

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

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

ADDITIONAL KEYWORDS: antenna – compound eye – diurnal – nocturnal – photic environment – sensory ecology.

## INTRODUCTION

Animals perceive information about their extrinsic environment, including the location and nature of potential mates, food sources, shelter or predators through a variety of modalities (e.g. light, odour, sound). As efficiency is essential for biological fitness, the considerable energetic resources required to develop and maintain elaborate sensory systems (Niven & Laughlin, 2008) mean that natural selection is expected to favour sensory organs with morphology optimized to detect salient cues and signals from the background information in the environment (Endler, 1992; Elgar *et al.*, 2018).

With millions of years of a stable light/dark cycle, the photic environment is a consistent selection pressure shaping the evolution of sensory structures. Indeed, sensory adaptations to the photic environment in which an animal is active are well documented. For example, populations of Mexican cave fish (*Astyanax mexicanus*) living in lightless caves no longer have functional eyes, while eyes are retained in populations that remain on the surface (Dowling *et al.*, 2002). Similarly, reduced investment in eyes is observed in arthropod troglifauna (cave-dwelling animals) including crustacea (Christiansen, 2012; Hobbs III, 2012), cave-crickets (Lavoie *et al.*, 2007), leiodid beetles (Peck, 1973; Friedrich *et al.*, 2011) and dytiscid beetles (Tierney *et al.*, 2018).

Many crepuscular (active during twilight) or nocturnal (active beyond astronomical twilight)

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–collectively referred to as dim-light active–arthropods frequently have sensory adaptations specific to their photic environment (Warrant, 2006; Wcislo & Tierney, 2009; Warrant & Dacke, 2011; Tierney *et al.*, 2017). Arthropod compound eyes are composed of ommatidia, each of which is an independent photoreceptive unit that distinguishes brightness and colour. For example, compared with their closest diurnal relatives, the average ommatidia diameter is greater in the compound eye of obligate dim-light foraging bees (order Hymenoptera, superfamily Apoidea) (Jander & Jander, 2002; Wcislo & Tierney, 2009) and wasps (Hymenoptera: Mutillidae, Polistinae, Vespinae) (Warrant, 2008), crepuscular or nocturnal *Myrmecia* ants (Hymenoptera: Formicidae) (Greiner *et al.*, 2007; Narendra *et al.*, 2011), night-flying leafcutter ants of the genus *Atta* (Hymenoptera: Formicidae) (Moser *et al.*, 2004) and night-flying onitine dung beetles (Coleoptera: Scarabaeidae) (McIntyre & Caveney, 1998). Larger ommatidia capture more photons and can thus detect changes in luminance in dimmer light (Land, 1997; Jander & Jander, 2002; Greiner *et al.*, 2007; Tierney *et al.*, 2017). Consequently, low levels of ambient light should favour larger ommatidia diameter to improve visual sensitivity. Larger ommatidia are often accompanied by a distinct arrangement of the internal structure of the compound eye (Land, 1997; Warrant, 2017) as well as physiological adaptations of the photoreceptors and of the neural circuitry involved in the processing of spatial and temporal visual information (Stöckl *et al.*, 2016; Warrant, 2017).

While there appear to be consistent adaptations of insect compound eyes to dim-light activity, most studies have been taxonomically limited to the Hymenoptera, Coleoptera and Lepidoptera. Furthermore, it is unclear how differences in compound eye morphology compare with differences in the sensory organs that insects use to detect odours and vibrations: the antennae. Selection pressures associated with dim-light activity may favour not only adaptations that increase the sensitivity to light but also adaptations that increase sensitivity to information in complementary modalities, such as odour and sound (provided that salient information is available in those modalities). For example, the nocturnal hawkmoth *Deilephila elpenor* (Lepidoptera: Sphingidae) preferentially uses olfactory rather than visual cues while the diurnal hawkmoth *Macroglossum stellatarum* shows the opposite preference (Balkenius *et al.*, 2006). This behavioural difference is accompanied by differences in the abundance of types of antennal sensilla (Balkenius *et al.*, 2006), which are the sensory hairs and pores on antennae that detect odours, vibrations, stretch, temperature, humidity and carbon dioxide (Chapman, 1982; Elgar *et al.*, 2018). The density (number per unit area) of sensilla is an ecologically relevant measure of resource investment

in insect antennae, and is positively associated with the strength of both behavioural (Gill *et al.*, 2013) and physiological (Spaethe *et al.*, 2007) responses to olfactory stimuli. Differences in the abundance of antennal sensilla between the nocturnal bull ant *Myrmecia pyriformis* and similarly sized diurnal ant species have also been documented (Ramirez-Esquivel *et al.*, 2014), although the observed differences may not be due solely to differences in the photic environment in which the ants are active (Ramirez-Esquivel *et al.*, 2014). Interestingly, the antennae of nocturnal fireflies (Coleoptera: Lampyridae) are relatively shorter than those of their diurnal relatives (Stanger-Hall *et al.*, 2018), although it is not known if this corresponds to differences in antennal sensilla density.

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

## MATERIALS AND METHODS

Compiling images of the eyes and antennae of a comprehensive sample of insects across taxonomic orders and fitting this into a phylogenetic comparative framework is not possible without a complete phylogeny of insects. Instead, we provide taxonomic generality by selecting 12 closely related pairs of species that vary in the photic environment in which they are active for foraging and reproduction. Thus, we compare a day-active (diurnal) and dim-light active (nocturnal and/or crepuscular) species in each pair, with each species pair belonging to a different family and spanning six taxonomic orders of insects (Table 1). We ensured that species within a pair overlapped in habitat type (e.g.

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

Taxonomic order	Taxonomic family	Day active			Dim-light active							
		Species			Species							
		Ommatidia	Eye surface area	Contact chemosensilla	Ommatidia	Eye surface area	Contact chemosensilla					
Coleoptera	Carabidae	<i>Cicindela semicincta</i>	5	5	5	5	4	4	4			
		<i>Phyllotocus macleayi</i>	6	6	6	5	5	5	5	5		
Diptera	Culicidae	<i>Aedes albopictus</i>	3	3	3	3	3	2	2	2		
		<i>Melliidtia tomentifera</i>	6	6	6	6	6	5	5	5		
Hymenoptera	Formicidae	<i>Myrmecia croslandi</i>	6	6	6	6	6	6	6	6		
		<i>Ephutomorpha ferruginata</i>	5	5	5	5	5	3	3	3		
Lepidoptera	Hesperiidae	<i>Netrocoryne repanda</i>	5	4	4	4	4	3	3	3		
		<i>Macroglossum nitaceae</i>	4	4	4	4	4	4	4	4		
Odonata	Austrocorduliidae	<i>Austrocordulia refracta</i>	4	3	0	2	5	3	0	3		
		<i>Austroaeschna atrata</i>	5	5	4	4	4	5	2	0		
Orthoptera	Gryllidae	<i>Bobilla victoria</i>	4	4	4	4	4	3	3	3		
		<i>Terpandrus jumbuna</i>	2	2	2	2	2	2	2	2		
Total			55	54	51	45	51	49	50	42	37	42

temperate forest) and geographical range. Two to six specimens of each species were obtained from Museum Victoria (Melbourne, Victoria, Australia) or the Australian National Insect Collection (Commonwealth Scientific and Industrial Research Organisation) for morphological analysis (Table 1); with the exception of the velvet ants (Hymenoptera: Mutillidae), our species pairs were confined to Australian taxa for sampling convenience and to provide continental consistency. As there are no nocturnal velvet ants found in Australia, the nocturnal species used in our analysis is North American with the specimens obtained from Utah State University (Utah, USA).

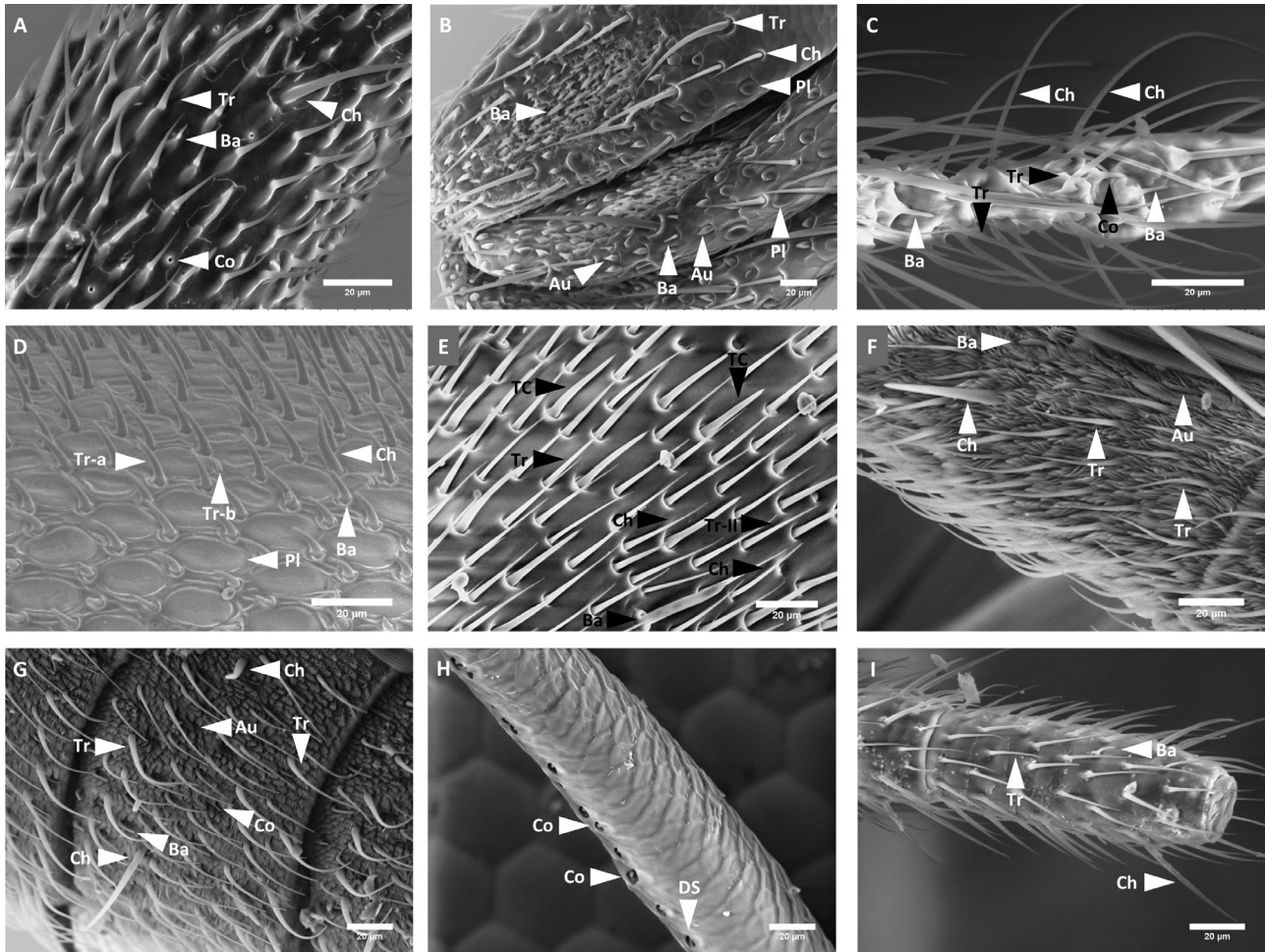
To image the sensory organs, each pinned uncoated specimen underwent low-vacuum scanning electron microscopy (SEM) using an FEI Quanta 200F scanning electron microscope (10 kV acceleration voltage, spot size 2.0, 0.5 mBar pressure) at the Bio21 Advanced Microscopy Facility (Bio21 Institute, The University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

We measured ommatidia from the anteromedial aspect of each compound eye (i.e. the ommatidia that face directly in front of the insect), thereby accounting for potential differences in ommatidia diameter between regions of the compound eye (Perl & Niven, 2016) and for potential differences between taxa related to whether a species spends most of its time looking above (terrestrial species) or below (aerial species). Antennal sensilla were identified and classified into three classes: olfactory (detects airborne odours), contact chemosensory (detects chemicals on a surface across which the antenna is palpated) and mechanosensory (responds to vibrations or mechanical deformation of the sensilla) (Fig. 1; Table 2). Pore-like sensilla were not consistently observed

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

As body size is generally larger for dim-light active species compared with closely related diurnal bee species (Wcislo & Tierney, 2009), we obtained relevant measures of body size to account for the potential influence of body size allometry on ommatidia size (Jander & Jander, 2002; Schwarz *et al.*, 2011; Smith *et al.*, 2015) and antennal sensilla density (Spaethe *et al.*, 2007). To obtain measures of body size, we either imaged the relevant body parts of the specimen under the scanning electron microscope or took digital images of the specimens using a Canon 6D DSLR with Canon EF-L 100mm f2.8 macro lens (Canon, Tokyo, Japan) with a ruler included as a scale. Body size was measured as average elytra length for the Coleoptera (Östman, 2005; Frank *et al.*, 2007), as the ratio of average wing length to thorax length for the Diptera (Barker & Krebs, 1995), as head width just posterior to the compound eyes for the Hymenoptera (Spaethe *et al.*, 2007; Wild, 2007; Boudinot & Fisher, 2013), as average forewing length for the Lepidoptera (van Hook *et al.*, 2012) and Odonata (Johnson *et al.*, 2013), and as average femur length for the Orthoptera (Whitman, 2008). All image analysis was performed using FIJI (Schindelin *et al.*, 2012).

We used the natural log of each of ommatidia diameter, density of contact chemosensory antennal sensilla and density of mechanosensory antennal sensilla to normalize the distributions. For each



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

metric, we fitted a linear model including active foraging time (day active, dim-light active) and body size as fixed effects and taxonomic family (equivalent to species pair ID) as a random effect, with variance partitioned using restricted maximum likelihood. All statistical analyses were performed using JMP 13.1.0 for Windows (SAS Institute, Cary, NC, USA).

#### DATA AVAILABILITY

The data analysed are available from figshare: <https://doi.org/10.26188/12824822>.

#### RESULTS

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

**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 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	<a href="#">Merivee <i>et al.</i> (2002)</a>
	Scarabaeidae	Trichodea, coeloconica, auricillica	Basiconica	Chaetica	<a href="#">Romero-López <i>et al.</i> (2010)</a> ; <a href="#">Handique <i>et al.</i> (2017)</a> ; <a href="#">Shao <i>et al.</i> (2019)</a>
Diptera	Culicidae	Trichodea, coeloconica	Basiconica	Chaetica	<a href="#">Seenivasagan <i>et al.</i> (2009)</a> ; <a href="#">Ibrahim <i>et al.</i> (2018)</a>
Hymenoptera	Halictidae	Trichodea, placodea	Basiconica	Chaetica	<a href="#">Frasnelli <i>et al.</i> (2010)</a> ; <a href="#">Carvalho <i>et al.</i> (2017)</a> ; <a href="#">Freelance <i>et al.</i> (2019)</a>
	Formicidae	Trichodea, trichodea curvata	Basiconica	Chaetica	<a href="#">Dumpert (1972)</a> ; <a href="#">Freelance <i>et al.</i> (2019)</a>
	Mutillidae	Trichodea, placodea	Basiconica	Chaetica	Undescribed; based on sensilla typing for Apiidae
Lepidoptera	Hesperiidae	Trichodea, auricillica	Basiconica	Chaetica	<a href="#">Xiangqun <i>et al.</i> (2014)</a> ; <a href="#">Abu-shall &amp; Tawfeek (2015)</a>
	Sphingidae	Trichodea, auricillica, coeloconica	Basiconica	Chaetica	<a href="#">Balkenius <i>et al.</i> (2006)</a>
Odonata	Austrocorduliidae	Coeloconica	N/A	Deeply-sunken	<a href="#">Rebora <i>et al.</i> (2008, 2010)</a>
	Telephlebiidae	Coeloconica	N/A	Deeply-sunken	<a href="#">Rebora <i>et al.</i> (2008, 2010)</a>
Orthoptera	Gryllidae	Trichodea	Basiconica	Chaetica	<a href="#">Kostromytska <i>et al.</i> (2015)</a>
	Tettigoniidae	Trichodea	Basiconica	Chaetica	<a href="#">Schneider &amp; Römer (2016)</a>

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

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

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

## DISCUSSION

Our results show that dim-light activity is associated with larger compound eye ommatidia and larger

overall compound eye size across taxonomic orders of insects, but there is no corresponding difference in antennal sensilla densities. There was evidence of body size allometry related to the distribution of some classes of antennal receptors.

The predicted and observed association between dim-light activity and larger compound eye ommatidia is consistent with results in bees (Jander & Jander, 2002; Wcislo & Tierney, 2009) and ants (Greiner *et al.*, 2007). Larger ommatidia enable greater photon capture, and therefore sensitivity, though at the expense of spatial resolution (Jander & Jander, 2002; Warrant, 2017); however, rhabdomere size and receptor photon-responses are also important considerations when assessing visual sensitivity (Horridge, 2005). Spatial (across ommatidia) and temporal (across time) summation of photons during visual information processing is also beneficial for vision in dim light for insects (Stöckl *et al.*, 2016; Warrant, 2017): future studies might explore whether the increased ommatidia diameter in dim-light active insects is consistently accompanied by this visual processing adaptation. The observation that dim-light activity is associated with larger compound eye size in

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

Model/parameter	Statistics				
<b>A. Ln (ommatidia diameter)</b>					
Model fit				$R^2$ adjusted: 0.917	$N = 104$
<i>Parameter estimates</i>	$\beta$	<i>SE</i>	<i>t ratio</i>	$P >  t $	
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	
<i>Random effects</i>				<i>% variation explained</i>	<i>Wald's P-value</i>
Taxonomic family				85.51	0.074
<i>Fixed effects</i>	<i>d.f.</i>			<i>F ratio</i>	$P > F$
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				$R^2$ adjusted: 0.966	$N = 104$
<i>Parameter estimates</i>	$\beta$	<i>SE</i>	<i>t ratio</i>	$P >  t $	
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	
<i>Random effects</i>				<i>% variation explained</i>	<i>Wald's P-value</i>
Taxonomic family				89.70	0.026
<i>Fixed effects</i>	<i>d.f.</i>			<i>F ratio</i>	$P > F$
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				$R^2$ adjusted: 0.700	$N = 93$
<i>Parameter estimates</i>	$\beta$	<i>SE</i>	<i>t ratio</i>	$P >  t $	
Intercept	11 422.2	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	
<i>Random effects</i>				<i>% variation explained</i>	<i>Wald's P-value</i>
Taxonomic family				54.05	0.041
<i>Fixed effects</i>	<i>d.f.</i>			<i>F ratio</i>	$P > F$
Foraging time [day, dim-light]	1,85.20			2.131	0.148
Body size	1,16.39			12.43	0.003
<b>D. Ln (contact chemosensory antennal sensilla density)</b>					
Model fit				$R^2$ adjusted: 0.736	$N = 82$
<i>Parameter estimates</i>	$\beta$	<i>SE</i>	<i>t ratio</i>	$P >  t $	
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>d.f.</i>			<i>F ratio</i>	$P > F$
Foraging time [day, dim-light]	1,77.23			2.399	0.126
Body size	1,25.51			8.680	0.007

**Table 3.** Continued

<b>E. Ln (mechanosensory antennal sensilla density)</b>				
Model fit			$R^2$ adjusted: 0.811	$N = 92$
<i>Parameter estimates</i>	$\beta$	<i>SE</i>	<i>t ratio</i>	$P >  t $
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>d.f.</i>	<i>F ratio</i>	$P > F$
Foraging time [day, dim-light]		1,85.28	2.341	0.130
Body size		1,25.29	3.516	0.072

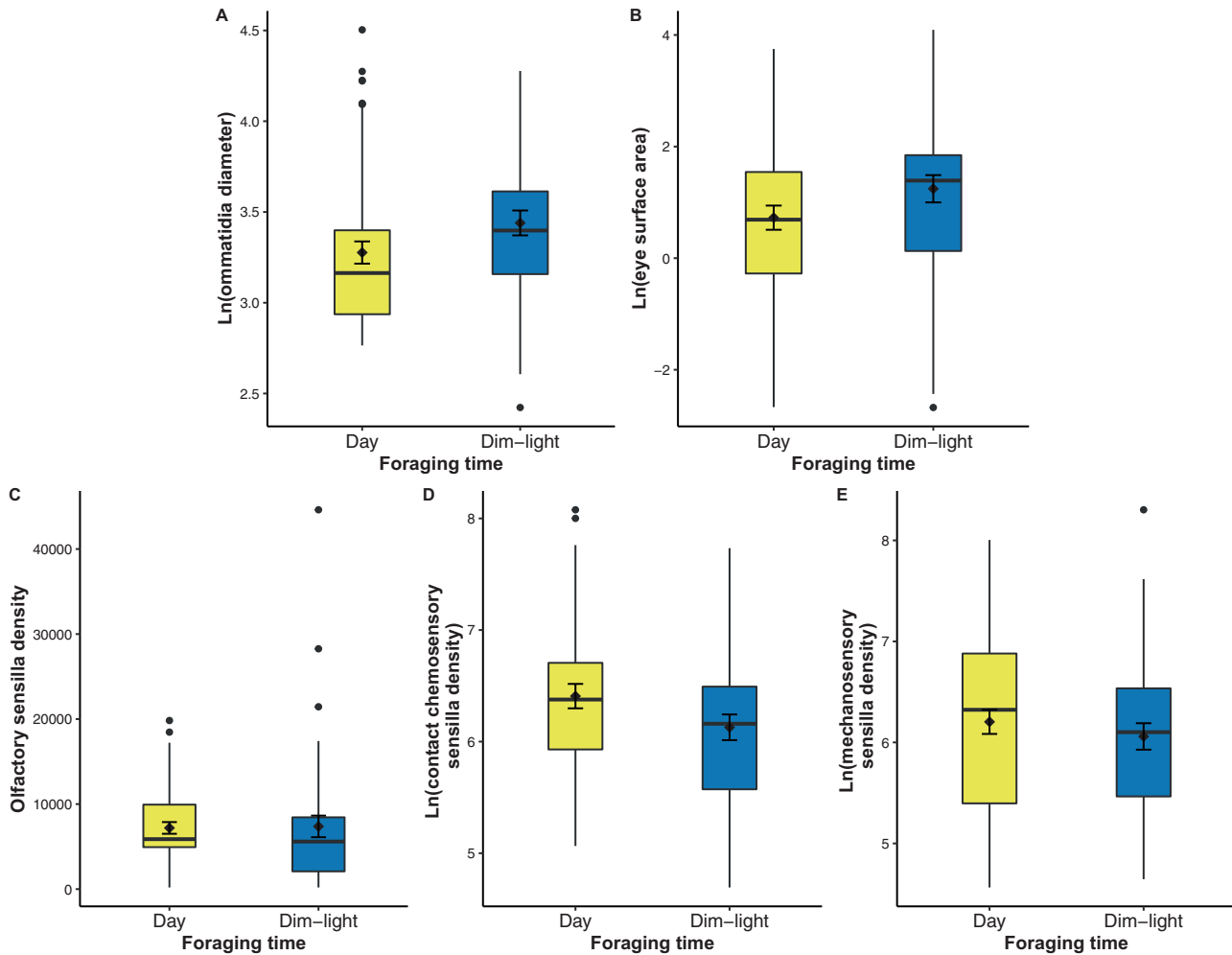
unsurprising, as an increase in ommatidia diameter would result in an increase in overall eye size unless the number of ommatidia were reduced, which is unlikely to be favoured by selection as it would reduce the visual acuity of the eye (Jander & Jander, 2002).

Enhanced sensitivity in other sensory modalities – manifested as elaborated antennae and/or more numerous antennal sensilla – in response to dim-light living may be expected, with such adaptations thought to compensate for reduced availability of visual information. For example, nocturnal hawkmoths (Lepidoptera: Sphingidae) tend to preferentially use olfactory cues over visual cues while their diurnal counterparts show the opposite preference (Balkenius *et al.*, 2006), suggesting increased reliance on non-visual sensory systems. However, our results do not provide evidence that dim-light activity is associated with increased antennal sensilla density and thus contradict the view that dim-light activity is associated with increased morphological investment in antennae. This view is also contradicted by recent findings in fireflies (Coleoptera: Lampyridae) that were in the opposite direction of the predicted pattern, with nocturnal firefly species having relatively shorter antennae than diurnal species (Stanger-Hall *et al.*, 2018). Investment in non-visual sensory organs may also depend on whether species are obligately or facultatively dim-light active, as selection for morphological specialization is expected to be stronger for obligately dim-light active species (Wcislo & Tierney, 2009). Indeed, facultatively nocturnal bees do not have the visual morphology adaptations that are typical of obligately nocturnal species, suggesting that behavioural change precedes structural adaptations (Wcislo & Tierney, 2009). Sufficiently detailed natural history information is not available for all species in our analysis to determine whether each dim-light active species was obligately or facultatively dim-light active, but future studies of this nature would ideally make this distinction. The availability of information in

non-visual sensory modalities is also likely to influence investment in antennal morphology, as the benefit of increasing sensitivity for a given sensory channel (e.g. olfaction) would depend on the availability of salient cues and signals in that sensory channel. Indeed, information in non-visual sensory channels may not be equally available for dim-light active species across taxonomic orders of insects, and such natural history differences potentially explain why our results do not support the view that dim-light activity is consistently associated with a higher density of antennal sensilla.

While our results do not provide evidence of increased investment in non-visual sensory organs in dim-light active insects, they also do not support complementary resource allocation between ommatidia and antennal sensilla that has been documented in fireflies (diurnal species have smaller eyes and longer antennae compared with nocturnal species) (Stanger-Hall *et al.*, 2018) and multiple species of *Drosophila* (Diptera: Drosophilidae) (Keeseey *et al.*, 2019), and is frequently characteristic of the troglomorphy exhibited of cave-dwelling arthropods (Christiansen, 2012; Hobbs III, 2012) including leiodid beetles (Peck, 1973, 1977, 1998). Finite energetic resources mean that elaboration of one morphological structure may be at the expense of another structure (Nijhout & Emlen, 1998; Emlen, 2001), and this might be especially evident across different sensory modalities, given the energetically expensive nature of complex sensory systems (Niven & Laughlin, 2008; Keeseey *et al.*, 2019). Nonetheless, our findings may be unsurprising in three ways. Firstly, animals typically use information in multiple sensory modalities (e.g. light and odour) simultaneously (Partan & Marler, 1999) and so it may be disadvantageous to invest heavily in receptors for one sensory modality at the expense of receptors for another modality; we note that taxa often differ in their reliance on information in a given sensory modality. Secondly, predicted negative correlations between investment in morphological structures are





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

not commonly observed (van Noordwijk & de Jong, 1986; Nijhout & Emlen, 1998): inverse resource allocation between traits can be context-dependent with variation in the direction of relationships between structures influenced by environmental conditions (Sgrò & Hoffmann, 2004) and, at least for animals which feed continuously, by changes in resource acquisition (Nijhout & Emlen, 1998). Thirdly, many instances of negative relationships in investment between sensory systems involve an absence of information in one sensory modality. For example, many species of cave-dwelling arthropods exhibit

regressed visual systems (e.g. smaller compound eyes with smaller and/or fewer ommatidia) and enhanced olfactory systems (e.g. longer antennae or higher densities of antennal sensilla) (Peck, 1973, 1977, 1998; Christiansen, 2012; Hobbs III, 2012). In the cavernous environment, characterized by the absence of natural light, natural selection would probably favour diversion of energetic resources from visual to non-visual sensory systems, as the energetically expensive visual system can no longer detect information that contributes to an individual's fitness (Stearns, 1989; Niven & Laughlin, 2008).

In conclusion, we show that dim-light active insects, across multiple taxonomic families, have larger compound eyes and ommatidia but no commensurate increase in the density of antennal receptors. This association of dim-light activity with comparatively greater ommatidia diameter and larger overall compound eye size is consistent with the predicted close relationship between sensory organ morphology, signal perception and the signalling environment (Endler, 1992), excluding radical departures in natural history among the taxa being compared. Given the potential for the use of insects to enhance restoration of anthropogenically degraded habitats (Prather & Laws, 2018; Elizalde *et al.*, 2020) and the need to inform conservation efforts with sensory ecology in response to the prevalence of anthropogenically induced environmental change (Lim *et al.*, 2008), understanding the interaction between sensory system adaptation and life history specialization is of increasing relevance. Knowledge of sensory organ morphology has implications for understanding how long-term anthropogenic changes to the photic environment – such as the penetration of artificial light at night into the once-dark night-time environment (reviewed by Tierney *et al.*, 2017; Hopkins *et al.*, 2018) or the presence of daytime light-reducing smog (White, 1976) – may influence species responses, especially because many insect species have relatively short generation times and temporally specific mating patterns. Such influences may have cascading effects upon insect community dynamics through altered signalling and communication behaviours. Insects provide important ecosystem services, including pollination, nutrient cycling, seed dispersal and bioturbation that are not only of obvious environmental importance but also considerable economic value (Losey & Vaughan, 2006; Elizalde *et al.*, 2020): effective signalling and communication within insect communities, at least for social insects, is essential to the efficiency of the provision of these ecosystem services (Dyer, 2002; Elizalde *et al.*, 2020).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Mean and standard deviation for each sensory morphology metric by active time, taxonomic order and taxonomic family. Note that where a metric has been Ln transformed (to normalize the distribution), this transformed metric rather than the untransformed metric was used in the statistical analysis. There are no contact chemosensilla density data for the Odonata as these sensilla are not present on their antennae.