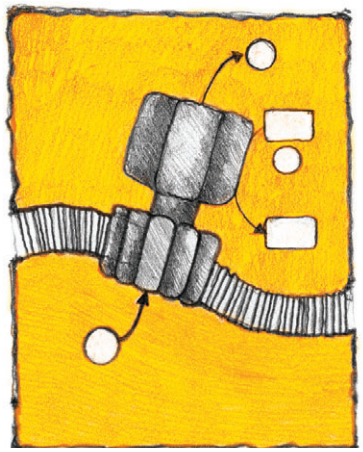
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

PHOTOTRANSDUCTION



## A NEW VIEW OF PHOTORECEPTORS

Eyesight relies on light-sensitive cells called photoreceptors, which convert light into electric signals that are passed on to the brain. Two types of photoreceptors emerged during animal evolution: ciliary photoreceptors (cones and rods) in vertebrates and microvillar photoreceptors in many invertebrates. The mechanism of visual signal transduction (phototransduction) has been worked out in great detail for vertebrate photoreceptors. However, there are many unanswered questions in invertebrates. In particular, how light leads to the opening of ion channels that generate the electric signal is not understood. In an exciting study published recently in *Science*, Roger Hardie and Kristian Franze from the University of Cambridge, UK, examined the phototransduction mechanism in the eyes of *Drosophila* flies. What they found was most surprising: photoreceptor cells contract slightly in response to light. Hardie and Franze postulated that a mechanical force contributes to gating of the ion channels that produce an electrical signal.

The basic optical unit of the fly's compound eye is the ommatidium, which is made of eight photoreceptor cells. Densely packed microvilli (tubular membrane protrusions) in the photoreceptors – which harbour the visual pigment (rhodopsin) and associated signal transduction components – assemble to form light-guiding structures called rhabdomeres. It is known that light absorption activates rhodopsin, which triggers a signalling cascade that activates an enzyme known as phospholipase C (PLC). The activity of this enzyme, in turn, somehow activates the ion channels, known as TRP channels, but how this occurred was not clear.

Knowing that TRP channels in some other systems are mechanosensitive, Hardie and Franze came up with the brilliant idea of testing whether photoreception in *Drosophila* is connected with a mechanical force that might contribute to channel gating. To answer this question they performed stunning experiments using atomic force microscopy (AFM) to measure small changes in photoreceptor height by connecting the microscope's cantilever to the photoreceptor tip.

Intriguingly, when they exposed the eye to brief flashes of light they recorded quick contractions of the photoreceptor cells that were even visible through a conventional microscope. They also showed that the contractions were dependent on PLC activity, because they were eliminated in *Drosophila* mutants lacking a functional PLC. But how does photoreceptor contraction trigger TRP channels to open and produce a light-activated electrical signal?

Hardie and Franze hypothesized that the contractions are due to small changes in microvillar membrane tension, which are amplified because the microvilli are arranged in large stacks. PLC cleaves a lipid in the microvillar membrane, removing a bulky head group from the inner membrane, which could alter membrane tension, and this is detected in turn by TRP channels that open to generate an electric signal. To support this hypothesis, the duo inserted gramicidin, a well-known mechanosensitive ion channel, into the plasma membranes of isolated photoreceptor cells that lacked functioning TRP channels and measured the cells' electric activity. The modified photoreceptors responded electrically to light, indicating that gramicidin and TRP channels function in a similar mechanosensitive manner. Finally, the duo manipulated membrane stiffness with a range of compounds and solutions and found that that membrane tension is likely to be an essential factor in phototransduction.

Hardie and Franze have provided evidence that phototransduction in *Drosophila* eyes involves a mechanical force. Thus, changes in membrane tension appear to couple PLC activity to the opening of mechanosensitive TRP channels.

10.1242/jeb.077727

**Hardie, R. C. and Franze, K.** (2012). Photomechanical responses in *Drosophila* photoreceptors. *Science* **338**, 260-263.

**Hans Merzendorfer**
**University of Osnabrueck**
**merzendorfer@biologie.uni-osnabrueck.de**

VISION

## GANNET'S GAZE STAYS FOCUSED UNDERWATER

Plunging birds' eyes are keen enough to detect fishy prey, even through the erratic shimmer of the ocean's surface, before the birds dive rapidly into the water. For some of these birds, however, merely seeing prey from the sky is insufficient for catching a meal. They must also have exceptional vision while submerged, which is no easy feat. While flying in air, the eye's ability to focus is provided by the refractive power of the cornea. However, while submerged, the refractive index of the cornea is about the same as that of the surrounding water – so there has to be some other mechanism for focusing an image on the retina.

Gabriel Machovsky-Capuska of Massey University, New Zealand, and colleagues from around the world wanted to know whether Australasian gannets, birds that plunge dive and swim to catch prey, have found a solution to this visual tradeoff. Gannets are unique in being one of the few species of bird that both plunge dive and 'wing flap' underwater. This suggested to the researchers that the gannets could be visually tracking fish even while submerged.

To determine whether gannets caught fish during the plunge section of their dive or after a visually guided underwater chase, Machovsky-Capuska and colleagues filmed diving gannets both above and below water in the field, noting when, and how many, successful prey captures resulted from each dive. The vast majority of successes occurred during the wing-flap stage of a dive – when the birds must be tracking the fish underwater.

Encouraged by these findings, the researchers photographed the eyes of several gannets both above and below the water. From the photographs, they used the reflection of light off the gannet's eyes to measure the curvature of the cornea, a proxy for its refractive power. They also used infrared photorefraction to determine how well focused an eye is from the position of light reflected off the retina.

The gannet's eyes were usually hyperopic, or far-sighted, in air and underwater. However, the birds were capable of achieving myopia, or near-sightedness, within about a tenth of a second of submergence. This ability to focus differently represented the birds' capacity to adapt to underwater vision even without the refractive power of their cornea.

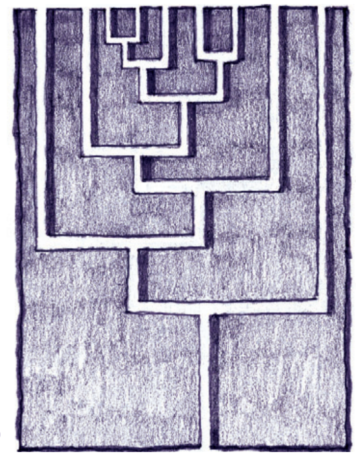
Machovsky-Capuska and colleagues suggest that gannets may change the shape of their eye lens, instead of the retina, to retain the ability to focus. Many aquatic animals, including fish, amphibians, whales and penguins have evolved spherical lenses to cope with the challenges of underwater vision. Specialized lens morphology may permit the gannet's remarkable ability to switch from aerial to aquatic vision quickly and compensate for the cornea's ineffectual refractive power in water. More research will undoubtedly reveal the mechanism of the gannet's remarkably flexible visual system. In the interim, New Zealand fish might consider camouflage.

10.1242/jeb.077701

**Machovsky-Capuska, G. E., Howland, H. C., Raubenheimer, D., Vaughn-Hirshorn, R., Würsig, B., Hauber, M. E. and Katzir, G.** (2012). Visual accommodation and active pursuit of prey underwater in a plunge-diving bird: the Australiasian gannet. *Proc. Biol. Sci.* **279**, 4118-4125.

**Kara Feilich**
**Harvard University**
**kfeilich@fas.harvard.edu**

SLEEP



## FOR SANDPIPERS, TO SNOOZE IS TO LOSE!

A considerable body of evidence suggests that sleep is essential to sustain the brain, with insufficient slumber linked to deficits in attention, motivation, sensory–motor processing and memory. Alternatively, some scientists propose that sleep may simply serve to conserve energy at times when activity is not constructive. In this manner, animals might evolve the ability to forego sleep when ecological demands favour wakefulness. The pectoral sandpiper (*Calidris melanotos*) is a polygynous Arctic seabird with strong sexual dimorphism. Males of this species expend extensive time and energy defending their territories and displaying for their less enthusiastic female counterparts. With no investment in their young post-copulation and, at such northerly latitudes during this season, no darkness to limit the chances to attract females, mating effort is all or nothing for these males. As John Lesku from the Max Planck Institute for Ornithology and his European colleagues realized, time spent dozing might limit opportunities for male sandpipers to pursue fertile females. As male reproductive fitness in these birds is determined by access to fruitful females, they hypothesized that sexual selection may favour the ability of males to forego sleep without experiencing the ill effects of sleep deprivation.

Lesku and his team deployed customized radiotelemetry-based systems to record activity patterns and log male–female interactions in a population of pectoral sandpipers on the Arctic tundra at times when females were fertile and post-fertile. They found that males were livelier than females in both periods, and that male activity decreased once fertile females were no longer available. One of the males was even active over 95% of the time for a 19 day stretch! Next, the researchers used a novel biologger to simultaneously measure brain and muscle activity – the latter indicative of neck movement – to determine whether sluggish males were actually sleeping more instead of just sitting peacefully. These results showed that the sandpipers quickly transitioned from being actively awake to sleeping, with no intermediate period of quiet restfulness: so inactivity and activity are accurate proxies for sleep and wakefulness in this bird.

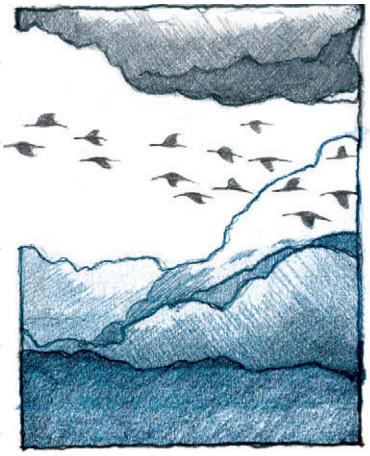
Focusing on the birds' activity patterns, the team found that the time spent sleeping per day was highly variable, ranging from 2.4 to 7.7 h and, in line with their hypothesis, males that slept the least sired the most offspring. Although the males that slept less did also sleep more deeply, they remained sleep deprived overall. This demonstrates that these males maintained the high level of performance necessary to 'score' a mate despite their sleep deprivation, challenging the view that sleep loss incurs inevitable costs. Continuing the project over several years, the researchers discovered that the birds that fathered more offspring were more prone to return to the study site. If sleep loss corresponds to reduced survivorship, the opposite should be true. In addition, males that returned were more likely to sire offspring in the subsequent year. This implies that reproductively successful males either have increased long-term survival or at least greater site fidelity. Lesku's team revealed that sacrificing sleep ensures paternity in pectoral sandpipers, suggesting that the capacity to forego sleep is adaptive for males of this species. For these birds, to snooze is most certainly to lose!

10.1242/jeb.077719

**Lesku, J. A., Rattenborg, N. C., Valcu, M., Vyssotski, A. L., Kuhn, S., Kuemmeth, F., Heidrich, W. and Kempenaers, B.** (2012). Adaptive sleep loss in polygynous pectoral sandpipers. *Science* **337**, 1654-1658.

**Jessica U. Meir**
**Harvard Medical School**
**jmeir@partners.org**

SEXUAL SELECTION



## COOL SONGS ARE SEXY FOR LINCOLN'S SPARROW CHICKS

Most people will agree that a nicely performed song by a guy hoping to impress a girl will go a long way. This is particularly true in the world of birds, where singing is one of the main ways males try to seduce females. Interestingly, many songbirds focus their serenading efforts at dawn, which is usually the coldest time of day. But why would they want to do this? Singing at dawn represents a thermal challenge: metabolic rate increases in the cold and therefore the task of singing becomes more energetically costly. But perhaps that is exactly why they do it, to impress females with their cold tolerance and dazzling performance. If so, then female birds would find songs sung in the cold sexier than songs sung in warm weather. To test this hypothesis, Michaël Beaulieu and Keith W. Sockman from the University of North Carolina, USA, studied the songs of Lincoln's sparrows at different temperatures.

Lincoln's sparrows are common throughout Canada and parts of the USA. The average temperature during their song chorus is 7.8°C, well below the temperature (23°C) beneath which metabolic rates rise above basal levels. To determine whether female Lincoln's sparrows are more attracted to songs performed at cold temperatures than songs performed in warm conditions, Beaulieu and Sockman divided females into two groups, and played them songs performed by two males. First, they exposed one group of females to one male's songs at 16°C and played the second male's songs at 1°C, recording how long the females spent next to the loudspeaker. However, they had to be sure that the females weren't simply hanging out by the speaker because they preferred that male's recital, so they reversed the temperatures when they played the songs to the second group of females, playing the first set at 1°C and the second set at 16°C. The researchers also tested whether the females would remember if a particular song had been sung in the cold and if they preferred it over a song that they had heard at warmer temperatures.

Having analysed the females' preferences, the team found that the female sparrows spent 40% more time close to the speaker when they were serenaded in the cold than when they were listening to love songs in mild conditions. Furthermore, even at 16°C, females preferred the song they had initially heard in the cold, so songs performed in the cold are clearly sexier than songs that are warbled when it's warm.

For songbirds, singing in the cold seems to be a way of advertising the quality of a male in the form of cold tolerance. The preferred choice of females for males singing at low temperatures might represent their choice of a male that may be energetically fitter and may be able to endure energetic challenges better than soft males who sing in the warm. The fact that females remembered which songs were performed in the cold might allow females to remain in the roost or perform other activities or while listening and then reciprocate the male's advances later in the day – when timing and temperature may be more convenient. Unfortunately, females' preferences for males with the stamina to serenade on chilly mornings may be severely affected by climate change as morning temperatures rise, although one thing is clear: cool singing is hot for birds.

10.1242/jeb.077735

**Beaulieu, M. and Sockman, K. W.** (2012). Song in the cold is 'hot': memory of and preference for sexual signals perceived under thermal challenge. *Biol. Lett.* **8**, 751-753.

**Viviana Cadena**
**University of Melbourne**
**viviana.cadena@melbourneu.edu.au**