

kind have enormous predictive power: no company that has existed for 100 years has achieved that without staying in the black figures for most of its branches for most of the time. The Hamiltonian paradigm holds that the same is likely to be true for the cooperative and altruistic adaptations that we study, because they are shaped by a long evolutionary history of prudent expenditure of gene-copy currency.

Do you believe there is a need for more crosstalk between biological disciplines? The genomic revolution that is upon us means that biology is rapidly becoming an even more data-driven science. I think this will at some point necessitate a renewed focus on the grand challenges that the biological sub-disciplines share. The increasing availability of genome-wide data for our own species is a case in point. It will make personalized medical treatment increasingly feasible, but full exploitation of these technological advances will require that medical practitioners are aware that many human adaptations, however plastic they may be, have become detached from the natural environments in which they evolved. Only evolutionary biology allows us to understand the consequences of such uniquely human mismatches. It is appropriate, therefore, that evolutionary theory about life history trade-offs, parent-offspring conflict, and selection for resistance against antibiotics and cancer drugs is now increasingly being applied and taught to understand pressing questions about human vulnerability to disease.

What do you think are the biggest problems science as a whole is facing today? It remains a huge privilege to receive a salary and funding for fundamental science and for mentoring young people into seeking their own careers in research, education, management, publishing or outreach. Well-functioning autonomous universities pursuing curiosity-driven academic goals have been the bearers of our civilization since the early Renaissance. However, that status is under threat when external

funding is increasingly reallocated towards directly or strategically applied programs, and core funding for faculty members dries up while teaching and admin burdens increase. At the same time, irrational denial of proven scientific achievement is on the rise, particularly on issues where science recommends the protection of public goods such as ocean fish stocks, the immunity of vaccinated populations or melting glaciers. The increasing public distrust in science is now becoming a global tragedy fuelled by almost unlimited electronic information that makes it hard to distinguish between evidence-based information and politically-motivated or commercially-driven postures. The antidote of independent scholarship is needed more than ever before, but that no longer seems to be a general priority.

Does government have a role in producing innovation? Innovation is a rare emergent property. You are most likely to get it when you put the best people in the same premises, and give them the freedom to pursue internationally competitive excellence with minimal bureaucracy. While it is tempting to see strategic programs as more immediate solutions to the biggest problems facing society — antibiotics resistance, novel emergent diseases, food security — this approach is myopically self-defeating because applied research can at best be as good as the fundamental research that bears it. Are we as society best served by universities that train people to operate machines without having learnt to think? Or by academic curricula that steer young people to use existing knowledge for predefined problems, rather than developing new understanding to challenge the validity of present wisdom? Adopting an applied science agenda as a primary goal stunts the intellectual growth of the best young minds, just like selective logging of rainforest inevitably degrades the long-term resilience of ecosystems even though they will continue to appear green.

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Quick guide

Mating failure

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What is mating failure? Mating failure is the failure of a female to have her eggs successfully fertilised, therefore not producing offspring. Mating failure may be caused by either a lack of reproductive opportunities — for example due to early death — or by a failure to convert matings into fertilisations. This second category can be described as ‘cryptic mating failure’, due to the fact that the failure occurs during or after copulation, so that the reproductive processes that lead to mating failure are ‘out of sight’ of the researcher.

That’s strange! Shouldn’t natural selection minimise failure to reproduce? Yes. To put it bluntly: if an individual doesn’t mate and produce offspring, it doesn’t contribute any genes to the next generation. The existence of elaborate and costly sexual traits in many species is testament to the importance of achieving successful matings. Furthermore, securing a mate is often a dangerous or costly business, requiring considerable resources in order to fight rivals, avoid predation, locate and display to members of the opposite sex, and (in males) to maintain sperm levels. In many species, females are also directly harmed by males before and during mating. Given these costs of mating, and the potential high investment needed to gain them, individuals are under pressure to convert every mating into fertilised eggs and then offspring.

So that means mating failures should be rare? Theoretically! However, many studies have found non-trivial rates of infertile matings across a wide range of species. For example, a review of 32 insect species found that the frequency of infertile matings averaged 22%, ranging from zero in *Drosophila melanogaster* to 60% in the seed bug *Lygaeus simulans* (Figure 1). In birds, average hatching

failure seems to be around 10–12%, but can be as high as 40% in some species. This is only a small sample of species (more on that later), but it is clear that cryptic mating failures are frequent enough to significantly impact reproductive fitness across many species.

Why wouldn't fertilisation result from mating? Failure to convert mating success into fertilisation success can occur for a myriad of proximate reasons at any stage of copulation — from the improper coupling of genitalia to the unsuccessful fusing of egg and sperm due to genetic incompatibility. Males and females may be sterile or reproductively immature, or be in too poor a condition to produce eggs or sperm. Sperm depletion may also be common in polygynous species, such as Soay sheep (*Ovis aries*; Figure 1).

This seems very maladaptive... Could there be something else going on? Yes, it seems likely that there are contrasting selection pressures that in many species maintain a high failure rate. One example would be selection against polyspermy, which arises when multiple sperm penetrate the egg during fertilisation. Polyspermy is nearly always fatal to embryo development, and so this drives the evolution of female adaptations that reduce the number of sperm reaching the egg, such as a longer female reproductive tract. Females must tread a fine line between preventing any sperm reaching the egg and preventing too many from doing so. Falling either side of this optimum is likely to result in failure to produce any offspring.

Polyspermy may be more likely when females mate multiply, as this increases sperm competition between rival males, which can lead to the evolution of more competitive sperm and larger ejaculates. In this case, mating failure is maintained via sexual conflict, with different levels of sperm allocation favoured by each sex. Sexual conflict may also occur when males harm females during mating, leading to increased female resistance to mating. Here, choosy females risk mating failure by never accepting a mate, whereas non-choosy females risk considerable fecundity and



Figure 1. Cryptic mating failures in animals.

Top left: The frequency of infertile matings has been observed to be very high in some species, such as 60% in the seed bug *Lygaeus simulans*. This high frequency may be due to the long time needed to thread the male intromittent organ along the female spermathecal duct (Photo: Liam Dougherty). Top right: Infertile matings may be common in species in which dominant males mate multiply and so risk becoming sperm depleted, as in Soay sheep (*Ovis aries*) (Photo: Arpat Ozgul). Bottom left: Mating failures may be common in species in which females can exercise cryptic female choice. For example, red jungle fowl (*Gallus gallus*) females are frequently observed to eject male sperm from the cloaca after mating (Photo: Dominic Cram and Tom Pizzari). Bottom right: Mating failures can still lead to the production of offspring in haplodiploid species such as the parasitoid wasp *Nasonia vitripennis*, as unfertilised eggs are able to develop into fertile haploid males (Photo: Peter Koomen and Leo Beukeboom).

longevity costs from mating with too many males.

So, is mating failure always bad for females? It depends. If males are abundant enough that females can afford to be choosy, it may even be advantageous for females to cause mating failures as a form of cryptic female choice. By preventing complete intromission or ejaculation, or by expelling sperm transferred by a male, such as in red jungle fowl (*Gallus gallus*) (Figure 1), they can assert control over which male fathers their offspring, whilst taking advantage of any direct benefits that males may provide, such as nuptial gifts or parental care. However, even when the likelihood of remating is low, mating failure might not always be disastrous. For example, in haplodiploid species such as the parasitoid wasp *Nasonia vitripennis*,

females are capable of producing male offspring from unfertilised eggs in the absence of sperm (Figure 1). These females may have reduced reproductive success but they do at least avoid total reproductive failure.

What wider implications does mating failure have? The frequency of mating failure may influence many aspects of a species' mating system. High levels of cryptic mating failure are predicted to lead to increased levels of female remating (i.e. polyandry) in order to gain fertilisations. On the other hand, multiple mating by males may increase the mating failure rate via depletion of sperm stores. High levels of failure may also lead to an increased ability to discriminate against infertile mates, possibly through mate choice for condition-dependent traits in the opposite sex.

Rates of mating failure are themselves likely to be influenced by the mating system, such as the sexual conflict mentioned above. We suggest that accurate estimates of the failure rate, as well as the mechanisms leading to mating failure, may be important in order to understand the patterns of sexual selection acting in a population.

Why don't we think about it more? Is this a new concept? Mating failure is by no means a new concept, but most of what we know about it comes from experiments focusing on other aspects of reproductive behaviour. Individuals that don't produce any offspring for unknown reasons may frequently be removed from analyses. Mating failure is therefore likely to be significantly under-reported, and as such the proportion of species showing considerable rates of failure may be much higher than we realise. It might also mean that the rates of infertility seen in humans are perhaps not as unusual as many people think. Furthermore, a lack of clarity and consistent terminology has made gathering data on this topic challenging. Uniting multiple terms used in the literature — such as 'copulation failure', 'insemination failure', and 'female constraint' — under the umbrella of 'mating failure' may help to bring together researchers from different study systems to understand the causes and consequences of this widespread phenomenon.

Where can I find out more?

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Quick guide

Brown

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What's so special about brown (and yellow)? There are four bright primary perceptual hues — red, green, blue and yellow. When red, green, or blue are dimmed, the resulting dark hues still retain perceptual elements of red, green, or blue (Figure 1 top); only yellow changes categorically, to brown. Thus, unlike all other basic hues, yellow and brown are one-directional hues that are dependent on the brightness context in which they are viewed. The bright primary hues are yellow, red, green, and blue — but the dark primary hues are brown, red, green, and blue.

When do we see brown? Any surface that looks yellow when it's brighter than its surroundings will look brown when it's made sufficiently darker. This can be accomplished by making either the surroundings brighter or the surface darker. Thus, as a pure yellow light is dimmed, it starts to take on increasing amounts of brown over the 'butterscotch' range until it eventually becomes just brown, with no trace of yellow (Figure 1 middle). This explains why we never encounter brown signal lights: lights brighter than their surroundings can be yellow, red, green, or blue, but never brown, because brown is only a dark color.

How is brown similar to yellow? Yellow and brown can both be seen in isolation, with no trace of any other hue. Both can mix perceptually with either green or red: for example, orange is a reddish yellow, olive is a greenish brown. Also, neither yellow nor brown can perceptually mix with blue: blue is perceptually opponent to both yellow and brown and can cancel either hue when mixed with them. It has long been recognized that we don't see hues that have perceptual components of both yellow and blue, but the same is true for brown and blue.

How is brown different from yellow?

Although yellow and brown can mix in different proportions over the range of butterscotch hues, each can be seen in the absence of the other. Different

proportions of red and green lights are needed to produce a red–green balanced yellow compared to a red–green balanced brown, so a surface that looks like a red–green balanced yellow when surrounded by black will look greenish brown against bright white. Similarly, a red–green balanced brown will look reddish yellow (orange) against a dark surround. This change of red–green balance gave rise to the longstanding notion that the bright counterpart of brown is orange. In fact, any hue that has a yellow component when bright will have a brown component when dark. Thus, the bright counterpart of brown is yellow, not just orange.

What determines the light level at which we see brown? The brighter the surrounding lights, the higher will be the light level at which a surface looks brown. But brown is not simply a result of simultaneous contrast with its immediate environment. Even distant bright surround stimuli can cause a surface to appear brown, although they will be more effective the closer they are to the surface. Thus, brown induction resembles other contextual phenomena, such as brightness and color induction and color constancy. As a group, these phenomena reveal that the visual system uses the context of the entire scene to create our perceptions of hue and brightness of a surface, not just the light coming directly from the surface. Contexts that modulate perceived brightness generally appear to modulate perceived brownness in similar ways (Figure 1 bottom). At the same time, the spectral reflectance of a surface does influence its brownness; for example, reducing the perceptual saturation (making it more pastel) of a surface can increase the light level at which the surface appears brown, essentially giving brown an advantage over yellow.

So, is brown just darkening of yellow induced by the bright surround? No, there is nothing about the darkening effect of the bright surround that explains why the visual system categorically changes the hue from yellow to brown. There is no categorical hue change for red, green, or blue, even though a bright surround will darken them. However, the physical light level at which brown occurs does seem