example, polarised light — as soon as the beetle began to roll the ball. The test was to remove the green light before the second roll to see whether the direction of the polarised light introduced during the first roll had been learnt and would set the beetle's direction during the second roll. The results were unambiguous: the beetles had learnt nothing about the orientation of cues that were presented only during the roll (Figure 1E): the celestial cues must be recorded exclusively during the dance.

It is always satisfying when a paper poses intriguing questions that demand to be answered. In this case it is: Why do beetles record the sky pattern during the dance on the ball? There seem to be several possible kinds of answer. The first is that from the vantage point of the ball, the beetle has a less interrupted view of the sky. The beetle, while rotating on the ball could, for instance, select the most reliable celestial cues — ones that remain clear and/or rotate at a speed that matches the speed signalled by idiothetic cues. At a neuronal level, it could mean selecting for guidance the output of those compass neurones that respond unambiguously at particular orientations during the beetle's scan and are thus suited to the celestial cues that are currently present.

The second sort of answer is that rotating on the ball helps the beetle decide on the best direction for ball-rolling. One reason for choosing a direction could be to avoid obstacles like the dung pile itself or other beetles. Another could be to select a direction that takes advantage of the landscape; for instance, to avoid upward slopes and to choose downward ones. The beetle's limited visual field and possible acute zones might then account for the rotational scanning that occurs during the dance. A final possibility is that dancing on the ball is a form of display that indicates to competitors the dancer's possession of the ball and a willingness to defend it from others. These possibilities are not mutually exclusive so teasing out which, if any, are correct may be challenging. Nonetheless, we can anticipate that unravelling the meaning of the dance will expose more of the dung beetle's remarkable surprises.

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Gradient Sensing: Engineering the Yeast Love Affair

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A new study in fission yeasts promotes the notion that transient polarity patches that wander the cell surface at the onset of mating are discrete agents of gradient sensing. This concept unexpectedly bridges the modes of gradient sensing in eukaryotes and prokaryotes.

The ability of cells to sense gradients of relevant environmental factors and align the direction of migration (chemotaxis) or growth (chemotropism) along these gradients is critical for their life functions and survival. Detailed molecular mechanisms and general biophysical principles of gradient sensing are thus of much interest and have remained the focus of continuous experimental and theoretical efforts for decades. The general consensus has been that prokaryotes and eukaryotes utilize distinct biophysical strategies. Temporary sampling of chemical gradients via biased random walk has been firmly established as the principle of chemosensing for small bacterial cells [1]. In contrast, the field of eukaryotic chemotaxis, led by the studies on large motile cells, such as *Dictyostelium* amoeba and neutrophils [2], concluded that eukaryotic cells sense gradients spatially, by detecting differences in the occupancy of chemosensory receptors along their surface. However, it remained unclear

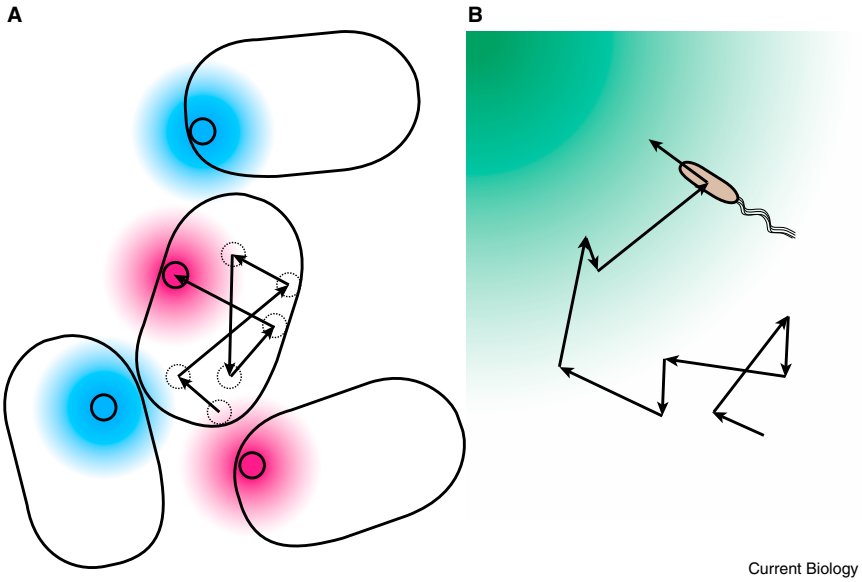

Figure 1. Fission yeasts play 'hot and cold' dating game during the exploratory phase of mating.
(A) Transient polarity patches that emit mating pheromone and sense pheromone of the opposite sex (shown as colored gradients) undergo a biased random walk on the cell surface to establish efficient cell pairing. (B) Following a similar strategy, bacterial cells sense a chemical gradient (depicted here in shades of green) via a random, run-and-tumble motion that, on average, enables them to move up the gradient.

how small eukaryotes, such as yeasts, manage to accurately determine the direction of signalling gradients [3] despite their diminutive size, which places them closer to the prokaryotic world. Recent studies performed at a higher spatial and temporal resolution revealed a trial-and-error process that underlies gradient sensing in budding and fission yeasts and the conclusions from these studies began to question the validity of the spatial gradient sensing hypothesis in these unicellular fungi [4–7]. In a recent issue of *Current Biology*, Merlini *et al.* [8] approach fission yeast mating with an engineering perspective and conclude that the biophysical principle of gradient sensing in this organism may, after all, be not too different from the strategy employed by the prokaryotic microbes.

Under inducing conditions, fungal haploid cells secrete mating pheromones and express receptors for the pheromone of the opposite sex. During mating, cells pair up by sensing the secreted pheromones, grow towards each other by forming mating protrusions, also known as shmoos, and eventually fuse to form a diploid zygote. In filamentous fungi, in addition to this sexual process, cells fuse during the vegetative life cycle to form large branching colonies. This process, best understood in *Neurospora crassa* [9,10], involves chemotropism between genetically identical cells and, therefore, is mediated by a common signalling molecule. To avoid self-activation, *N. crassa* evolved a peculiar 'ping-pong' mechanism of pulsatile signal exchange that ensues between the paired-up cellular protrusions during their homing towards each other [11,12].

Studies in budding yeast mating have been instrumental in informing the efforts in eukaryotic gradient sensing for over three decades [13]. Early work mainly focused on three molecular modules directly responsible for pheromone sensing: pheromones and their secretory machinery; pheromone receptors and associated G proteins; and the downstream Fus3 MAP kinase cascade. Research in the Herskowitz and Peter labs also identified that the molecular link between pheromone-induced G-protein signalling and the emergence and growth of the shmoo [14] is the activation of small GTPase Cdc42, a master regulator of eukaryotic cell polarity. Thus, it has been assumed that the polarity module that controls chemotropic growth is activated downstream of choosing the direction towards the mating partner.

Recent progress in fluorescence microscopy and the development of fluorescent proteins and sensors for activated GTPases provided evidence that calls for the revision of this concept. Papers from the Lew and Martin groups [4,5] revealed that, prior to the shmooing proper, i.e., the phase of committed polarized growth towards the mating partner, there exists a transient exploratory phase, during which a weak polarity patch wanders the cell surface as if unsure of the right direction. Interestingly, in both budding and fission yeasts, these transient patches were smaller and weaker in fluorescence intensity than the polarity clusters observed during the vegetative polarized growth. Peter and colleagues [7] concluded that this property is the cause for the dynamic, wandering nature of an exploratory patch, whereas the intensification of a patch in response to stronger pheromone signal is a prerequisite for the conversion of a patch into the polarity cluster proper that drives the protrusion of the shmoo. As observed in the context of budding, emergence of the exploratory patch was shown to be independent of the actin cytoskeleton [4,6]. This confirmed that, both in budding and mating, the discrete polarity domain is a self-organized structure and it arises via positive feedback encoded by the molecular interactions within the Cdc42 polarity module [15–17]. In contrast, the mobility of the exploratory polarity patch was found to be largely actin dependent and negatively regulated by the strengthening of the Cdc42 positive feedback [4,6]. Unlike in budding yeast, Martin and colleagues observed that, in fission yeast, the exploratory patch moves by large jumps, disassembling in one spot and re-assembling in the other [5].

In their new contribution, Merlini *et al.* [8] first address a question that naturally flows from the earlier studies: is the exploratory polarity patch actually a locus of signal release and signal sensing? Starting with a demonstration of co-localization of the patch with some components of the secretory and sensory machineries, they

proceed to analyze mating efficiency in a set of computational models varying in the scope (total cell surface vs. only the patch) of signal sensing and signal releasing. In this analysis they rely on a powerful quantitative assay that allows them to measure the kinetics of yeast mating (as the percentage of paired cells vs. time) under various perturbations and compare the results with model predictions. Their conclusion is clear: the model in which the release and sensing of the pheromone are co-localized with the polarity patch outperforms other models and its simulated mating efficiency reaches that of the wild-type yeast population. It is interesting that in *N. crassa* the analogs of the polarity patches detected by the activity of Cdc42 and another small GTPase, Rac-1, coincide with the sites of signal reception as reported by the localization of the signal-responding MAP kinase Mak-2 (the Fus3 homologue) [18,19]. It is tempting to speculate that, even in large filamentous fungi, there exist localized zones of heightened signal sensing (and, very likely, release) that coincide with and are defined by the self-organized clusters of GTPase activity. In support of this conjecture, chemical inhibition of Rac-1 activity resulted in cessation of pulsatile Mak-2 recruitment [19].

Merlini *et al.* [8] further ask if patch mobility, which in their experimental system is essentially determined by the patch lifetime, affects the mating efficiency. An increase in the patch lifetime in experimental studies reduced the efficiency of mating by increasing the proportion of cells that formed unreciprocated shmoos. Likewise, modelling analysis suggested the existence of the optimal patch lifetime that maximizes the efficiency of mating. These results are in good qualitative agreement with budding yeast studies where both overly mobile and static patches were found to be detrimental to mating [4,6,7].

Taken together, these new findings from Martin, Vavylonis and colleagues [8] strengthen the concept of transient polarity patches as discrete platforms for gradient sensing. Cumulative evidence from several fungal systems suggests that these platforms are equipped with signal-sending and signal-receiving capabilities and can translocate along the surface of cells either gradually, as reported in budding yeast cells, or in jumps due to the repeating cycles of assembly/disassembly, as observed in the larger cells of fission yeast and filamentous fungi. Their discrete nature and characteristic size, which varies across fungi much less than the size of the cells themselves, are likely determined by the pattern-forming ability of Cdc42 and the other small GTPases involved. Given that the nature of the exploratory patches is akin to that of vegetative polarity clusters, it remains to be seen if competition for the common molecular resources that ensure the uniqueness (i.e. singularity) of the yeast bud [17,20] also provides for the unique exploratory patch per mating cell. As in the case of budding, fusing with multiple mating partners would be unproductive due to the uniqueness of the yeast nucleus. This, however, is not a restriction in the multinucleated cells of *N. crassa*, where formation of multiple signalling patches per cell has indeed been observed.

Considering an exploratory-phase patch as an independent agent of a sub-micron size that performs a biased random walk, constrained only by the surface of the 'host' cell, makes for a surprising analogy between the gradient-sensing strategies of bacteria and fungi (Figure 1). Indeed, in both cases the agent (bacterial cell or sensing patch) moves randomly in the complex spatial profile of the signalling molecule, biasing its walk towards the increase in signal amplitude and thus using the temporal averaging strategy, previously attributed solely to bacteria. In case of populations of mating or fusing vegetative cells, such a walk is bound to have multiple attractors, and frequent switches of partners have indeed been seen among cells of fission yeasts and *N. crassa*. Remarkably, in this novel hybrid mechanism, the eukaryotic cell still utilizes its entire cell surface. However, it does so by supporting a random walk of a searching agent rather than by attempting a complex and error-prone calculation of receptor occupancy differences. The thought-provoking study by Merlini *et al.* [8] promotes our understanding of eukaryotic gradient sensing and vividly illustrates the power of the systems biology approach towards complex biological problems.

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Palaeobiology: Born and Gone in Global Warming

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Why ichthyosaurs — marine Mesozoic reptiles — disappeared before the dinosaur extinction has remained a mystery. New research suggests they may have gone extinct stepwise, during one of the most extreme greenhouse periods in the history of complex life-forms.

In 1811, Mary Anning and her brother found the fossil skull of a giant reptile on a beach in Lyme Regis in Dorset, England. This find triggered an era of paleontological discoveries that eventually led Richard Owen to christen a new class of extinct reptiles, the Dinosauria, in 1842 [1]. But ironically, the first skull was not of a dinosaur — it belonged to *Temnodontosaurus platyodon*, an ichthyosaur (Figure 1). Ichthyosaurs are an iconic group of marine reptiles that are best known for the evolution of a fish-shaped body, which is reflected in their name that means 'fish lizard' [2]. They are often portrayed as the reptiles that were best-adapted to marine life [3]. Ranging from half a meter to over 20 meters in body length, most ichthyosaurs were pelagic predators of fish, squid-like cephalopods and sometimes other marine reptiles. They are noted for the records for the largest eyeball among vertebrate animals [4], and the highest number of digits, with at least eight [5,6]. Ichthyosaurs were indeed very successful and remained a major component of marine predator guilds for more than 150 million years [7]. One of the greatest mysteries surrounding this celebrated group is their extinction.

Ichthyosaurs became extinct long before the dinosaur extinction, when some other, seemingly less well-adapted marine reptiles survived. The cause of this 'unreasonable' extinction has never been clearly explained. Finally, a new study by Valentin Fischer and colleagues casts new light on this issue [8].

It had been known for a few decades that the ichthyosaurian fossil record ends in a time period called the Cenomanian (~100.5 to ~93.9 million years ago) [9,10], the first geologic age of the Late Cretaceous epoch. The Cenomanian was an unusual time period. The extinction rate of marine life was elevated in the late Cenomanian [11], which ended with a notorious event during which a large percentage of the seafloor became anoxic [12]. Natalie Bardet pointed out in 1992 that the disappearance of the ichthyosaurs may have been related to this marine extinction event [10], based on a pivotal investigation of the time ranges of ichthyosaurian species in the Cretaceous. One of the questions has been whether the evolutionary diversity and disparity of ichthyosaurs were already declining in the Early Cretaceous [13], ahead of the anoxic event, making them susceptible to extinction. However, a recent careful examination of the ichthyosaurian fossil record concluded that their diversity remained high until the Cenomanian [14]. The new study by Fischer *et al.* [8] builds on these early works by improving the temporal resolution to the subage level (i.e., an average data resolution of about three million years, as opposed to about 7.3 previously) and refining statistical treatments in a trial to clarify what may have happened during the last chapters of ichthyosaurian existence.

The new study [8] reaches three novel conclusions: first, the extinction of ichthyosaurs occurred in two steps within the Cenomanian, where early and final extinction peaks are recognized. Second, the Early Cenomanian extinction reduced ichthyosaurian diversity and variation in feeding strategy, without the subsequent origination of new phenotypes to fill the ecological vacancy until the final extinction in the Late Cenomanian. Fish and squid feeders were eliminated, leaving only a group of apex predators. And third, the extinction rate increased with rising environmental volatility, including changes in sea levels and carbon dioxide levels in the atmosphere, which, according to the rising consensus,