



**Figure 1 | Chagyrskaya Cave in Siberia.** Skov *et al.*<sup>1</sup> analysed genomic data from Neanderthal remains found in this cave.

segments that are shared between individuals. These approaches are better suited to identifying distant relatives and determining the nature of second-degree relationships (for example, distinguishing aunt and niece from grandparent and grandchild).

The Chagyrskaya genomes, like that of an earlier Neanderthal from Denisova<sup>4</sup>, contain signatures of inbreeding, in the form of long stretches of identical DNA inherited from each parent. In isolation, an individual with signs of inbreeding as extreme as one of these Neanderthals might be mistaken for the offspring of second-degree relatives. However, when a whole population shows this profile, the interpretation moves towards less-recent but more-numerous ancestors shared between parents, as a result of consistently small population sizes. The authors draw parallels with endangered mountain gorillas, a subspecies that recent decades comprised fewer than 1,000 individuals<sup>5</sup>. An outstanding question is whether this level of inbreeding was a common predicament for Neanderthals, or a specific feature of Altai populations isolated at a geographical extreme.

It is fairly well accepted that Neanderthals lived in small communities – comprising perhaps 10–30 individuals per group – with very low population densities in many regions<sup>6</sup>. What is less clear is the nature and level of interaction between these communities. Perhaps, then, Skov and colleagues' most provocative finding is that women seem to have been frequently on the move between groups. Chagyrskaya provided an unprecedented haul of Neanderthal Y chromosomes (six in total), which were notably lacking in diversity – on average, two male individuals could expect to share a male-line ancestor around 450 years before they lived. By contrast, the equivalent estimate for female individuals (generated using mtDNA) was around 4,350 years.

Several scenarios could account for the greater diversity of maternal lineages, including the possibility that a subset of men fathered most children. But, through modelling, the authors found that their data are best explained by female-biased migration between communities of about 20 individuals, with more than 60% of women being born elsewhere. There are, of course, many caveats to consider. The authors' sample size is small; the sequenced remains might be a skewed representation of the community or derive from multiple communities; and models are always wrong to some extent. But, in line with the group's hypothesis, a study of mtDNA has previously hinted that some Neanderthals practised patrilocality<sup>7</sup>

(women residing with their partner's family), and Skov *et al.* provide the most convincing evidence yet for such behaviour.

Our own species has a uniquely fluid social structure within which bonds of marriage are a central feature. Detailed analysis of present-day hunting and gathering societies shows that both men and women frequently move between groups<sup>8</sup>, and that dispersed relatives often maintain lifelong ties – which is not the case for apes<sup>9</sup>. A father whose daughter moves to another community is able to recognize his grandchildren as kin, and to bond with (or at least tolerate) his son-in-law. This can allow vast social networks to form, if population densities are high enough. Whether this level of flexibility and cooperation is unique to *Homo sapiens* (and perhaps part of our success story) or a trait shared with our closest relatives remains to be seen. Chagyrskaya Cave and other sites across Eurasia have many more secrets to yield.

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## Engineering

# Embrace wobble to level flight without a horizon

**Graham K. Taylor**

The apparent motion of a flier's surroundings is shown to stabilize its flight by providing information about its orientation. Lapses in information are overcome through the effects of sensor noise and body oscillations. **See p.485**

These days, a buzzing sound overhead is perhaps just as likely to signal the approach of a camera drone as that of a bee. Either way, the sound results from wings or rotors whose fast cyclical motion serves the joint functions of supporting the flier's weight, and stabilizing and controlling its flight. Achieving stability through feedback control requires an accurate estimate of the attitude angle that describes a

flier's orientation with respect to the direction of gravity. Drones estimate their attitude using gravity-sensing devices called accelerometers, but it's not yet clear how insects do so without accelerometers<sup>1</sup>, because vision offers a direct estimate of attitude only when the horizon is visible. On page 485, de Croon *et al.*<sup>2</sup> show how vision can be used to infer attitude dynamically from the apparent motion of features in a flier's

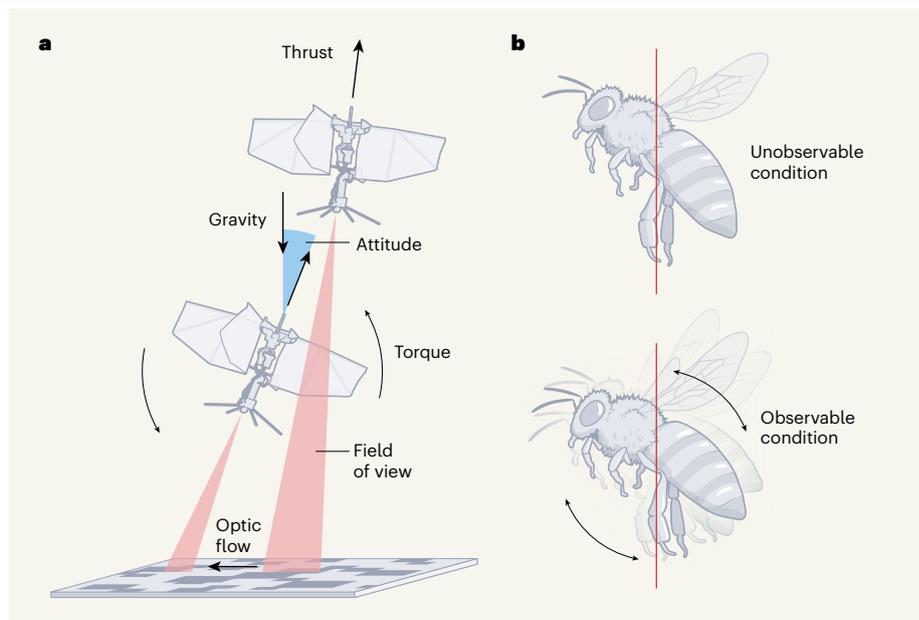
surroundings – and demonstrate their point by flying unstable drones without accelerometers.

Miniaturized accelerometers aren't well suited to controlling insect-scale drones<sup>3</sup>. The key problem can be demonstrated with a smartphone that switches its display from portrait to landscape mode as it rotates, by using accelerometers to sense how the screen is oriented. This approach to attitude estimation works well when the phone is still, but fails if the phone is shaken to mimic flapping or is swung around in imitation of a flight manoeuvre. Either way, the phone's own acceleration obscures the accelerometer's reading of gravitational acceleration, making its estimation of the direction of gravity ambiguous. The same ambiguity arises in agile flapping flight at small scales, which might explain why insects have not evolved to use accelerometers in flight control. So how might insects estimate attitude, and could their solution improve drone design?

To answer these questions, de Croon and colleagues developed a generic model of flight control applicable to unstable fliers that manipulate their attitude to direct their thrust (Fig. 1a). This is a reasonable approximation of an insect or helicopter whose wings or rotors sweep a fixed path. In the simplest version of their model, the authors assume that the flier's height remains constant, which amounts to assuming that its thrust is adjusted to balance its weight. The flier is free to move forwards or backwards by tilting its thrust in the direction in which it means to move. It achieves this by applying a torque to control its rotation rate, as measured by a sensor called a gyro. More sophisticated versions of the model incorporate the effects of drag, wind, variable height and a sloping floor – but, for each variation, the underlying question is the same. Can attitude be estimated without an accelerometer?

By increasing the complexity of their model in a stepwise fashion, the authors produced an elegant theoretical analysis showing how a flier's attitude can be estimated from the way that contrasting features on the ground below seem to move. This apparent motion is known as optic flow, and is used by bees and other insects for navigation and flight control<sup>1,4</sup>. Quadrotors (helicopters with four rotors) and other drones already use optic flow to stabilize their position against drift and to control landing<sup>5</sup>, so the idea that they could also use it to estimate attitude is appealing.

At first sight, it might seem surprising that optic flow can be used to estimate attitude at all. For one thing, optic flow is generated by translation as well as rotation. Moreover, rotational optic flow depends only on the rotation rate, whereas translational optic flow varies with distance as well as with speed – which is why nearby trees seem to move faster than distant hills when viewed from a moving car. Nevertheless, for a flier that must tilt its body to redirect its thrust, changes in speed and



**Figure 1 | Flight stabilized by apparent motion.** **a**, Drones and insects that use thrust to support their weight typically manipulate their attitude (orientation with respect to the direction of gravity) by applying a torque to direct this thrust. They perceive the resulting coupling of rotational and translational motion visually, through the relative motion of contrasting features in their field of view: a phenomenon known as optic flow (the direction of which is opposite to that of the flier's own motion). De Croon *et al.*<sup>2</sup> showed that changes in optic flow can be used to estimate attitude, given a model of the flier's characteristic flight dynamics and knowledge of its rotation rate. **b**, This method fails when the rotation rate is zero, a flight condition in which their attitude is 'unobservable', as occurs if a drone or an insect is in a perfect hover. In practice, a flier can withstand short lapses in attitude information until noise – from the flier's sensors or its own flight dynamics – kicks it back out of this condition. Wingbeat-driven oscillations therefore enhance attitude estimation using optic flow, which the authors demonstrated using a flapper drone.

height are tightly coupled with attitude<sup>5</sup>. Hence, given a suitable dynamical model of the flier's motion, it is possible to estimate attitude from information about the flier's rotation rate and changes in the optic flow beneath it.

But there's a catch. Crucially, the authors identify certain motion conditions in which flight attitude cannot be estimated from optic flow – notably, when the rotation rate is zero, as occurs, for example, in a perfect hover (Fig. 1b). Under these conditions, the state of the system is said to be unobservable, because it cannot be inferred unambiguously from the available sensor information. Unobservability is a deal-breaker for most engineered systems, and is typically remedied by adding extra sensors, such as the accelerometers on a quadrotor. But what if no suitable sensors are available, as might be the case at insect-like scales?

The authors' central idea, which they demonstrate using a quadrotor flown indoors over flat, sloping and uneven floors, is that this unobservability can be accommodated if the system can tolerate passing through any locally unobservable flight conditions. To know how it is oriented, the flier must simply wait until the necessary information becomes available. This will happen quickly enough in the real world, where sensor noise and control error will push the system back into an observable flight condition almost as

soon as it encounters an unobservable one.

This intriguing idea is particularly pertinent for flapping fliers, whose dynamics are forced periodically by their wingbeat. Such fliers experience the unobservable condition of zero rotation rate periodically, but only at the extremes of each body oscillation. For flapping fliers, the same body oscillations that impair attitude estimation using accelerometers should therefore improve attitude estimation using optic flow, by guaranteeing that the flier's state remains observable most of the time. Going beyond their experiments with quadrotors, de Croon *et al.* demonstrate this in practice for a flapper drone with an artificial compound eye.

These impressive results from engineered systems align closely with the 'mode-sensing hypothesis' from biology<sup>1</sup>, which is the idea that the sensory systems of flying insects are specifically tuned to detect excitation of their modes of motion. These natural modes describe the characteristic ways in which an insect, or any other dynamical system, moves. Examples include the periodic swinging of a pendulum, and the analogous coupling of attitude, speed and height that allows a drone's attitude to be estimated from measurements of rotation rate and optic flow. In this context, de Croon and colleagues' findings provide insight into why optic-flow information sensed

by an insect's compound eyes is fused with information on rotation rate from its ocelli, a trio of light-sensitive organs on its head<sup>6</sup>.

Optic flow contains much richer information about an individual's motion and its environment than the authors exploit in this study, especially when sensed across the entire visual field<sup>1,2</sup>. It follows that widefield optic-flow sensing, coupled with a model more closely resembling the natural flight dynamics of insects, might not produce the same unobservability that de Croon and colleagues identify using their simple model of flight control. Even so, as their groundbreaking work shows, quadrotors and flapping fliers that use optic flow to control attitude can

accommodate unobservability by embracing their wobble.

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have almost no species in common and yet look very similar to each other – a tall, dense canopy of mostly evergreen, broadleaved trees with many vines and most of the nutrients locked up in plants, rather than in the soil. Organizing ecosystems into biomes not only advances research, but is also crucial for conservation efforts. No government can feasibly create a policy without an inventory of what it is managing<sup>2</sup>. There have already been dozens of attempts to make an authoritative list of biomes, with each attempt having its own limitations.

Keith and colleagues have developed a list of six criteria for an optimal catalogue of ecosystem classifications. Finding no existing system that met all of these criteria, the authors assembled a series of committees to develop a new, definitive list under the auspices of the International Union for Conservation of Nature (IUCN), which is a large, influential non-governmental organization working in the area of conservation. The resulting classification system is called the Global Ecosystem Typology, hereafter referred to as IUCNGET.

Just as Carl Linnaeus developed a system for classifying organisms that uses subcategories such as kingdom, class, genus and species, IUCNGET has three main category levels: realm, biome and functional group. This new classification system identifies ten realms: four core realms (terrestrial, freshwater, marine and subterranean) and six interface realms that capture transitions between two core realms. These 10 realms are divided into 25 biomes, which are further subdivided into 110 functional groups that have more-subtle distinctions, driven by factors such as temperature, precipitation and seasonality. This system can be explored, complete with maps and pictures, at the website for this project (<http://global-ecosystems.org>).

A tropical rainforest, for example, would be in the terrestrial realm (denoted T), which is

## Ecology

# New catalogue of Earth's ecosystems

Brian J. McGill & Stephanie N. Miller

Echoing the hierarchical Linnaean system for naming species, ecologists have developed a definitive classification of Earth's ecosystems. This feat, achieved by a massive effort, could anchor conservation efforts for decades to come. **See p.513**

How should Earth's ecosystems be categorized in a systematic manner? On page 513, Keith *et al.*<sup>1</sup> propose a solution.

An ecosystem is a set of plants and animals and their associations with each other and the environment. A biome is a category of ecosystem whose members share similar vegetation structure and processes and are found repeatedly in different locations around the globe. Many examples of biomes, such as

tropical rainforest, are immediately familiar, whereas others, such as succulent semi-desert, have names that are probably recognized only by an ecologist. And it might come as a surprise that ecologists would even bother to name certain biomes: for example, human-generated subterranean freshwater systems such as flooded mines.

The biome concept suggests that tropical rainforests can exist on different continents,



**Figure 1 | Classifying ecosystems.** Keith *et al.*<sup>1</sup> present a new system for classifying any ecosystem on Earth. **a**, A tropical/subtropical dry forest and thicket, such as this one, has T1.2 as its ecosystem designation. This designation corresponds, respectively, to the terrestrial (T) realm, the first biome (a grouping of similar vegetation and processes) of this realm, and the second functional group of this biome. **b**, A succulent or thorny desert and semi-desert ecosystem,

such as the example shown, is assigned to the ecosystem called T5.2 (for the second functional group of the fifth biome of the terrestrial realm). **c**, The ecosystem in this flooded quarry tunnel is placed in the SF2.2 grouping. It is in the subterranean–freshwater (SF) realm, the second biome of this realm, which is a human-generated biome, and its second functional group – flooded mines and other voids.