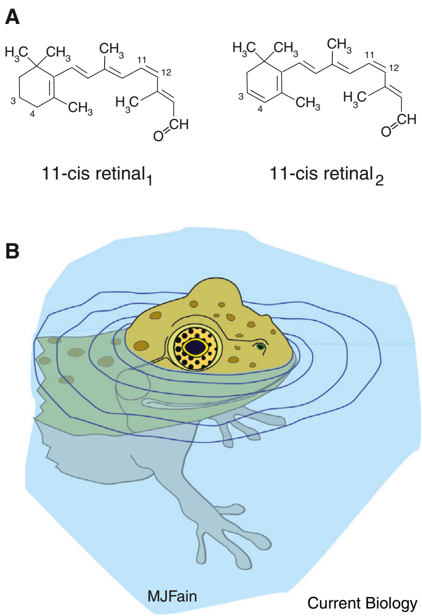

Figure 1. Visual chromophores of bullfrog.
(A) Structures of 11-*cis* retinal$_1$ and 11-*cis* retinal$_2$ (3,4-didehydroretinal). (B) Bullfrog swimming or floating with eye just above water. Dorsal retina containing retinal$_2$ would look downward into water, and ventral retina containing retinal$_1$ upward into air.

leaves unresolved the pathway leading to the synthesis of 11-*cis* retinal$_2$. The substrate for the 3,4-dehydrogenase could be retinol, retinal, or retinyl ester either as 11-*cis* or as the all-*trans* isomer. Is the Cyp27c1 protein in the endoplasmic reticulum along with the enzymes that convert all-*trans* retinol to 11-*cis* retinal (such as LRAT and the RPE65 isomerase), or is it somewhere else in the RPE? Do melanopsin-containing ganglion cells in freshwater vertebrates also use retinal$_2$? If not, where is the retinal$_1$ for melanopsin synthesized, and how is it kept separate from the retinal$_2$ produced by the retinal pigment epithelium? How does thyroid hormone induce Cyp27c1 expression? What is the evolution of Cyp27c1? It is probably present in jawless vertebrates such as lamprey, which are known to synthesize retinal$_2$ and make retinal$_2$-based photoreceptor pigments [12]. Is it found in any of the primitive chordates? What about arthropods, for example in crayfish which are known to use retinal$_2$ as a chromophore [13]? The answers to these questions will greatly enrich our understanding of the fascinating role of alternative chromophores in the natural history and physiology of vision.

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Collective Behaviour: Leadership and Learning in Flocks

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A new study has decoded which birds become leaders in homing pigeon flocks, finding an unexpected benefit of leadership: faster birds emerge as leaders, and these leaders learn more about their environment than their followers.

Flocks of homing pigeons circling overhead display remarkable feats of coordination (Figure 1). These movements are the product of leader–follower dynamics, with some individuals influencing the group's movements more than others [1]. But the explanation to which individuals emerge as leaders within these flocks has remained elusive. New work reported in this issue of *Current Biology* by Pettit *et al.* [2] reveals a simple

Figure 1. Flying in flocks.
Homing pigeons (*Columba livia*) form consistent leadership hierarchies during their homeward journeys. New research deciphers which birds become leaders in flocks, and also finds an unexpected benefit of leadership. Photo by Zsuzsa Ákos.

mechanism showing how some individuals rise to the top of the flock. Using an elegant experimental protocol and high-resolution spatial and temporal tracking data, the researchers also find a surprising benefit of becoming a leader.

The ability of homing pigeons to return to their home site has long fascinated the public, scientists and pigeon fanciers alike. Incredibly, pigeons can return to their home loft even after being released 1800 kilometres away [3]. They accomplish this navigational marvel by using a smorgasbord of senses and navigational techniques. These include utilising celestial, olfactory, magnetic and visual cues that help them navigate home [4–7]. But pigeons don't just rely on their own senses and navigational skill to find their way home: when released as a flock, birds have access to social information and can pool their own imperfect estimates of their homeward routes [8]. Doing so results in pigeons navigating more effectively as groups compared to when on their own [8].

Whilst information pooling allows flocks to navigate more efficiently, this process is by no-means an egalitarian affair. Leader–follower dynamics are observed in flocks of up to 30 pigeons, and these relationships are consistent over time [1,9,10]. Here, leadership is defined when an individual's direction of movement is copied by another individual after some time delay [1]. As in other animals [11], leaders usually occupy positions at the front of the group, as information on direction changes tends to pass from positions at the front of the group to the back [1,12,13]. Not all individuals, therefore, contribute equally to the decision of which route to take during the group's homeward journey.

One question that has remained unresolved is what makes some individuals leaders and others not. Pigeons have social dominance hierarchies, and these can be measured by seeing which birds have priority access to food and which birds are involved in antagonistic interactions [9]. One possibility for the leadership observed in flocks was that individuals were following those more socially dominant than themselves. However, this hypothesis was previously rejected when researchers compared the leader–follower relationships in flight to the dominance hierarchies observed on the ground: there was no observed relationship between the two [9]. Another possibility was that leadership was related to the navigational experience of an individual, with leaders having more efficient routes home. Whilst this explanation was partially supported in pairs of pigeons [14], this did not appear to be true for larger groups of 10 individuals [10]. In these bigger flocks, the mystery of leadership remained unanswered.

In their new study, Pettit *et al.* [2] have unravelled this mystery. Using an elegant experimental design, the authors first released pigeons individually from unfamiliar release sites. By fitting the birds with miniature GPS loggers, the researchers could recreate their solo journeys home, and gather high-resolution data on the pigeons' movements. Individuals not only differed in their navigational efficiency — calculated as the ratio between the bee line distance between the release site and home, and the actual distance the pigeon travelled — but also their average flying speed. Whilst some pigeons were 10 times better navigators than others, some were also 5 ms^{-1} faster flyers.

Next, Pettit *et al.* [2] took the pigeons and composed groups of 10 individuals. They then released these birds together from the same release sites as before. As in previous studies, the birds formed leadership hierarchies during their homeward journeys, and these hierarchies were consistent over four different releases. The researchers could therefore assign individuals a leadership score according to their position in these hierarchies. By comparing an individual's leadership score in the flock with how it behaved during its initial solo flight, the mechanism driving leadership was revealed. Pigeons that flew faster during their solo flights were more likely to occupy positions at the front of the group and lead the flock. Similar results have been observed in pairs of pigeons [15]. An individual's leadership score, however, was not related to its navigational efficiency: faster, but not necessarily more informed pigeons, emerged as flock leaders.

In other animal groups, informed individuals do occupy positions at the front of groups [16], but this did not appear to be the case in the pigeon flocks. Instead, faster moving individuals occupied leadership positions, which had been previously predicted by theoretical models [17]. But Pettit *et al.* [2]

took their study one step further. After releasing the birds in flocks, the authors then split the groups up again, and re-released birds individually one last time. During these second solo flights, almost all birds had improved their navigational efficiency as compared to their first solo flight. This was presumably because they had learnt new information about their routes home when in groups. However, leaders had improved their navigational efficiency significantly more than followers. Hence, whilst leaders were initially no better navigators than their followers, by the time they had finished their flock flights, they had become more informed than their other group members.

The costs and benefits associated with different positions in the group have usually been attributed to predation risks or foraging rewards [18]. This is the first demonstration that the spatial position an individual occupies in a group can affect how it learns information about its environment. But why might followers be ineffective learners compared to leaders? Perhaps individuals in the back of the flock pay more attention to social information, and less attention to environmental landmarks during flight. This lends important insights into the cognitive demands individuals are under when trying to maintain flock cohesion, but at the same time navigate home. Indeed, other studies have recently highlighted the need for individuals in groups to balance their own goal-orientated behaviours with social cohesion [19]. The new study [2] also raises new questions surrounding the processes underlying collective decisions. Even though these groups have hierarchical leader–follower relationships, and initially do not follow the most informed individuals, groups still outperform singletons in a navigational challenge. How individuals integrate information in these hierarchical flocks, and exactly how much influence different individuals have in the collective decision, are the next key challenges to understand.

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Ecology: Dynamics of Indirect Extinction

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The experimental identification of the mechanism by which extinctions of predators trigger further predator extinctions emphasizes the role of indirect effects between species in disturbed ecosystems. It also has deep consequences for the hidden magnitude of the current biodiversity crisis.

Species do not go extinct one at a time. Instead, it looks as though ecosystems change in a kind of chain reaction, just like in bowling. The impact of the ball knocks down one or two pins, but they hit other pins and this ultimately

