <sup>2</sup> adjusted: 0.917		n = 104
<b>Parameter estimates</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t ratio</b>	<b>p &gt;  t </b>
Intercept	3.194	0.131	24.45	<0.0001
Foraging time [day]	-0.045	0.015	-2.970	0.004
Body size (mm)	0.011	0.005	1.970	0.057
<b>Random effects</b>		<b>% variation explained</b>	<b>Wald's p-value</b>	
Taxonomic family		85.51	0.074	
<b>Fixed effects</b>		<b>df</b>	<b>F ratio</b>	<b>p &gt; F</b>
Foraging time (day, dim-light)		1,94.73	8.794	0.004
Body size		1,35.61	3.868	0.057
<b>B. Ln (compound eye surface area)</b>				
Model fit		R <sup>2</sup> adjusted: 0.966		n = 104
<b>Parameter estimates</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t ratio</b>	<b>p &gt;  t </b>
Intercept	-0.392	0.341	-1.150	0.267
Foraging time [day]	-0.073	0.035	-2.100	0.038
Body size (mm)	0.088	0.013	6.820	<0.0001
<b>Random effects</b>		<b>% variation explained</b>	<b>Wald's p-value</b>	
Taxonomic family		89.70	0.026	
<b>Fixed effects</b>		<b>df</b>	<b>F ratio</b>	<b>p &gt; F</b>
Foraging time (day, dim-light)		1,96.35	4.423	0.038
Body size		1,63.98	46.50	<0.0001
<b>C. Olfactory antennal sensilla density</b>				
Model fit		R <sup>2</sup> adjusted: 0.700		n = 93
<b>Parameter estimates</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t ratio</b>	<b>p &gt;  t </b>
Intercept	11422.2	1823.06	6.270	<0.0001
Foraging time [day]	-597.3	409.2	-1.460	0.148
Body size (mm)	-311.9	88.47	-3.530	0.003
<b>Random effects</b>		<b>% variation explained</b>	<b>Wald's p-value</b>	
Taxonomic family		54.05	0.041	
<b>Fixed effects</b>		<b>df</b>	<b>F ratio</b>	<b>p &gt; F</b>
Foraging time (day, dim-light)		1,85.20	2.131	0.148
Body size		1,16.39	12.43	0.003

**D. Ln (contact chemosensory antennal sensilla density)**

Model fit		R <sup>2</sup> adjusted: 0.736		n = 82
<i>Parameter estimates</i>	<i>β</i>	<i>SE</i>	<i>t ratio</i>	<i>p &gt;  t </i>
Intercept	6.701	0.234	28.64	<0.0001
Foraging time [day]	0.073	0.047	1.550	0.126
Body size (mm)	-0.043	0.015	-2.950	0.007
<i>Random effects</i>		<i>% variation explained</i>		<i>Wald's p-value</i>
Taxonomic family		64.43		0.052
<i>Fixed effects</i>		<i>df</i>	<i>F ratio</i>	<i>p &gt; F</i>
Foraging time (day, dim-light)		1,77.23	2.399	0.126
Body size		1,25.51	8.680	0.007

**E. Ln (mechanosensory antennal sensilla density)**

Model fit		R <sup>2</sup> adjusted: 0.811		n = 92
<i>Parameter estimates</i>	<i>β</i>	<i>SE</i>	<i>t ratio</i>	<i>p &gt;  t </i>
Intercept	6.545	0.275	23.78	<0.0001
Foraging time [day]	0.064	0.042	1.530	0.130
Body size (mm)	-0.024	0.013	-1.880	0.072
<i>Random effects</i>		<i>% variation explained</i>		<i>Wald's p-value</i>
Taxonomic family		75.97		0.031
<i>Fixed effects</i>		<i>df</i>	<i>F ratio</i>	<i>p &gt; F</i>
Foraging time (day, dim-light)		1,85.28	2.341	0.130
Body size		1,25.29	3.516	0.072

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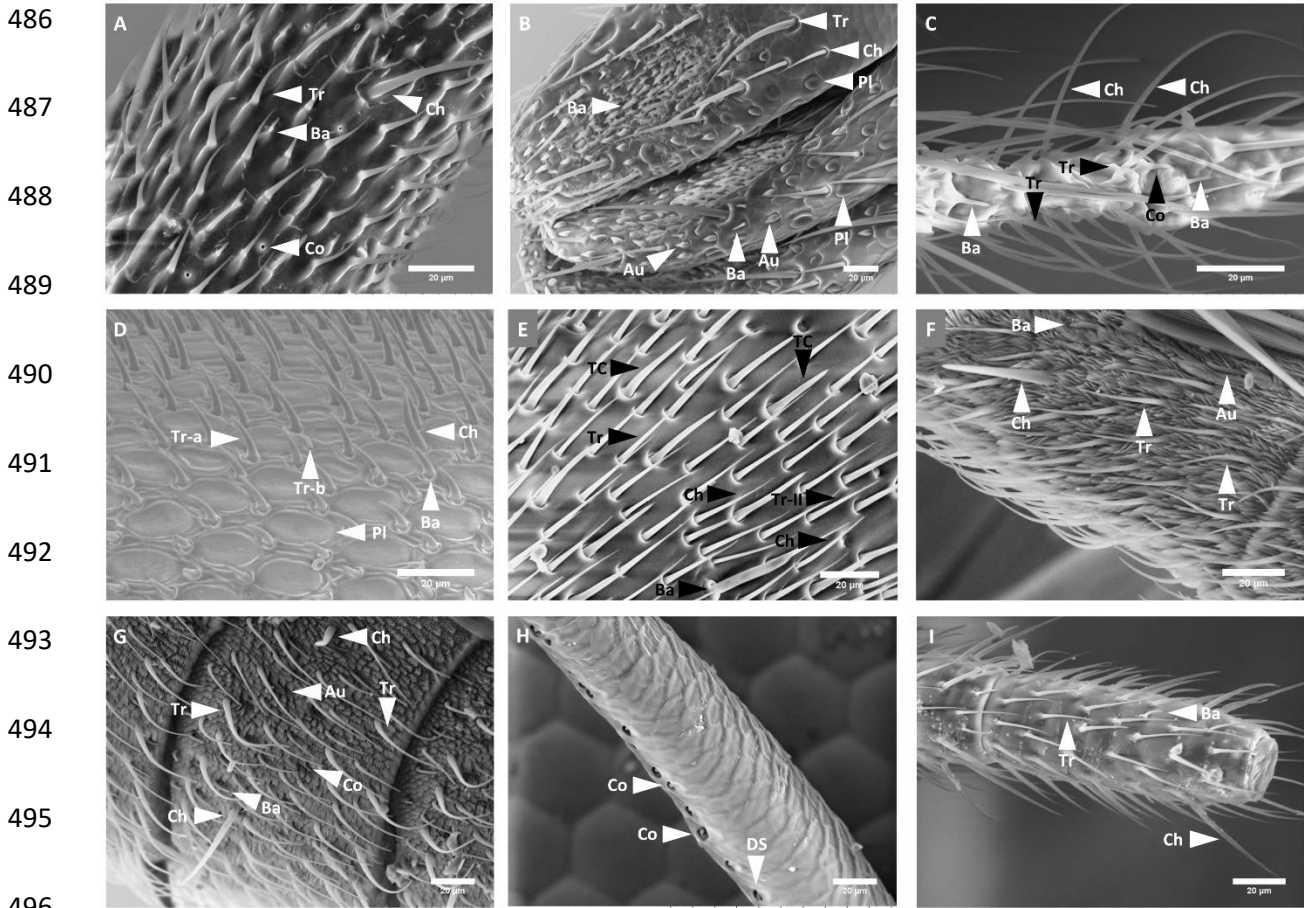
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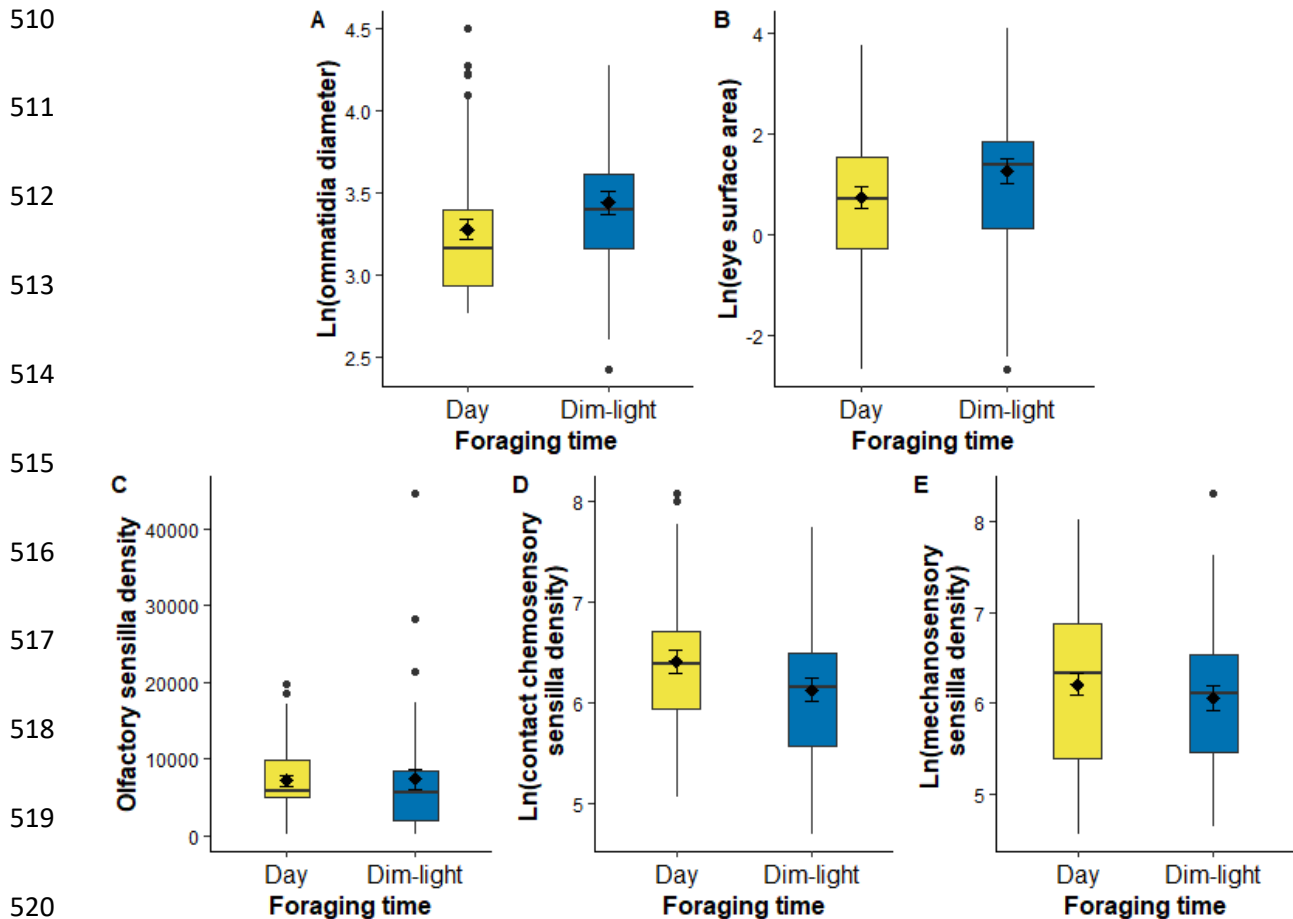
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497 **Figure 1.** Electron micrographs displaying the types of antennal sensilla identified and included in the  
 498 analysis for each taxon. Au = auricillica; Ba = basiconica; Ch = chaetica; Co = coeloconica; DS =  
 499 deeply sunken; Pl = placodea; Tr = trichodea; Tr-a = trichodea type a; Tr-b = trichodea type b; TC =  
 500 trichodea curvata; Tr-II = trichoid type II. The class (olfactory, contact chemosensory,  
 501 mechanosensory) for each type of sensilla identified for each taxon is listed in Table 2; note that the  
 502 antennae of Odonata do not possess contact chemosensilla. All scale bars are 20µm in length. **A.**  
 503 *Cicindela semicincta* (tiger beetle; Coleoptera: Carabidae). **B.** *Phyllotocus macleayi* (flower scarab  
 504 beetle; Coleoptera: Scarabaeidae). **C.** *Aedes albopictus* (Asian tiger mosquito; Diptera: Culicidae). **D.**  
 505 *Mellitidia tomentifera* (an Australian native bee; Hymenoptera: Halictidae). **E.** *Myrmecia pyriformis*  
 506 (bull ant; Hymenoptera: Formicidae). **F.** *Netrocoryne repanda* (butterfly; Lepidoptera: Hesperidae).  
 507 **G.** *Macroglossum micacea* (hawkmoth; Lepidoptera: Sphingidae). **H.** *Austrocordulia refracta* (eastern  
 508 hawk dragonfly; Odonata: Austrocorduliidae). **I.** *Bobilla victoria* (cricket; Orthoptera: Gryllidae).

509



521 **Figure 2.** The influence of the photic environment on compound eye and antennal morphology. Tails  
 522 indicate the range; box indicates the interquartile range; horizontal line within the box indicates the  
 523 median; black diamonds indicate the mean; black capped error bars indicate standard error of the mean.  
 524 **A.** The natural log of average compound eye ommatidia diameter ( $\mu\text{m}$ ) is larger for dim-light active  
 525 than for day active species ( $F_{1,94.73} = 8.794, p = 0.004$ ). **B.** The natural log of compound eye surface  
 526 area ( $\text{mm}^2$ ) is larger for dim-light active than for day active species ( $F_{1,96.35} = 4.423, p = 0.038$ ). **C.** The  
 527 density of olfactory antennal sensilla does not vary between day active and dim-light active insects  
 528 ( $F_{1,85.20} = 2.131, p = 0.148$ ). **D.** The density of the natural log of contact chemosensory sensilla does  
 529 not vary between day active and dim-light active insects ( $F_{1,77.23} = 2.399, p = 0.126$ ). **E.** The density of  
 530 the natural log of mechanosensory sensilla does not vary between day active and dim-light active insects  
 531 ( $F_{1,85.28} = 2.341, p = 0.130$ ).