St. Kilda Ho^R alleles are those that have been present since the island was first colonized or reflect subsequent, perhaps recent, admixture of sheep form elsewhere. For instance, coat colour polymorphisms in Soay sheep reflect admixture with modern breeds in the last 150 years [5]. So the Soay population might have been introgressed by superior Ho^R alleles that conceivably confer positive fitness effects through pleiotropy or close linkage with other genes. This view gains some support as over the last 20 years the Ho^R allele has been increasing in frequency in the population by ~20%. However, this rate of increase need not be the result of selection as it is not distinguishable from random fluctuations through drift [5].

The lesson from this study is simple. Pin-pointing the genetic basis of sexual traits in natural populations is likely to throw up challenging observations. It’s too early to conclude that overdominance at single loci will play a large role in explaining the lek paradox, or that genetic capture and sexual antagonism play no part. But, the vast diversity of bizarre and extravagant ornamentation and weapony used in courtship is ripe for an unraveling of its genetic basis.

References
Specific retinal ganglion cells, while signals from green cones inhibit them. In birds, both pathways are believed to be completely separated: achromatic vision uses signals from broadly tuned receptors, the double cones, while color vision uses signals from four types of narrowly tuned single cones [9].

**Insect Colour Vision**

Crustacean and insect compound eyes share similarities (Figure 1) that give hints to the evolution of insect colour vision [10]. Their compound eyes consist of up to several thousand individual units, the ommatidia, each with a separate optic apparatus and several photoreceptor cells. Many crustaceans and most insects have two, three or more different spectral types of receptor cell [11]. In a decapod crustacean with basic colour vision, spectral sensitivity is linked to two anatomical classes of receptor cell. Seven long-wavelength-sensitive (LWS) receptors have proximal rhabdoms and short visual fibres projecting to the first ganglion of the visual pathway, the lamina. A single UV-sensitive receptor has a distal rhabdom and a long visual fibre projecting to the second visual ganglion, the medulla [12]. Colour vision must rely on comparing signals from these two types of receptors.

Insect ommatidia, as a rule, have six receptors with axons terminating in the lamina. In bees, they are LWS [13] and used as an input channel to their achromatic pathways analysing information on patterns, shape and motion [9]. The remaining photoreceptors project directly to the medulla. Two of these have distal rhabdoms and are short-wavelength-sensitive, just as the distal receptor in decapods. Their sensitivities differ between ommatidia [14–16], giving rise to a random array of three ommatidial types: ommatidial type one has one blue and one UV receptor, type two has two UV receptors and type three has two blue receptors. It is obvious that — just as in decapod crustaceans — colour vision depends on signals from receptor cells with axons terminating in the lamina and those with axons terminating in the medulla. LWS receptors with short visual fibres contribute to colour vision and achromatic pathways.

In flies, just as in other insects, six LWS receptors (R1–6) project to the lamina with short fibres. An additional UV-sensitive accessory pigment and the neural wiring result in broad spectral tuning and high sensitivity [4]. Just as in bees, these six receptors are the basis of achromatic vision [4]. Based on the remaining two receptors, R7 and R8, which have long visual fibres projecting to the medulla, flies have two types of ommatidia: in ‘pale’ ommatidia, R7 is UV-sensitive (335 nm) and R8 is blue-sensitive (460 nm). In ‘yellow’ ommatidia, R7 is also UV-sensitive but expresses a different opsin (355 nm), and R8 is green-sensitive (530 nm) [17].

At the time when the spectral sensitivity of fly receptors was first studied, it seemed most sensible to assume that fly colour vision builds exclusively on the spectral classes found in R7 and R8, without any contribution from the broadly tuned receptors R1–6. The highly sensitive achromatic pathway of flies, based on signals from R1–6, was assumed to be completely separated from the parallel colour vision pathway that uses signals from R7 and R8 [18]. This general belief — fly R1–6 and R7–8 being analogues to human rods and cones — has not been challenged for
decades. Only five years ago, a concise study [19] describing all medulla neurons connected to R7 and R8 could claim to list the entire colour vision pathway of Drosophila.

The new study by Schnaitmann and colleagues [8] now shows convincingly that, contrary to these expectations, photoreceptors R1–6 do indeed contribute to colour vision in Drosophila. Using a blind mutant and GAL4-drivers they generated flies with restricted sets of functional photoreceptors and tested their colour discrimination. Flies with functional ‘yellow’ ommatidia, but not those with ‘pale’ ommatidia, discriminated green and blue as well as normal flies, even with reversed intensities. As expected, flies which had no functional receptors except R7 and R8 in ‘yellow’ ommatidia also did well. However, even flies which only had functional receptors R8 and R1–6 in ‘yellow’ ommatidia could do the job.

This came as a surprise. It implies that the broadly tuned receptors R1–6 contribute to both the achromatic pathway and the colour vision pathway in flies. Schnaitmann et al. [8] went one step further and generated flies lacking neurons in the lamina. They showed that the colour vision pathway depends on neurons known as ‘lamina monopolar cells’ to convey the signals from R1–6 to the medulla, where they can be compared neurally with signals from R7 and R8. Further studies can now unravel the full colour vision pathway of Drosophila. The results by Schnaitmann and colleagues [8] strongly suggest that flies may have a rather conserved insect colour vision system. Thus, anything we learn from Drosophila will help us to understand colour vision not only in this tiny fly that did not seem to care much about colour, but even in bees and other insects.

More generally, we learn that flies use information more efficiently than previously thought. The analogy that fly receptors R1–6 serve a similar function as human rods, while fly receptors R7 and R8 are comparable to our cones, no longer holds. More adequately, flies use their receptors in a similar way as we use our cones: all receptors are involved in colour vision, and most—in flies six out of eight receptors in each ommatidium, in humans the red and green cones (93% of all cones) — are additionally used for achromatic vision, in a parallel pathway. Birds remain the challenge: why do the animals that have the sharpest vision of all use only half of their cones — the double cones — for high acuity achromatic vision? Or did we, just as in fruit flies, miss something? The new results on Drosophila [8] have challenged a paradigm: parallel visual pathways may share the same input more often than we thought.

References

Lund Vision Group, Department of Biology, Lund University Sölvegatan 35, 22362 Lund, Sweden.
E-mail: Almut.Kelber@biol.lu.se, Miriam.Henze@biol.lu.se
http://dx.doi.org/10.1016/j.cub.2013.10.025

Nuclear Division: Giving Daughters Their Fair Share

How do nuclear components, apart from chromosomes, partition equally to daughter nuclei during mitosis? In Schizosaccharomyces japonicus, the conserved LEM-domain nuclear envelope protein Man1 ensures the formation of identical daughter nuclei by coupling nuclear pore complexes to the segregating chromosomes.

Alison D. Walters and Orna Cohen-Fix

When we consider what constitutes a successful mitosis, we immediately think of the correct segregation of chromosomes into two daughter nuclei. However, it takes more than chromosomes to make a nucleus. The integrity of the daughter nuclei and the organization of the chromatin within them rely on the presence of an intact nuclear envelope (NE). The NE is a double lipid bilayer, with an outer membrane that is continuous with the ER, and an inner nuclear membrane (INM) that contains proteins that interact with chromatin and other nuclear components. The NE is perforated by nuclear pore complexes (NPCs) that allow selective passage of proteins between the nucleoplasm and cytoplasm. In metazoans, a filamentous network,