Birds do it, bees do it: evolution and the comparative psychology of mate choice

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ABSTRACT The primary theoretical framework for the study of human physical attraction is currently Darwinian sexual selection. Not only has this perspective enabled the discovery of what appear to be strong universals in human mate choice but it has also facilitated our understanding of systematic variation in preferences both between and within individuals. Here we briefly summarise the background to the area and then discuss two key examples of where an evolutionary and comparative approach to understanding our behaviour has been particularly useful. Classroom activity suggestions and links to key stage 4 (age 14–16 years) teaching requirements are also explored.

Background

As late as 1974, Berscheid and Walster stated that '*identification of the physical characteristics considered attractive in Western culture, or in any other, seems a hopeless task*' (as quoted by Berscheid and Reis, 1998). Nearly four decades later, however, a vast literature has accumulated showing strong intra- and cross-cultural agreement on the attractiveness of a variety of physical traits. The primary reason for this explosion in research was the integration of Darwinian theory into psychology and the wealth of novel hypotheses this created regarding human mate choice.

Under Darwinian theory, the process of evolution occurs through two distinct forms of selection: firstly, natural selection, which in its narrow definition refers to the effects of differential mortality on the frequency with which a given gene is passed on to the next generation (that is, survival of the fittest or, rather, those best adapted to their environment); secondly, sexual selection, which refers to the effects of differential success in mating on gene frequency in the following generation. Importantly, in a sexually reproducing species, survival is evolutionarily meaningless without mating and, furthermore, traits that may seem bizarre or even impossible under natural selection can frequently be explained by their impact on mating. The classic example is the peacock's tail, which must hinder survival by acting as a physical burden to the male but yet has been shown to increase the males' chances of mating: females seem to be attracted to the complexity of the tail's patterning (Petrie, Halliday and Sanders, 1991).

Selection should favour the evolution of physical and behavioural traits that can attract (or otherwise monopolise) members of the opposite sex; likewise, it should also favour the development of preferences for opposite sex traits that contribute to successful reproduction. After all, an individual can mate a thousand times but if none of those matings produces offspring that survive to maturity then the energy has been wasted and that individual's genes are lost. Thus female peacocks may be attracted to complex male tails because such complexity can only be produced by healthy males who are not overburdened with parasites and who will give her healthy, viable offspring; the tail is what we call an 'honest signal' (Zahavi, 1975) and indicates the male's 'good genes'. Research with humans has suggested that our attraction, for instance, to symmetry in our partners may likewise be a selected preference for an honest signal of 'good genes' that promote even growth in the face of environmental assaults and illness (Gangestad and Thornhill, 1998; Jones *et al*., 2004); see Activity Box 1 for possible classroom demonstrations of symmetry in human attraction.

Perhaps the most interesting examples of commonality between human and non-human mate choice, however, are the mechanisms that may underlie variation in mate preferences. Variation in

ACTIVITY BOX 1 Bilateral symmetry

1. Have students run their tongues along the roof of their mouths: they will feel a line along the centre where the two halves of the palate are fused together. This can help us to imagine the line running through the centre of our bodies around which we should be symmetric (if we grow perfectly).
2. Take digital photographs of familiar individuals' faces (celebrities, or your own if feeling brave!) and present them on screen in both their original form and flipped over left–right. Because we primarily focus on one side of the face, it's easier to see the differences between left and right sides of the face this way. The more similar the two versions look, the more symmetrical they are, and the more symmetrical they are, the more attractive they may be considered.

our own preferences is intuitively obvious: a class of children will agree that some actors are hugely popular but many will have different people they consider 'most' attractive. It may not, however, occur to them (or, indeed, to most adults) that many animals also show variation, and thus the discovery of the possible biological basis of our own differences is likely to be a powerful example of evolution acting on human behaviour. Here we will use two well-established examples of variation in mate choice, both of which are amenable to classroom demonstration: condition dependence/ biological markets, and sexual imprinting.

Biological markets

The notion of 'biological markets' was put forward by Noë and Hammerstein (1995) and refers to the manner in which individuals in a species (or even between species) will 'trade' what they 'have' for what they 'want' – for instance, capuchin monkeys may 'trade' grooming for support in conflicts (Manson *et al*., 1999). When applied to the mating arena, this phenomenon is termed 'condition dependence' because individuals must achieve the best mate they can (for example, the most fertile or with the best genes) given their own 'condition'. For instance, Kraak and Bakker (1998) showed that, among sticklebacks, the more brightly coloured a male (which suggests better health), the more likely he is to swim towards and try to mate with a fatter female (who is likely to produce more offspring) versus a thinner female. Essentially, duller males don't waste precious energy trying to court a 'better' female!

Among zebra finches, on the other hand, we can experimentally manipulate a male's condition and observe its effects. It was fortuitously discovered that female zebra finches are very attracted to certain coloured ankle bands. Thus, by putting one of these ankle bands on a male, he became more desirable; researchers also found that these newly desirable males tended to spend less time engaging in nest building and tending young and more time mating with (other males') females (Burley 1986). Given that males do not produce eggs, they are able to pass on more of their genes by multiple mating, so being higher condition has allowed them to 'negotiate' mating encounters more to their advantage. And we can see the exact same pattern in humans: more symmetrical males report engaging in less relationship-maintenance behaviour and may have more sexual partners (Simpson *et al*., 1999). Furthermore, like the sticklebacks, women who consider themselves to be very attractive, or who have more attractive body shapes (smaller waist compared to hips, which *may* indicate fertility (Jasienska *et al*., 2004), prefer more symmetrical men than other women. Activity Box 2 describes a classroom demonstration of biological markets that shows just how simple a process it may be.

Sexual imprinting

Sexual imprinting, on the other hand, has little to do with the absolute value of a given trait and may have more to do with individual couples' compatibility. While many people are familiar with the notion of imprinting – where chicks will famously lock on to the first face they see as their 'parent' – sexual imprinting refers to the manner in which offspring will use their parents' features as a model for their future mates. In cross-fostering studies, we can see that sheep raised by goats, and goats raised by sheep, will try to mate in adulthood with individuals of their adoptive parents' species rather than their own. Similarly, Vos (1995a; 1995b) found that painting the beaks of white zebra finches to manipulate the natural sex difference in colouration leads to male chicks choosing a mate with a beak like that of their mother, no matter what sex that mate really is. Perhaps most strikingly, Japanese quails will

ACTIVITY BOX 2 Biological markets in operation

A good question, of course, is how we 'know' our own condition – especially if one has a brain the size of a stickleback's! It may be that we and other animals use others' reactions to us to gauge our 'level' and expend our courtship energy accordingly.

A classic demonstration of this is to give every person in a group a sticker on their forehead, numbered from 1 through to *n* (where *n* is the number of children in the class) so that each child has a unique number, without them seeing what it is. Participants are then told to wander around the room and form a pair with the 'best' number they can (where smaller numbers are better, 1 being 'best'). Typically, within a short space of time, numbers 1 to 6 will have formed couples among themselves and stepped to one side; a while afterwards, those at the bottom will tend to end forming the last couples, and there will be strong similarity within couples in their 'ranks'. This shows how simple and easy it really is.

(Teachers will, of course, need to consider the safety of the space they use for this, and also the likelihood of their students being willing to abandon their personal likes and dislikes regarding their classmates for the duration of the activity.)

preferentially mate with unfamiliar first cousins or unrelated individuals, perhaps based on similarity of the cousins to their nest-mates (Bateson, 1978). Sexual imprinting may be evolutionarily advantageous because finding mates is enhanced by using successfully mated parents as models (Todd and Miller, 1993). Alternatively, it is argued that a certain degree of similarity between mates may increase genetic compatibility between mates (Tregenza and Wedell, 2000) and/or increase the extent to which one's own genes are represented in offspring (via the mate). Using parents as a model for mates, therefore, can increase mate similarity. However, using parents as models could simply be an efficient way for our genes to guide us to an appropriate member of the same species and opposite sex, and all imprinting thereafter is just a by-product of 'cognitive miserliness'!

Evidence for imprinting in humans is very recent but has been rapidly replicated using a variety of methods. Both men and women seem to imprint on their opposite-sex parents and have been shown to choose partners, or be attracted to faces, which resemble their parents in terms of age (Perrett *et al*., 2002), colouring (Little *et al*., 2003), general facial appearance (Bereczkei *et al*., 2002; Berezckei, Gyuris and Weisfeld, 2004) and even facial proportions (Wiszewska, Pawlowski and Boothroyd, 2007). Following the publication of the study by Wiszewska *et al*. (2007), media coverage included several striking examples of celebrity couples who demonstrated imprinting effects: Charles Saatchi bears an uncanny similarity to his father-in-law Nigel Lawson; Johnny Ball looks more like Nigel 'Fatboy Slim' Cook than would be expected if Zoë had selected her husband by chance. Figure 1 shows an illustration of the methods of Bereczkei *et al*. (2004) that can also easily be used for in-class demonstrations.

However, one key problem is raised by sexual imprinting: if we are attracted to people who look like our parents, why don't we mate with our siblings? This is where human mate choices show a wonderful example of balanced selection pressures. Just as the giraffe's neck is maintained at optimum length by the opposing pressures of reaching the most leaves and the physical strain of actually being able to support that length (Figure 2), in humans our attraction to familial features is balanced against what is known as the Westermarck effect. The effect was named after the man who first observed that individuals generally never mate with anyone with whom they were raised: communally reared children from kibbutzim typically do not marry anyone in their nursery cohort, and in Taiwan the old practice of child-marriage suffered because those children typically found each other sexually aversive when they reached adulthood. In contrast, where siblings have been raised apart and meet as adults, they are surprisingly likely to report feelings of sexual attraction (Bevc and Silverman, 2000). This 'genetic attraction' has been covered several times in popular culture, from recent soap opera storylines (*Hollyoaks*) to melodrama literature (reunited relatives are a recurring theme in the Virginia Andrews novels), and has been the subject of recent news stories and documentaries. It is, of course, a matter for careful consideration by individual teachers whether their class is suitable for this kind of potentially delicate discussion.

By considering imprinting and the Westermarck effect together, however, we can

Figure 1 Spot the daughter-in-law – a demonstration of the method used by Bereczkei *et al*. (2004) (images our own). Participants were asked to choose the face (from 1 to 4) most similar to the target face on the left. The better the mother–son relationship, the more likely participants were to guess correctly. Copies of this image can be downloaded from www.boothlab.org/NSLC/ for use in class; the correct answer here is bride number 2.

Figure 2 The balance between different selection pressures in the fixation of giraffe neck lengths. As taller giraffes can reach more leaves, and thus gain superior nutrition, selection should favour giraffes with longer necks. However, supporting long necks requires massive ergonomic adjustments; necks any longer than this would be damaging to maintain. This leads to counteracting selection against necks that are *too* long.

see that, as with the giraffe's neck, evolution can produce perfectly balanced adaptations that lead to the optimal genetic outcome: in this case, we hypothesise, a balance between the benefits of genetic compatibility/similarity and avoiding the problems of inbreeding (see Figure 3 for a visual representation of this balance).

A tale of three species

Sticklebacks, zebra finches and humans: these three species differ vastly in many respects and yet share some striking similarities in their mating behaviour. It is likely that some of these similarities arise from 'convergent evolution' where the same solution to a problem arises separately in different lineages. It does not, however, diminish the powerful lesson of these examples: certain aspects of our behaviour show precisely the same patterns as species as various and small-brained as fish and birds, and either we are so bizarrely special that we do the same things as they do for completely different reasons or we must accept the influence of evolution on our behaviour.

That is not to say, however, that human behaviour should be considered to be totally

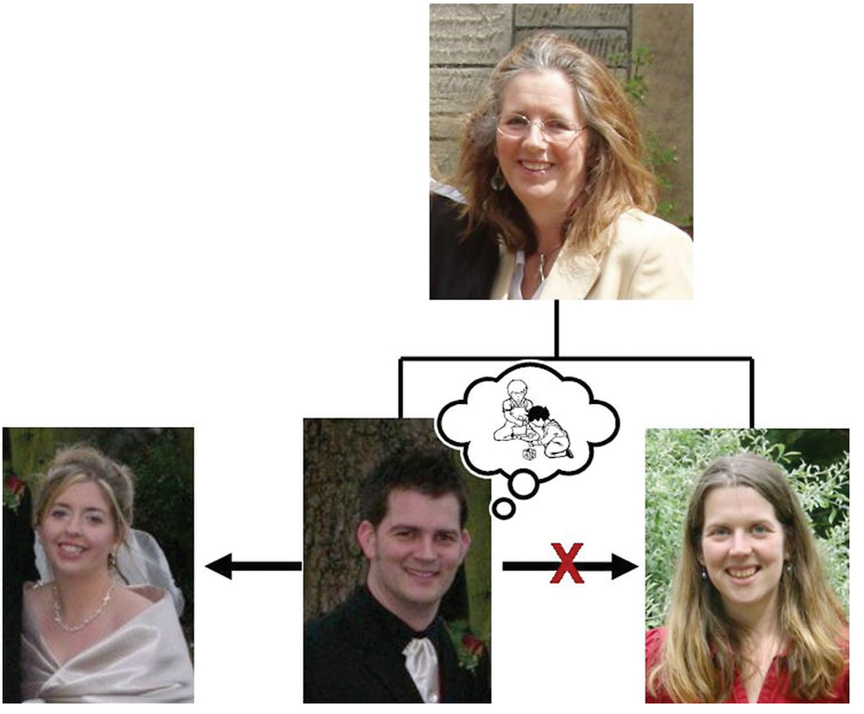

Figure 3 How imprinting may be balanced by the Westermarck effect

homologous to non-human animal behaviour. Humans are uniquely large-brained and our expanded frontal cortex allows us to make abstract connections and consider both ourselves and our environment in ways that no other creature is capable of. Thus we have a remarkable degree of control over our instinctive behaviours and are able to actively reject them if we choose. 'Biological determinism' and the 'naturalistic fallacy' both refer to the assumption that our genes control us and that we must accept what is 'natural' as desirable. This represents an excellent discussion point: males in most mammal species seem to have been subject to selection favouring multiple mating over strict monogamy but how many girls in the class would tolerate being cheated on? Does biology have to be destiny?

On the other hand, we must not anthropomorphise other animals. Japanese quails do not 'fancy' their cousins; they respond to visual and hormonal signals in an involuntary manner. Because we are aware of our feelings and experience them through the filter of our own thoughts about ourselves, it may be difficult for us to conceive of animals not sharing the same experience (how many pet owners can't help but view their animals as 'people'?) but they almost certainly do not. Similarly, our complex culture adds many layers to human interaction and courtship that other animals lack, and these powerful influences should not be underestimated.

Conclusion

Recent advances in our understanding of human attraction provide stimulating and engaging examples of the influence of biological evolution on human behaviour. With careful consideration of the potential sensitivities and common misconceptions involved, they represent excellent potential teaching examples for both key stage 4 biology (age 14–16 years) and also A-level psychology (age 16–18 years). We have identified many areas of the National Curriculum for England and Wales that could be effectively delivered using the evolution of mate choice as a platform for learning. Furthermore, the topic meets a number of cross-curriculum ideals as laid out by the Government. Examples of these can be seen in Table 1. For those interested in exploring this area further, Activity Box 3 provides links to online research sites that have a range of textual and practical resources as well as data collection projects.

Table 1 Integrating attraction research into the National Curriculum for England and Wales

Curriculum section	Potential application
Key stage 4 Science curriculum	
(1) HOW SCIENCE WORKS 1c how explanations of many phenomena can be developed using scientific theories, models and ideas	*Evolutionary theory can help us understand many aspects of human behaviour, including attraction.*
1d that there are some questions that science cannot currently answer, and some that science cannot address	*See discussion questions in section 4.*
(2) PRACTICAL AND ENQUIRY SKILLS 2c collect data from primary or secondary sources, including using ICT sources and tools	*The exploration of science by students is highly encouraged through practical means and, by utilising an area that they find interesting and relevant, we can foster 'ownership' of the curriculum for students. The classroom activities suggested in Activity Box 1 can help students engage in data collection and interpretation.*
2d evaluate methods of collection of data and consider their validity and reliability as evidence	*Attraction research primarily uses computer-based attraction tests, and questionnaires, and often utilises the internet or is biased towards undergraduate populations. Students may be well placed to discuss the benefits and drawbacks of some of these issues. Real-life examples of research can be found on the websites in Activity Box 3.*
(3) COMMUNICATION SKILLS 3a recall, analyse, interpret, apply and question scientific information or ideas	*As above regarding 2c.*
(4) APPLICATIONS AND IMPLICATIONS OF SCIENCE 4b to consider how and why decisions about science and technology are made, including those that raise ethical issues, and about the social, economic and environmental effects of such decisions	*A useful discussion to be had here revolves around the impact of discoveries regarding attraction and evolution on lay folks' understanding/assumptions about themselves and each other: firstly, what are the implications of an understanding that we are one species amongst many; secondly, how appropriately do we tend to interpret information about research into attraction and should such considerations impact on the course of research?*
4c how uncertainties in scientific knowledge and scientific ideas change over time and about the role of the scientific community in validating these changes	*The vast increase in physical attraction research since the introduction of evolutionary approaches clearly demonstrates how early uncertainty was revolutionised into a deep understanding.*

Curriculum section	Potential application
Key stage 4 Science curriculum	
(5) ORGANISMS AND HEALTH 5a organisms are interdependent and adapted to their environments 5b variation within species can lead to evolutionary changes and similarities and differences between species can be measured and classified	*The comparative element to evolutionary psychology is a particularly pertinent example of these curriculum points.*
Key stage 3 and 4 cross-curricular dimensions	
(1) IDENTITY AND CROSS-CULTURAL DIVERSITY Who do we think we are?	*There are differences but also similarities between organisms, as highlighted by mate choice research. Consideration of how evolution and genes shape our being can help us understand who we are as a species – are we distinct from nature or a product of it? This also then puts into context who 'we' are as a more distinct local group, by embedding inter-group differences within inter-specific differences.*
What connects us with and distinguishes us from others in the UK and the rest of the world?	*Attraction research has highlighted many cultural universals in mate preferences, but also certain cross-cultural patterns of variation. Discussion of that cultural impact would also address this question.*
(2) TECHNOLOGY AND THE MEDIA Can I believe what I see and read?	*Research addressed in this article has been widely reported on in the media and, by giving students both the academic discussion here and the media reports, teachers can promote discussion of authenticity in media views on science.*
(3) CREATIVITY AND CREATIVE INDUSTRIES What are the creative industries and why are they important to me?	*Science involves a lot of creative thinking and development of new approaches to problems. Attraction research has moved on from a stagnant past to a cross-disciplinary, dynamic field thanks to new approaches.*

ACTIVITY BOX 3 Online resources and experiment websites

Website	Lead researcher	Website content
www.boothlab.org	Dr Lynda Boothroyd, Durham	Online studies and lay-readers' research summaries
www.facelab.org	Dr Lisa DeBruine and Dr Ben Jones, Aberdeen	Online studies and face-morphing application
www.perceptionlab.com	Prof. David Perrett, St Andrews	Online studies and face-morphing application
www.alittlelab.com	Dr Tony Little, Stirling	Online studies and research summaries
www.psy.uwa.edu.au/facelab/	Prof. Gill Rhodes, Western Australia	Lay readers' research summaries and published images
homepage.psy.utexas.edu/homepage/group/LangloisLAB/	Prof. Judith Langlois, Texas	Lay readers' research summaries

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