be pivotal to solving the mystery of high-temperature superconductivity. ■

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EVOLUTIONARY BIOLOGY

Animal personalities

Alison M. Bell

That different people differ in their readiness to take risks is an obvious feature of human personality. Theoretical advances now help in making sense of observations of analogous behaviour in animals.

Personality might seem to require a complexity and subtlety that is unique to humans. But evidence for individual variation in traits that we would recognize as personality, for example aggressiveness in fighting or boldness in the face of a predator, has cropped up in animals ranging from fish to monkeys to squid. Even an individual spider behaves differently from other spiders, through time and in different situations[1]. Wolf *et al.* (page 581 of this issue[2]) now show how such variation in behaviour can make evolutionary sense.

Personality has been difficult to explain from an evolutionary perspective because, at first glance, it could seem maladaptive[3]. An individual that is consistently uninhibited and bold is going to end up eaten by a predator. The optimal animal should be bold only when it makes sense to be bold, and adjust its behaviour when the situation changes. Although animals are legendary for their remarkable 'behavioural plasticity' (think migration or camouflage, for example), there is growing evidence that animals do not always change their behaviour as much as they should. In other words, behavioural plasticity is limited[3].

One possible explanation for this is that individuals should behave consistently if it's simply too hard to undergo a personality transformation. If turning off a general tendency to be aggressive requires time and energy to entirely rewire neural machinery, or to build a physiology that can support a different metabolism, then individuals might be better off sticking to an intermediate strategy[4]. Similarly, if information about the immediate environment is uncertain, then it makes sense just to behave the same way and avoid the risk of making a mistake[5].

This line of reasoning can help to explain why a given individual behaves consistently, but not, for example, why some individuals are always more aggressive than others. Such variation is puzzling, because natural selection will favour individuals with characteristics that perform the best, and less 'fit' individuals will be removed from the population. If a trait is heritable and linked to survival or reproductive success, then evolutionary theory tells us that variation will eventually disappear from the population. But, empirically, we know that personality traits are heritable[6], are linked to fitness[7] and are quite variable.

So how is all this behavioural variation maintained? One way is if the fitness of one strategy depends on the frequency of other strategies in the population[8,9]. Imagine, for example, a group composed entirely of individuals that accumulate resources by guarding them — territorial male birds, for example. An individual using a different strategy — say, dashing in to sneak the resource while a guard is otherwise occupied — would do well in that situation (so long as it is rare), because it would effectively occupy an 'open niche', devoid of competitors.

Alternatively, behavioural variation can be maintained if the best strategy depends on an individual's 'state', which effectively anchors a personality type[8]. This state can be anything from sex or health to body size, and the idea is that an individual should behave consistently so long as its state does not change. This explanation leaves the question of what maintains variation in state.

Wolf *et al.*[2] offer an answer by proposing that an individual's strategy for survival and reproduction — its life-history strategy — is a relatively unchanging state (unlike hunger level, for example), and that individuals adopt different life-history strategies because of fitness trade-offs. Any behaviour that is related to a life-history strategy will be stable through time and differ between individuals with different strategies.

The authors' model starts by assuming that an individual can either reproduce now, but

50 & 100 YEARS AGO

50 YEARS AGO

"Incorporation of radioactive amino-acids in the proteins of bull spermatozoa" — It is widely held that ribonucleic acid is directly involved in protein synthesis, and there have been several recent demonstrations of the necessity for the presence of ribonucleic acid during synthesis of proteins. In view of this, it seemed to be of interest to examine protein turnover in mature, ejaculated spermatozoa, which apparently contain at most only traces of ribonucleic acid... The absence of the acid from bull semen has been confirmed in the present investigation... It is possible that in this case deoxyribonucleic acid may be involved in the synthesis of proteins... The other possibility would be to regard protein synthesis in spermatozoa as an enzymatic process independent of nucleic acids.

From *Nature* 1 June 1957.

100 YEARS AGO

Mr. Walter Wellman, who proposes to make another attempt to reach the North Pole by means of his airship *America*, has left for Norway, on the way to Spitsbergen, where the balloon will be inflated. In the first week of July there will be trials of the airship until it is demonstrated that it is ready for the voyage... Mr. Wellman has given Reuter's representative the following particulars of his plans:— The airship has been made 18 feet longer and its lifting power increased by 3000 lb., giving a total lifting force of 19,500 lb. The balloon is 184 feet long and 52 feet in its greatest diameter, its cubic volume being 265,000 cubic feet. With the single exception of Count Zeppelin's airship, this is the largest ever built...The total radius of action is believed to be 2500 miles, or double the distance from the base to the Pole and back again. The balloon will not ascend more than 300 feet to 500 feet, and a guide-rope will trail over the surface of the earth.

From *Nature* 30 May 1907.

having acquired low-quality resources, or delay reproduction by one year, having acquired high-quality resources. For example, an individual that becomes sexually mature at a young age will have to balance the benefit of early reproduction against the cost of reproducing at a smaller size. Individuals that postpone reproduction must be able to survive to realize their reproductive expectations, and should therefore be generally risk-averse, whereas the opposite is true for those planning to reproduce early. So stable individual differences in risk-taking behaviours can evolve and be maintained when there is a trade-off between early versus late reproduction.

Along the same lines, Stamps[10] argues that another life-history trade-off — this time between growth and mortality — can favour the evolution of personality. Individuals can either opt to grow fast but risk dying young, or instead elect to take the safe route and grow slowly. Because individuals can benefit from growing at a consistent rate, any behaviour or suite of behaviours that is related to growth rate will be consistent through time. And because both the fast-growing and the slow-growing strategy can be maintained in a population when the two strategies have equal fitness owing to a trade-off with mortality[11], behavioural variation can result.

These models[2,10] not only explain why personality occurs, but also predict what form it should take (that is, behaviours that affect the trade-off are likely to co-vary). And they can explain why personality doesn't always evolve[12]. Moreover, an explanation invoking variation in life-history strategies is particularly powerful because life-history trade-offs are something that all living creatures confront — no one can live for ever and produce an infinite number of healthy offspring. Therefore, life-history trade-offs might help to explain why we see something akin to personality in such a wide variety of species.

However, there is room for further theory that allows more dynamic feedback between life-history strategy and behaviour. For example, imagine that a bold and aggressive individual on the 'reproduce early' schedule is successful in acquiring resources. If so, it has effectively changed its state, and its chance of successfully reproducing in the future ('residual reproductive value') has increased. So it is easy to envisage cases in which it would make sense for that individual to switch to the 'delay reproduction' strategy, and change behavioural tactics accordingly. In other words, transitions between life-history strategies might be mediated by personality, and vice versa.

Nonetheless, these models[2,10] offer an adaptive explanation for animal personality and show that its evolution is logically plausible. They should help to convince sceptics that animal personality is not merely an anecdotal topic. Ironically, the search for evolutionary explanations for why individual animals consistently behave differently might also help to answer a fundamental question about ourselves: why do we have unique personalities? ■

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SOLID-STATE PHYSICS

A polariton laser

Leonid V. Butov

Polaritons — particles comprising both light and matter — can form a coherent state, just as light and matter can individually. This fact has now been exploited to make the first room-temperature polariton laser.

At the foundation of modern quantum physics, waves in nature were divided into electromagnetic waves, such as the photon, and matter waves, such as the electron. Both can form a coherent state in which individual waves synchronize and combine. A coherent state of electromagnetic waves is known as a laser; a coherent state of matter waves is termed a Bose–Einstein condensate. But what if a particle is a mixture of an electromagnetic wave and matter? Can such particles form a coherent state? What does it look like? Writing in *Physical Review Letters* Christopoulos *et al.*[1] provide insight into these questions, demonstrating a coherent state of matter–light excitations, or polaritons, in a semiconductor microcavity: the first reported room-temperature polariton laser.

A semiconductor microcavity is built by placing a semiconductor layer between two mirrors. Excitation by an external source, typically a laser, can populate the cavity with different types of particle. The first of these is an exciton, a bound pair of an electron and a 'hole' — an empty state in the band of allowed electron states in the semiconductor. Excitons act as matter particles with a mass equal to the combined mass of an electron and a hole (typically about the vacuum electron mass, m_e), and can form a coherent state similar to a Bose–Einstein condensate.

The second occupant of the cavity is a photon. Although in an empty space a photon is massless, when it is confined in a planar cavity its dispersion relation — the dependence of its energy on its momentum — is modified to the same form as that of a particle with a mass $m = (n\lambda_c/2L)m_e$. Here, n is the refractive index of the cavity medium, L the cavity width and λ_c a constant, the Compton wavelength. For a typical gallium arsenide (GaAs) semiconductor cavity of width 1 micrometre, this mass is about 100,000 times smaller than the electron mass.

If the microcavity is the right width, the energies of the cavity photon and the exciton can be made to match up. When this happens the two mix, forming a new particle. This is a combination of matter and electromagnetic waves — an exciton-polariton, or simply 'polariton'. These polaritons inherit some of the lightness of the cavity photons, and have masses much smaller than m_e.

By varying the parameters of the semiconductor microcavity, several types of coherent state can be obtained. The first forms when the densities of electrons and holes in the cavity medium are so high that the polaritons are essentially destroyed (typically because of dephasing, screening and phase-space filling owing to the carrier Coulomb interaction[2]). In this regime, which is known as weak coupling, the protagonists are the cavity photons and the electron–hole pairs. The system is analogous to a conventional laser: the photon is amplified by stimulating the electron and hole to recombine, emitting a second, coherent photon of the same energy. It is, in fact, a close relative of a type of laser known as a VCSEL (vertical-cavity surface-emitting laser). In contrast to conventional edge-emitting semiconductor lasers, VCSELs emit their beam perpendicular to the active region of the laser, so they can be built in a dense two-dimensional array. Moreover, the beam of a VCSEL is characterized by a lower divergence angle compared with that of the edge-emitting lasers; as a result they are favoured for use in fibre-optic communications.

After the demonstration of lasing in the weak-coupling regime, research moved on to creating a coherent state in the strong-coupling, or polariton, regime. This required prevention of the polariton's destruction before a coherent