



## Research

**Cite this article:** Sheehan MJ, Jinn J, Tibbetts EA. 2014 Coevolution of visual signals and eye morphology in *Polistes* paper wasps. *Biol. Lett.* **10**: 20140254.  
<http://dx.doi.org/10.1098/rsbl.2014.0254>

Received: 24 March 2014

Accepted: 11 April 2014

### Subject Areas:

behaviour, evolution

### Keywords:

sensory drive, visual signals, insect vision, coloration, paper wasps, perception

### Author for correspondence:

Michael J. Sheehan

e-mail: [mjsh1@berkeley.edu](mailto:mjsh1@berkeley.edu)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2014.0254> or via <http://rsbl.royalsocietypublishing.org>.

## Animal behaviour

# Coevolution of visual signals and eye morphology in *Polistes* paper wasps

Michael J. Sheehan<sup>1,2</sup>, Judy Jinn<sup>1,3</sup> and Elizabeth A. Tibbetts<sup>1</sup>

<sup>1</sup>Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

<sup>2</sup>Integrative Biology and Museum of Vertebrate Zoology, and <sup>3</sup>Department of Psychology, University of California, Berkeley, CA, USA

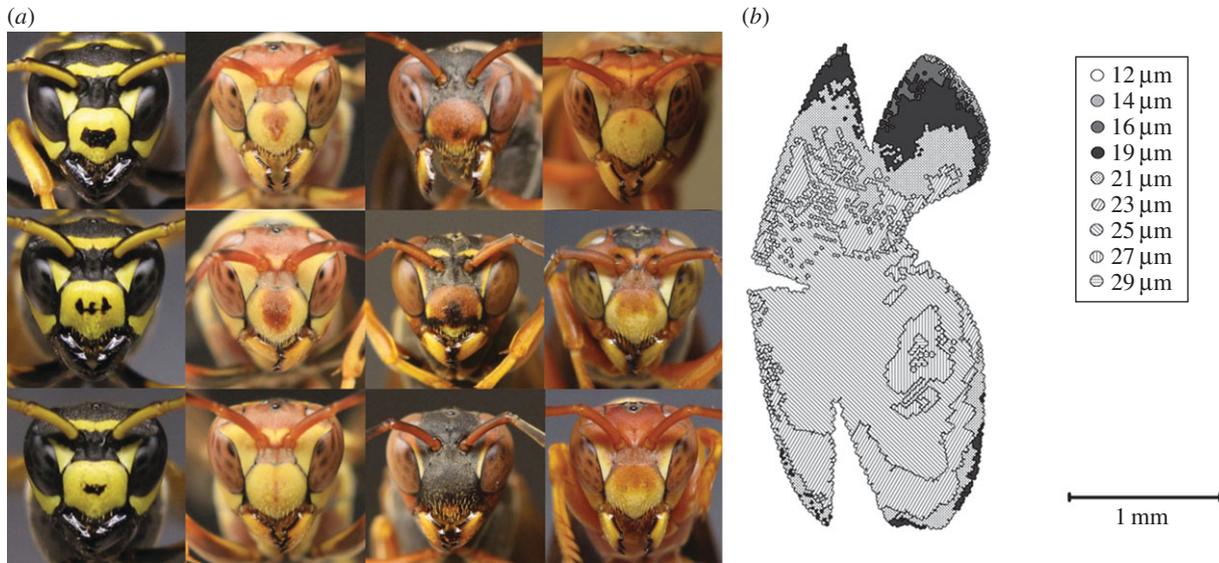
To be effective, signals must propagate through the environment and be detected by receivers. As a result, signal form evolves in response to both the constraints imposed by the transmission environment and receiver perceptual abilities. Little work has examined the extent to which signals may act as selective forces on receiver sensory systems to improve the efficacy of communication. If receivers benefit from accurate signal assessment, selection could favour sensory organs that improve discrimination of established signals. Here, we provide evidence that visual resolution coevolves with visual signals in *Polistes* wasps. Multiple *Polistes* species have variable facial patterns that function as social signals, whereas other species lack visual signals. Analysis of 19 *Polistes* species shows that maximum eye facet size is positively associated with both eye size and presence of visual signals. Relatively larger facets within the eye's acute zone improve resolution of small images, such as wasp facial signals. Therefore, sensory systems may evolve to optimize signal assessment. Sensory adaptations to facilitate signal detection may represent an overlooked area of the evolution of animal communication.

## 1. Introduction

Signal detectability depends on the interaction between signal form, receiver sensory system and transmission environment. Theory predicts complex coevolutionary dynamics among all of these factors [1]. Thus far, most research has focused on how prevailing environmental conditions shape sensory systems and how sensory systems constrain signal form. For example, the environment influences spectral sensitivity of cichlid visual systems, which in turn shapes the sexually selected coloration of males [2]. While there are well-known examples where receiver sensory systems evolve to facilitate eavesdropping on existing signals of predators or prey [3], less work has explored sensory system evolution in the context of intraspecific communication (though see [4]). Unlike eavesdropping on existing heterospecific signals, sensory system evolution in response to conspecific signals may play a crucial role in shaping the evolution of novel signals within a species. Recent work has demonstrated a surprising level of intraspecific sensory variability [5], indicating that some individuals are better at detecting and assessing signals than others. If receivers benefit from accurate signal assessment, selection could favour sensory organs or neural systems that improve detection and discrimination of established signals. Over time, this process could substantially influence the evolution of receiver sensory systems.

Here, we tested whether visual signalling is associated with differences in eye anatomy in *Polistes* paper wasps. Many *Polistes* have variable facial patterns that are signals of quality or individual identity while other species lack visual signals [6,7]. In all paper wasps with visual signals, information is conveyed by the relative differences in the size and shape of facial markings among individuals (figure 1a).

Visual signal perception is expected to be relatively challenging for wasps because insect compound eyes are poor at detecting and differentiating fine detail [8]. The effects of diffraction limit the spatial resolution of compound eyes



**Figure 1.** (a) Examples of the intraspecific pattern variability used for signalling in *Polistes* wasps. Species shown from left to right are *Polistes dominula*, *Polistes exclamans*, *Polistes fuscatus* and *Polistes bellicosus*. (b) A map of a compound eye of *Polistes bahamensis* with each facet grey shaded to show its relative size. The largest facets are clustered in an acute zone in the forward facing region of the eye. The grey scale indicates the relative size of the facets. (Online version in colour.)

because each lens that composes the eye is small. Where high visual resolution is favoured, insects evolve localized regions of larger lenses known as acute zones [8] (figure 1b; electronic supplementary material). Increased facet size within the acute zone improves resolution by reducing the acceptance angle and increasing photon capture.

If signal detection has favoured improved vision in wasps, we expect visual signalling in *Polistes* to be associated with increased maximum facet diameter. Visual signalling should be relatively more challenging for smaller species because space for signal display and visual resolution are constrained by body size [8]. Therefore, we predict that smaller species will evolve proportionally larger facets in their acute zones than larger species.

## 2. Material and methods

A common method for studying the apposition eyes of insects is to make replicas of the eye surface with clear nail lacquer which is allowed to dry [9]. Using Adobe PHOTOSHOP CS5, we measured the surface area of the eye and estimated the maximum facet diameter from photographs of the flattened replica taken at 45 $\times$  using a camera mounted to a dissecting scope. For each eye, we located the frontal region with the largest facets and then sampled facets sizes in a regular grid within and around this area, to cover the entire fronto-medial region of the eye. Measures were taken blind to the identity of the species. We estimated facet diameter by measuring the length of five facets along the X, Y and Z axes of the hexagonal grid of the eye in pixels [10]. By averaging the axes and dividing by 5, we derived an estimate of facet diameter. We used the largest estimate of facet size for each eye in our analysis. Species were classified as signalling or non-signalling based on the presence or absence of intraspecific colour pattern variation as previously described in the literature ([7]; electronic supplementary material). Theory suggests that intraspecific colour pattern variation is often used for social signalling [11]. All *Polistes* species with variable colour patterns that have been studied to date use the colour pattern variation for social signalling [12–15], and species lacking colour pattern variation have been shown to lack signals [6].

We used the topology inferred from recent phylogenetic hypotheses for *Polistes* in our analyses [16,17] (figure 2a). We

estimated branch lengths for comparative analyses using Pagel's method [18] in MESQUITE [19]. We considered four models: maximum facet diameter as a function of (i) eye surface area, (ii) signals, (iii) both eye surface area and signals as main effects and (iv) both main effects and their interaction using phylogenetic generalized least squares (PGLS) in the program 'caper' in R [20]. Results from each of these four models are reported in table 1. We first compared the fit of different models using AIC to a null model in which maximum facet diameter was included as a random effect and report  $\Delta$ AIC, where the better models have more negative  $\Delta$ AIC values. Next, we provide the significance values for individual factors for the best-fit model. Values for  $\lambda$  and  $\delta$  were estimated using maximum likelihood. Eye size was used to correct scaling relationships between body size and facet size, following previous studies of vespid eye morphology [21].

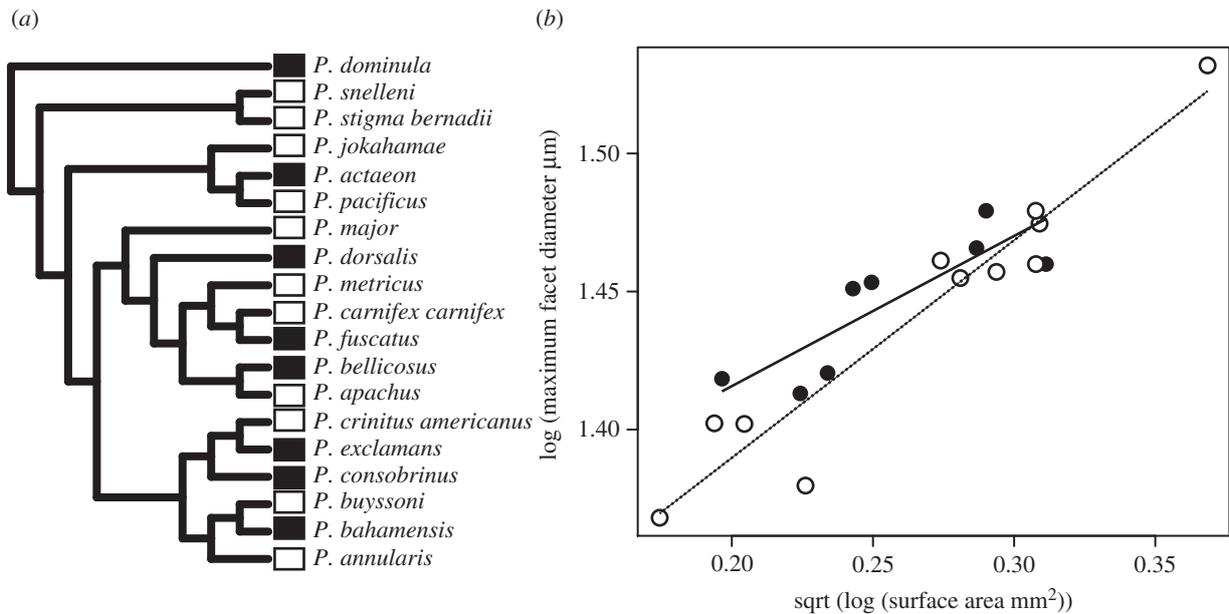
## 3. Results

The best-fit model to our data includes signalling status, surface area of the eye and their interaction (table 1). Other models explain less of the variation in maximum facet diameter. The results of the best-fit model support the hypothesis that signals can shape the evolution of sensory systems, as visual signalling is associated with significantly increased maximum facet diameter (PGLS,  $t = 2.76$ ,  $p = 0.014$ ). The maximum facet diameter of wasp eyes was also strongly influenced by eye surface area (PGLS,  $t = 10.87$ ,  $p < 0.0001$ ). Additionally, there was a significant interaction between surface area and signalling where visual signalling species with smaller eyes showed a greater increase in maximum facet diameter than visual signalling species with larger eyes (figure 2b, PGLS,  $t = -2.45$ ,  $p = 0.027$ ).

## 4. Discussion

Visual signals in *Polistes* influence the evolution of eye morphology; species with visual signals have increased maximum facet diameter in the acute zone relative to non-signalling species. Larger facets within the acute zone are expected to improve visual resolution [7], allowing for better signal detection.

Although visual signalling is associated with generally increased facet size, the data suggest that enlarged facets are



**Figure 2.** (a) The phylogenetic relationships among *Polistes* wasps examined in this study as well as their signalling status (filled circles, visual signals; open circles, no visual signals; see the electronic supplementary material for details of the phylogeny). (b) The relationship between surface area of the eye and the maximum facet diameter. Species with signals have larger facets than expected in their acute zone, as predicted if signals favoured increase visual acuity in receivers. The positive effect of signalling on maximum facet diameter is strongest in smaller species.

**Table 1.** PGLS model comparisons.

model terms	$r^2$	$F_{(d.f.)}$	$p$	$\lambda$	$\Delta AIC$
surface area	0.84	95.97 <sub>(2,17)</sub>	<0.0001	0.0	-32.98
signals	-0.06	0.002 <sub>(2,17)</sub>	0.97	0.51	2.00
surface area + signals	0.86	56.53 <sub>(3,16)</sub>	<0.0001	0.0	-34.21
surface area $\times$ signals	0.87	40.90 <sub>(4,15)</sub>	<0.0001	0.87	-37.03

not a requisite precursor for signal evolution. There is overlap in the facet size of species with and without visual signals. *Polistes* are highly visual species that live in open nests and are visual predators [22], so all species may have the baseline acuity necessary to perceive visual signals. Therefore, it is unlikely that differences in sensory biology among wasps have given rise to variation in signalling across *Polistes*. Nevertheless, assessing visual signals is sufficiently challenging that it has selected for larger maximum facet size to facilitate signal detection and discrimination.

Despite studies considering the potential importance of variation in sensory systems as a factor in signal evolution [5], surprisingly little work has considered the potential selective force that signals may exert on sensory systems. There is abundant evidence that signal features evolve to improve efficacy [23,24], and this study provides evidence that sensory abilities of receivers may also evolve to facilitate signal detection. Indeed, previous studies have provided evidence of cognitive adaptations in receiver processing to improve signal

detection and discrimination [25–27]. The present results suggest that selection may also act to improve sensory inputs.

Communication has important consequences for both senders and receivers. Therefore, it is important to understand how selection acts on both signal form and receiver sensory abilities to facilitate effective communication. Whenever signal detection is sufficiently challenging for receivers, receiver sensory systems may evolve to improve signal detection and discrimination. The results reported here highlight the need to consider sensory systems as dynamic entities in future models of signal evolution.

**Acknowledgements.** We thank Floria Uy, Brian Sedio and Darlene Bhavnani for assistance during data collection. James Carpenter and the AMNH generously provided access to their *Polistes* collections.

**Funding statement.** Collecting of specimens was financially supported by a grant to M.J.S. by the E.S. George Reserve of the University of Michigan. This material is based in part upon work supported by the National Science Foundation under grant no. IOS-1146139 to E.A.T.

## References

- Endler JA. 1992 Signals, signal conditions and the direction of evolution. *Am. Nat.* **139**, S125–S153. (doi:10.1086/285308)
- Seehausen O *et al.* 2008 Speciation through sensory drive in cichlid fish. *Nature* **455**, 620–626. (doi:10.1038/nature07285)
- Fullard JH. 1998 The sensory coevolution of moths and bats. In *Comparative hearing: insects* (eds RR Hoy, AN Pepper, RR Fay), pp. 279–326. New York, NY: Springer.
- Bybee SM, Yuan F, Ramstetter MD, Llorente-Bousquets J, Reed RD, Osorio D, Briscoe AD. 2012 UV photoreceptors and UV-yellow wing pigments in *Heliconius* butterflies allow a color signal to serve both mimicry and intraspecific communication. *Am. Nat.* **179**, 38–51. (doi:10.1086/663192)
- Ronald KL, Fernández-Juricic E, Lucas JR. 2012 Taking the sensory approach: how individual

- differences in sensory perception can influence mate choice. *Anim. Behav.* **84**, 1283–1294 (doi:10.1016/j.anbehav.2012.09.015)
6. Sheehan MJ, Tibbetts EA. 2010 Selection for individual recognition and the evolution of polymorphic identity signals in *Polistes* paper wasps. *J. Evol. Biol.* **23**, 570–577. (doi:10.1111/j.1420-9101.2009.01923.x)
  7. Tibbetts EA. 2004 Complex social behaviour can select for variability in visual features: a case study in *Polistes* wasps. *Proc. R. Soc. Lond. B* **271**, 1955–1960. (doi:10.1098/rspb.2004.2784)
  8. Land MF. 1997 Visual acuity in insects. *Annu. Rev. Entomol.* **42**, 147–177. (doi:10.1146/annurev.ento.42.1.147)
  9. Kelber A, Jonsson F, Wallén R, Warrant E, Kornfeldt T, Baird E. 2011 Hornets can fly at night without obvious adaptations of eyes and ocelli. *PLoS ONE* **6**, e21892. (doi:10.1371/journal.pone.0021892)
  10. Merry JW, Kemp DJ, Rutowski RL. 2011 Variation in compound eye structure: effects of diet and family. *Evolution* **65**, 2098–2110. (doi:10.1111/j.1558-5646.2011.01285.x)
  11. Dale J. 2006 Intraspecific variation in coloration. In *Bird coloration, volume 2, function and evolution* (eds GE Hill, KJ McGraw), pp. 36–86. Cambridge, MA: Harvard University Press.
  12. Tibbetts EA, Dale J. 2004 A socially enforced signal of quality in a paper wasp. *Nature* **432**, 218–222. (doi:10.1038/nature02949)
  13. Tibbetts EA, Sheehan MJ. 2011 Facial patterns are a conventional signal of agonistic ability in *Polistes exclamans* paper wasps. *Ethology* **117**, 1138–1146. (doi:10.1111/j.1439-0310.2011.01967.x)
  14. Sheehan MJ, Tibbetts EA. 2009 Evolution of identity signals: frequency-dependent benefits of distinctive phenotypes used for individual recognition. *Evolution* **63**, 3106–3113. (doi:10.1111/j.1558-5646.2009.00833.x)
  15. Tannure-Nascimento IC, Nascimento FS, Zucchi R. 2008 The look of royalty: visual and odour signals of reproductive status in a paper wasp. *Proc. R. Soc. B* **275**, 2555–2561. (doi:10.1098/rspb.2008.0589)
  16. Pickett KM, Wenzel JW. 2004 Phylogenetic analysis of the New World *Polistes* (Hymenoptera: Vespidae: Polistinae) using morphology and molecules. *J. Kans. Entomol. Soc.* **77**, 742–760. (doi:10.2317/E-18.1)
  17. Pickett KM, Carpenter JM. 2010 Simultaneous analysis and the origin of eusociality in the *Vespidae* (Insecta: Hymenoptera). *Arthropod Syst. Phyl.* **68**, 3–33.
  18. Pagel MD. 1992 A method for the analysis of comparative data. *J. Theor. Biol.* **156**, 431–442. (doi:10.1016/S0022-5193(05)80637-X)
  19. Maddison W, Maddison DR. 2001 MESQUITE: a modular system for evolutionary analysis. Version 2.76. See <http://mesquiteproject.org>.
  20. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2012 *Caper: Comparative analyses of phylogenetics and evolution in R. R package version 0.5*. See <http://cran.us.r-project.org/>.
  21. Barlow HB. 1952 The size of ommatidia in apposition eyes. *J. Exp. Biol.* **29**, 667–674.
  22. Downing H, Jeanne R. 1986 Intra- and interspecific variation in nest architecture in the paper wasp *Polistes* (Hymenoptera, Vespidae). *Insectes Sociaux* **33**, 422–443. (doi:10.1007/BF02223949)
  23. Rowe C. 2013 Receiver psychology: a receiver's perspective. *Anim. Behav.* **85**, 517–523. (doi:10.1016/j.anbehav.2013.01.004)
  24. Endler JA, Westcott DA, Madden JR, Robson T. 2005 Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* **59**, 1795–1818. (doi:10.1111/j.0014-3820.2005.tb01827.x)
  25. Sheehan MJ, Tibbetts EA. 2011 Specialized face learning is associated with individual recognition in paper wasps. *Science* **334**, 1272–1275. (doi:10.1126/science.1211334)
  26. Loesche P, Stoddard PK, Higgins BJ, Beecher MD. 1991 Signature versus perceptual adaptations for individual vocal recognition in swallows. *Behaviour* **118**, 15–25. (doi:10.1163/156853991X00175)
  27. Parr LA. 2011 The evolution of face processing in primates. *Phil. Trans. R. Soc. B* **366**, 1764–1777. (doi:10.1098/rstb.2010.0358)