

experimenter or a conspecific achieve a goal that did not involve food. In one such study, chimpanzees would hand an object to an experimenter who was reaching for it, suggesting helpful motivations. In another experiment, chimpanzees would open doors — a novel action — for conspecifics who were unable to get through. However, chimpanzees in captivity are trained to give objects back to their caregivers and are therefore used to fetching things, and releasing doors to watch them opened is intrinsically interesting. Benefits to others could arise as by-products of the experimental design. When confronted with superficially similar tasks, one which benefits conspecifics and one which prevents them from eating, chimpanzees could be initially attracted and then lose interest when not rewarded for their choices.

While evidence for prosociality in chimpanzees has not been robust, other, perhaps less competitive species might be better candidates. Yet, to date, there has been no clear evidence for prosociality in experiments on bonobos, the more socially tolerant of the two *Pan* species. Cooperatively breeding New World monkeys (cotton-top tamarins and common marmosets) do provision food to offspring in the wild, and in captivity will make prosocial choices under limited circumstances, but it is not entirely evident that they fully understand the benefits to others. In other tasks, such as rescuing trapped conspecifics, rats — ever the go-to animal for psychological testing — have been shown to be prosocial. But again, ulterior motives need to be ruled out. Rescues can come about as by-products of exploratory behaviour. As for imbuing psychological mechanisms such as empathy onto the animals, caution is needed. Ants, for instance, also ‘rescue’ trapped ants. Empathy is less likely to play a role here, and may not play a role in rats. As with all behaviours, the more similar a species is to us, the more prone we are — and the more cautious we must be — to anthropomorphising.

We have just begun to rigorously scratch at prosocial behaviour in other species, and we continue to dig beneath the skin of human prosociality. Humans, while not always

prosocial, have a concern for the welfare of others. Other species, while sometimes acting for the benefit of others, may not rely on homologous mechanisms. The intention to help others, with an understanding of the consequences of the actions and the means to identify with the needs of others, may be uniquely human. While our closest living relatives can recognise something of the intentions of others, they do not appear to care so much. If so, it is possible that direct reciprocity springs from a concern for the welfare of others, and that motivational rather than cognitive factors account for the limited evidence for reciprocal altruism in other animals. Prosociality will have evolved from mechanisms seen in other species — perhaps emotional contagion, parental attachment or ownership — but somewhere after the split from *Pan*, a concern for the welfare of others, including non-kin, allowed for our species to engage in large-scale cooperation. So, while intuitively obvious, prosociality is not as widespread as one would expect and is surprisingly difficult to distinguish from look-alikes.

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Polarization vision seldom increases the sighting distance of silvery fish

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Although the function of polarization vision, the ability to discern the polarization characteristics of light, is well established in many terrestrial and benthic species, its purpose in pelagic species (squid and certain fish and crustaceans) is poorly understood [1]. A long-held hypothesis is that polarization vision in open water is used to break the mirror camouflage of silvery fish, as biological mirrors can change the polarization of reflected light [2,3]. Although, the addition of polarization information may increase the conspicuousness of silvery fish at close range, direct evidence that silvery fish — or indeed any pelagic animal — are visible at longer distances using polarization vision rather than using radiance (i.e. brightness) vision is lacking. Here we show, using *in situ* polarization imagery and a new visual detection model, that polarization vision does not in fact appear to allow viewers to see silvery fish at greater distances.

We independently imaged 154 individuals of 12 species of silvery fish *in situ* using a custom-built polarization-sensitive camera [4] deployed on the Great Barrier Reef (depth 5–10 m, angle of view typically within 15–30° of horizontal; Supplemental information). As expected, the Weber radiance contrasts of the lateral surfaces of the imaged fish (compared to the background water) were low, ranging from –0.2 to 1, with 50% of the values falling between –0.07 and 0.16. The differences between the polarization characteristics of the fish and the background were also low. The degrees of

polarization of the fish were tightly correlated with, but consistently lower than, those of the backgrounds (Supplemental information). The angles of polarization of the fish were also correlated with those of the backgrounds, with the difference following a normal distribution with a standard deviation of 3.1° (Supplemental information).

We then calculated radiance and polarization sighting distances. Radiance distance was based on Weber contrast and excluded polarization information, while polarization distance was based on the visual detection model developed by How and Marshall [5] and excluded radiance information (Supplemental information). The average polarization sighting distances for each species were always less than the average radiance sighting distances (Figure 1), even when: first, the polarization sensitivity of the putative viewer's visual system (S_p) was set to the extremely high value of 10; second, the images were limited to cases where the background polarization (DoLP_{bkgd}) was greater than 25%; and third, the putative viewers were allowed to rotate their eyes from -45° to $+45^\circ$ and choose the orientation that gave them the longest sighting distance. The effect of S_p on polarization sighting was large when S_p increased from 2 to 5, but minor when S_p was further increased from 5 to 10 (Figure 1). The effect of selecting only images with more highly polarized backgrounds (40 of a total of 154 images) was typically minor to moderate (Figure 1; columns 1 and 2 versus columns 3 and 4). Eye rotation produced similarly minor effects (Figure 1; columns 2 and 4 versus columns 1 and 3). Further analysis showed that polarization and radiance contrasts attenuated at nearly the same rate, and that differences in sighting distance were primarily due to inherent contrast differences (i.e. contrasts at zero viewing distance). Once normalized by their respective detection thresholds, the inherent radiance contrast of a given fish nearly always exceeded its inherent polarization contrast (Supplemental information). At least two factors may limit the utility of polarization vision underwater.

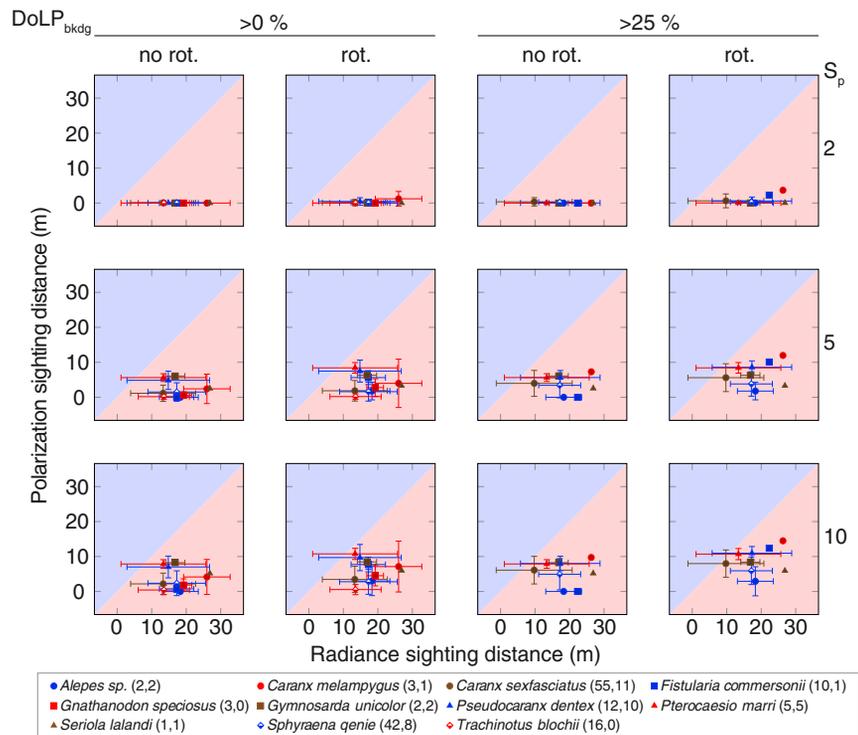


Figure 1. Polarization versus radiance sighting distances estimated from the radiance and polarization information captured by the polarization camera.

In columns 1 and 2, all images were included. In columns 3 and 4, only those images for which the background polarization (DoLP_{bkgd}) was greater than 25% were included. Within each pair of columns, two cases were considered: 1) the viewer's head was oriented such that the polarization photoreceptors are oriented horizontally and vertically ('no rot.'). 2) the viewer tilted its head (over a range of -45° to $+45^\circ$) such that the polarization sighting distance was maximal for each image ('rot.'). The polarization sensitivity of the microvilli S_p varies by row from 2 to 5 to 10. The two numbers following each species name in the legend are the total N and the N for which the background polarization was greater than 25% respectively. The error bars indicate standard deviation. Each graph is divided into two regions. In the pink region (which contains nearly all the data), the radiance sighting distance is greater than the polarization sighting distance. In the blue region, the opposite is true.

The first is that the underwater light field is typically not highly polarized [6]. Even in the clear waters of the Great Barrier Reef and even in the horizontal viewing direction, where underwater polarization is typically greatest, the degree of polarization of the background water in the sampled images never exceeded 40% (Supplemental information). This, together with the fact that all but five of the 154 silvery fish examined had degrees of polarization less than that of the background, limited the polarization information available. This natural situation is quite different from most lab-based studies on behavioral responses to polarized light, where the degree of polarization of the target and/or the background (created by sheet polarizers) are near 100% [7]. Recent

approaches [8] have begun to address this issue.

Second, the polarization sensitivities (S_p) of animals are relatively low [9]. Therefore, images taken by a polarization-sensitive camera often show more features than what is perceived by an animal's visual system. The effect is less than might be expected, however. Although S_p for a research-quality sheet polarizer is near 500, the sighting distance that would be achieved using it is only roughly double what would be achieved using a filter with an S_p of 10. This is both because it is $(S_p - 1)/(S_p + 1)$ that matters [10], not S_p itself, and because contrast is attenuated exponentially (Supplemental information).

Of course, animals with polarization vision may not choose between this

ability and radiance vision but instead employ both simultaneously, much as humans use both chromatic and achromatic information to assess a scene. Thus, at close range, a polarization-sensitive animal can likely use both polarization and radiance cues to obtain a more complete and potentially more discernible view of an object. However, it is unlikely that an animal can combine the two visual modalities to increase sighting distance. Once one modality drops below the threshold for detection, it cannot improve the other modality's sighting distance limit. This is analogous to underwater color vision, which can provide additional information at close range, but does not increase sighting distance because the image of the target at long range generally has the same color as the background due to the effects of the intervening water (i.e. at a great enough distance, all fish in blue water eventually look blue).

While our study is limited in location and number of species, it is the first to combine *in situ* polarization imagery with a realistic model of visual perception that allows us to quantitatively compare the utility of polarization vision versus radiance vision when viewing silvery fish. The results show clearly that silvery fish, while by no means cryptic relative to polarization vision, are nevertheless seen at the greatest distances using radiance information alone. This should be examined in other species, habitats, and especially at viewing angles further from horizontal to determine if there is a situation in which polarization vision can increase detection range. In addition, it is known that various polarization-based haze-reduction algorithms [1] can, in certain situations, increase the sighting distance of any target, silvery or not. Because it is not known whether these algorithms have been implemented by any animal, they were not the focus of this study. However, preliminary modeling of the simplest of these strategies — using the vertical channel to minimize the background light and thus boost achromatic contrast — show some, though often minimal, benefit for two-thirds of the sampled fish (Supplemental information), but at the cost of reducing the sighting distance for the remainder of the fish. Further research should explore whether this

algorithm or other more complex ones are used by extant visual systems.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and one figure can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.07.030>.

AUTHOR CONTRIBUTIONS

S.J. conceived the study, V.G. and S.P. developed and calibrated the polarization camera, N.J.M. collected the imagery, S.J. and Y.L.G. developed and implemented the visual model, and all interpreted the results and wrote the manuscript.

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Correspondence Evidence for meiotic sex in bdelloid rotifers

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In their study of genetic exchange in the bdelloid rotifer *Adineta vaga*, Debortoli *et al.* [1] conclude that the patchwork pattern of allele sharing among three individuals in the genomic regions they examined is “...unlikely to arise in cases of PTH (*Oenothera*-like) meiosis since haplotypes are transferred as entire blocks...” and therefore that “Genetic exchange among bdelloid rotifers is more likely due to horizontal gene transfer than to meiotic sex.” This assumes without justification that horizontal gene transfer (HGT) in bdelloids precludes the sexual transmission of entire haplotypes, for which we have reported evidence in the bdelloid *Macrotrachela quadricornifera* [2]. And it does not consider the contribution to such a patchwork pattern that would result from conversion and subsequent outcrossing, even in *Oenothera*-like systems.

Moreover, the group of three individuals studied by Debortoli *et al.*, in which the shared sequences are considerably diverged, is not well suited to the detection of sex in a population that may include numerous distinct *Oenothera*-like haplotypes. For that purpose, one should employ individuals whose shared sequences are identical or nearly so in order to enrich for direct descendants of the F1 from a cross. Otherwise, subsequent outcrossing could replace the shared haplotypes with others, removing the evidence for transmission of entire haplotypes. It is therefore important to note that in the group of three individuals we studied the shared sequences were either identical or very nearly so, allowing us to observe the specific and unusual pattern of sharing expected for *Oenothera*-like meiosis. To explain the presence of such