

CHAPTER 2

What do humans maximize?

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2.1 INTRODUCTION

Natural selection results in organisms that appear designed to maximize their inclusive fitness (Figure 2.1; Hamilton 1964, 1970). Our null hypothesis is therefore that people, like all organisms, behave in ways which reveal that their ultimate goal is inclusive fitness maximization. Saying that people appear designed to maximize their inclusive fitness does not imply that they are aware of this design objective or that they will achieve maximum possible inclusive fitness. Evolutionary theory does not predict that humans will intentionally try to maximize anything. This statement does not imply an absence of individual autonomy of action; natural selection has not hard-wired all of our behaviours and decisions. However, in large part, it has defined which things cause people to experience pleasant or unpleasant emotions and sensations. For example food, sex, friendship, being of use to others, a sense of security and social recognition are enjoyable, while hunger, pain, fear, failure and ostracism are unpleasant. These preferences mean that people derive pleasure from, and direct their behaviour toward, evolutionarily beneficial outcomes. In short, humans are largely free to do what they want (they can choose how to satisfy their desires), but they are not free to want what they want (their desires are shaped by evolved preferences).

Humans have an unrivalled capacity for problem solving, reasoning and both individual and social learning. These cognitive tools allow individuals to use their experiences to follow a unique path toward happiness throughout their lives. If people have different experiences to learn from, they will behave differently so we expect people of different age groups, sexes, institutions, classes, communities and cultures to behave differently and to hold divergent beliefs about how to achieve the same goals.

While human preferences may be the result of natural selection, there are good reasons to expect people to make mistakes. There is

whether humans behave optimally as fitness/happiness/income maximizers (we know they will not). Instead, we advocate the biological approach, which uses economic tools to generate predictions that provide a framework to help us study human decision making and to understand why humans show the adaptations they do.

In the next part of this chapter, we discuss the purpose of adaptation and the reasons why organisms are expected to be neither perfect nor optimal. Then, in the second part, we go on to ask ‘what does evolutionary theory predict humans will maximize?’ In the third section, we discuss the reasons why human actions sometimes appear not to maximize inclusive fitness (or anything else) and finally, given these reasons, we discuss when humans will match the predictions of optimality models.

2.2 WHAT IS THE PURPOSE OF ADAPTATION?

In crossing a heath, suppose I pitched my foot against a *stone*, and were asked how the stone came to be there, I might possibly answer that, for anything I knew to the contrary, it had laid there for ever ... But suppose I had found a *watch* upon the ground, and it should be enquired how the watch happened to be in that place, I should hardly think of the answer which I had before given, that, for any thing I knew, the watch might have always been there. Yet why should not this answer serve for the watch, as well as for the stone?

The opening lines of *Natural Theology* (Paley 1802, p. 7).

What is the difference between a watch and stone? Unlike stones, Paley explains that watches consist of many parts, and that the form of these individual parts may only be understood when we realize they are all contrived for a common purpose (in this case to tell the time). In other words, unlike stones, watches appear designed. Paley argues that organisms resemble watches, not stones by demonstrating that the parts of an organism are like watches, made up of related parts, contrived for common purposes. Consider the eye; the function of an eye’s retina, cornea, lens, muscles and nerves cannot be understood unless we appreciate these parts are contrived for the common purpose of seeing. So when Paley asked ‘what is the difference between a watch and a stone?’, he had identified the question which lies at the heart of evolutionary biology: why does the natural world appear designed (Darwin 1859; Williams 1966; Leigh 1971; Maynard Smith 1982; Gardner 2009)? Fifty years later, Darwin provided the answer.

Darwin’s (1859) theory of natural selection accounts for both the *process* and the *apparent purpose* of adaptation (Gardner 2009). The process is simple: as more individuals are born than survive to reproductive age, any heritable traits associated with increased individual reproductive success

will tend to accumulate in populations. As a consequence of this process, Darwin argued, successive generations of organisms will appear increasingly well designed to maximize their reproductive success. Darwin therefore answered Paley's question in two ways: first, he showed how complex design (adaptation) could result from a natural process; second, he explained what natural design was ultimately for – to maximize Darwinian fitness.

The *Origin of Species* is a masterpiece, but its central argument is informal (non-mathematical) and it was written before the mechanism of biological inheritance (genes) was known. This meant Darwin's ideas were not precisely defined. In the 1930s, Fisher formally linked the dynamics of population genetics to the process of natural selection in his seminal work *The Genetical Theory of Natural Selection* (Fisher 1930). In this work he proposed his 'Fundamental Theorem of Natural Selection', which formally defines natural selection in terms of changes in gene frequencies and defines Darwinian fitness as an individual's genetic contribution to future generations. His theorem shows that genes associated with a greater individual fitness are predicted to accumulate in natural populations. Given this result, Fisher concluded that organisms would appear as if they are striving to maximize their Darwinian fitness (see also Grafen 2002, 2007).

Fisher's theory contained an important caveat; while he knew that behaviours may be favoured because of their indirect effect on relatives who share genes, he explicitly chose to ignore this added complexity. It was Hamilton (1964, 1970) who first formally incorporated the effect of relatives into fitness, and thus made what is arguably the most important contribution to evolutionary theory since Darwin. The result was inclusive fitness theory, which provides a more complete understanding of the process of natural selection, and is the modern view of what natural selection maximizes. An individual's inclusive fitness may be divided into two components (Figure 2.1). The first component is direct fitness, which is a measure of an individual's genetic contribution to future generations via its own reproduction. The second component is indirect fitness, which measures the genetic contribution an individual achieves by affecting the reproduction of related individuals. Grafen (2002, 2006, 2007) has confirmed Hamilton's result more formally, by demonstrating that the phenotypes resulting from the dynamics of natural selection on gene frequencies in a related population match the result of an optimization program where an agent is set to maximize its inclusive fitness within a phenotypic strategy set. Put simply, the fitness that organisms should appear designed to maximize is inclusive fitness.

Table 2.1. *A Hamiltonian classification of social behaviours.*

Effect on actor (direct fitness)	Effect on recipient (indirect fitness)	
	+	-
+	Mutually beneficial	Selfish
-	Altruistic	Spiteful

A social behaviour refers to any trait that has fitness consequences for another. A Hamiltonian (or evolutionary) classification is determined by the effect the behaviour has on the individual's average lifetime fitness and not by the fitness consequences of single interactions. Both mutually beneficial (+/+) and selfish (+/-) traits may evolve between relatives or non-relatives. Altruistic behaviours (-/+) are favoured when the benefits to related individuals outweigh the cost to self. Spiteful traits (-/-) are very rare, because of the need for negative relatedness (where the actor and recipient on average share fewer genes than two individuals drawn at random from the population).

This expanded view of fitness was instrumental in explaining the diversity of sociality in the natural world (Hamilton 1996). A behaviour is cooperative if it has been selected for, at least in part, because of the beneficial effect it has on others (West et al. 2007b). Explaining the presence of such behaviours appears problematic given that – all else being equal – they reduce the relative fitness of the actor. However, inclusive fitness theory showed that natural selection could favour cooperation or the limitation of conflict under a wide range of conditions. One explanation is that seemingly disadvantageous genes can increase their transmission indirectly by helping other individuals (typically close relatives) that are likely to share the same gene (Hamilton 1964). Yet cooperation also occurs between unrelated individuals and even between different species.

The inherent instability of cooperation between non-relatives is often conceptualized with the aid of the prisoner's dilemma (Axelrod and Hamilton 1981) or the tragedy of the commons (Hardin 1968), whereby individuals do best by not cooperating (cheating), no matter what their partners do. When there is no scope for repeated interactions or sanctions, this results in an inevitable outcome (the 'tragedy') in which all rational actors cheat, even though they would have been better off if they had all cooperated, hence the dilemma. Thus for cooperative behaviour between non-relatives to be evolutionarily stable, it must be favoured by hidden direct fitness benefits that outweigh any apparent costs and, when

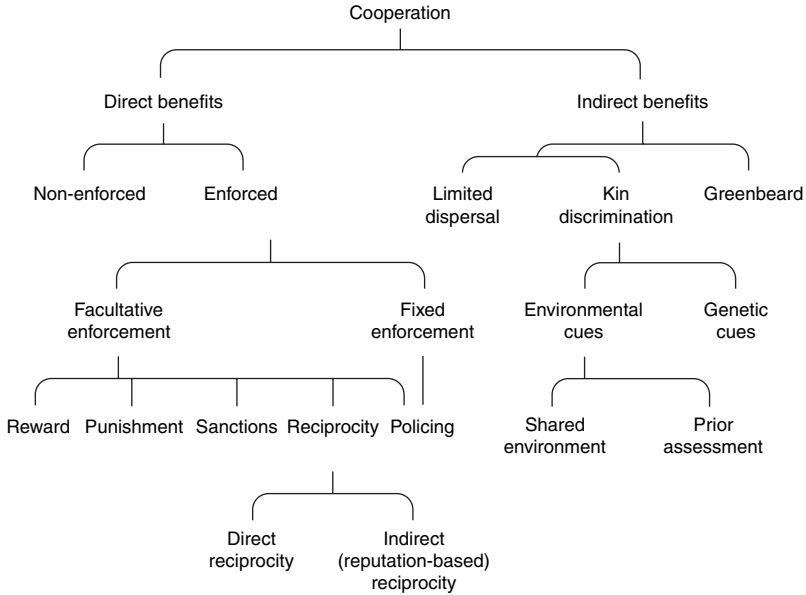


Figure 2.2. Evolutionary explanations for cooperation. Direct benefits explain mutually beneficial cooperation, which may be between non-relatives, whereas indirect benefits explain altruistic cooperation, which is always between relatives (Hamilton 1964). Within these two fundamental categories, different mechanisms can be classified in various ways (Frank 2003; Sachs et al. 2004; Lehmann and Keller 2006; Bergmüller et al. 2007; West et al. 2007b). This classification is intended for illustration only. Not all explanations are included (e.g. group competition, group augmentation and the effect of demography are excluded). A single act of cooperation may require multiple explanations; for example, it may evolve due to both direct and indirect fitness benefits, or interactions with relatives could be maintained by both limited dispersal and kin discrimination. Furthermore, it does not show how the relative importance of different mechanisms may shift through time. For example, group members may need to be related for a group to form so the benefits of cooperation are sufficient; but once established, cooperation may remain stable even if group members are unrelated, due to enforcement mechanisms. In most social species, different explanations will apply in different circumstances. For example, in humans, shared environment mechanisms help explain cooperation between kin, whereas reputation and punishment are important for cooperation between non-relatives. Finally, the way we divide up facultative enforcement strategies here is overly simplistic; a detailed discussion is beyond the scope of this chapter, and is provided elsewhere (Bergmüller et al. 2007). *Source:* adapted from West et al. 2007b.

confronted with a new instance of sociality, it is the job of evolutionary biologists to elucidate these (Sachs et al. 2004; Lehmann and Keller 2006; West et al. 2007b).

Over the past forty years, an extensive literature has developed within evolutionary biology, building upon Hamilton's work, to explain how natural selection may favour the formation and maintenance of cooperation at all levels of biological complexity, including between non-relatives and for different demographic and population structures (Table 2.1; Figure 2.2). Broadly speaking, such cooperation may be favoured for one or other of two reasons: because it is also directly beneficial in the long run to the performer, more so than it is costly (as, for example, in group augmentation effects; Kokko et al. 2001); or because it is enforced, through policing (Frank 1995, 2003; El Mouden et al. 2010), punishment (Clutton-Brock and Parker 1995; Gardner and West 2004; Lehmann et al. 2007) or sanctioning of cheaters (Kiers et al. 2003), and/or through rewards to cooperators, via mechanisms such as direct or indirect reciprocity (Trivers 1971). This work illustrates that individuals are not born selfish (contra Dawkins 1976, p. 3): they are born as inclusive fitness maximizers and this may favour their being selfish, spiteful, mutualistic or altruistic, depending on the circumstances in which they find themselves (West et al. 2007a).

2.3 ADAPTATION DOES NOT IMPLY PERFECTION OR OPTIMALITY

Watches vary. A stick in the ground can make a crude sundial, accurate to the nearest hour or so on a sunny day, while an atomic clock, cooled to near absolute zero, has a margin of error of about 1 second in 30 million years. Nevertheless, both sundials and atomic clocks are designed to tell the time. Even a broken watch that does not work at all shows evidence of design. According to Paley: 'It is not necessary that a machine be perfect, in order to shew with what design it was made ... the only question is, whether it were made with any design at all' (Paley 1802, p. 8). Applied to nature, Paley's point is that living organisms need not be perfect or optimal fitness maximizers to exhibit adaptations for 'fitness-maximizing' design (Gardner 2009).

The closest thing to perfect timekeeping is the atomic clock. If natural selection could produce its version of a 'perfect' watch, it would be a 'Darwinian Demon' (Law 1979). This imagined organism could simultaneously maximize all aspects of its inclusive fitness – it would live forever, in any environment, eat anything, be able to reproduce as soon as it was born and give birth to high-quality offspring at an infinite rate

while also helping its relatives produce their offspring at an infinite rate. Darwinian demons are a fantasy, for the same reason that we cannot wear atomic clocks on our wrists – constraints. In nature, phylogenetic, physical, time, developmental, information and resource constraints mean that organisms are unable to be perfect fitness maximizers. In addition to constraints, organisms must efficiently allocate limited resources to competing concerns. Therefore, from an evolutionary perspective, organisms can never be perfect. However, it is worth asking: when organisms make their complex trade-offs between different aspects of fitness (e.g. growth vs own reproduction vs relatives' reproduction), can they do so optimally?

Optimality is the achievement of maximum fitness given the constraints an organism faces. This means both atomic clocks and sundials may represent optimal designs in different environments. However, just as a broken watch still shows evidence of design, the presence of fitness-maximizing adaptation does not imply optimality of design. This is because in natural populations, in addition to genes, many other factors influence an organism's chances of survival and reproduction (i.e. its fitness). As the opening lines of Fisher (1930) famously read 'Evolution is not natural selection.' Stochastic effects (e.g. unpredictable weather), mutation and population movements all shift gene frequencies, so these are evolutionary forces too. If selection pressures are weak (most individuals survive and reproduce), these non-selective evolutionary forces can be the main drivers of phenotypic change, not natural selection. As these forces do not maximize anything, they divert phenotypes away from natural selection's goal of optimality, degrading any appearance of design. Therefore, even though organisms can be optimal, we expect measurably optimal behaviour to be extremely rare. There is no expectation that organisms will reach the goal of optimality, or even be anywhere near it, just that natural selection will direct genetic variation in that direction.

Although adaptation does not imply optimality, it is important to note that mechanisms under strong selection, such as those concerning life or death decisions or commonly encountered situations, will be more finely tuned toward optimality, as here, natural selection will be the dominant evolutionary force. Thus we expect to see organisms performing 'better' in the situations that they encounter most frequently. For example, as sex ratio theory predicts, a fig wasp will vary the sex ratio of her offspring depending upon the number of other females that lay eggs in the same fruit (Herre 1985, 1987). Studies have demonstrated that the sex ratios

the wasps produce are closer to the predictions of evolutionary optimality models in the situations they, as a population, encounter more frequently (Herre 1987).

2.4 WHAT DOES EVOLUTIONARY THEORY PREDICT HUMANS WILL MAXIMIZE?

Many animals have evolved the capacity for phenotypic plasticity in order to cope with variable environments. There are various ways phenotypic plasticity can be achieved. Natural selection may favour a range of phenotypes (Smith and Skúlason 1996; Halama and Reznick 2001). For example, many fish species have evolved discrete morphs, which feed in different habitats or adopt different mating strategies (Taborsky 1994; Ehlinger 1989). Alternatively, natural selection may favour the use of proximate cues to help determine optimal behaviour. For example, female great tits use increasing day length, temperature, food availability and social stimulation to time their egg laying with the peak emergence of caterpillars in spring. Studies of a great tit population in Oxford show that since the 1960s, great tits have used these cues to successfully track changes in the temporal availability of caterpillars (Dawson 2008). However, the main way animals achieve behavioural flexibility is through learning.

Learning occurs when an organism changes its behaviour in response to experience (Pearce 1997). By understanding and remembering the consequences of their actions, animals can react better to the behaviour of others and can cope with changes in their local environment (Sullivan 1988; Hollis et al. 1997; Mahometa and Domjan 2005). Many animals exhibit surprising abilities at learning. For example, goldfish, chickens, horses, cats and rhesus monkeys learn equally well to discriminate between two stimuli to gain a reward (Warren 1965). Despite the fact that many behaviours are not hard-wired, an animal's actions will still appear designed to maximize inclusive fitness as its learning is driven by cognitive mechanisms such as hunger, libido, pain and fear which are adapted to direct behaviour toward fitness-maximizing goals.

Humans differ from other organisms by degree not by kind. People derive pleasure from, and direct their efforts toward, fitness-maximizing outcomes (Darwin 1871). For example, people enjoy food, sex, friendship and social recognition and they dislike hunger, pain, fear, failure and ostracism. The diverse and growing literature on human behaviour illustrates that adaptive preferences underpin many aspects of our lives. We

summarize their effect to be that overall, humans strive to increase personal 'pleasure' and minimize 'pain', although what gives a person pleasure and pain changes often. We would predict that people are most happy when their conditions are improving, and are less happy when their conditions stagnate, even if they are doing well. This is because the positive emotions associated with happiness are evolved proximate mechanisms to guide our behaviour toward adaptive ends.

To illustrate how adaptive preferences can influence a person's behaviour, we use the literature on sexual preferences as an example. This work shows that men prefer plump women to thin women (81% of people in fifty-eight cultures surveyed; Brown and Konner 1987), and that this preference becomes more extreme when men are hungry (Swami and Tovee 2006), indicating the adaptive explanation may relate to the risk of food shortage (Sugiyama 2004). Men also prefer women with a low waist-to-hip ratio (Singh 1993), which may be adaptive as a low waist-to-hip ratio correlates with offspring with higher cognitive ability (Lasseka and Gaulin 2008). During the few days of the month when women are fertile, they are considered more attractive (Roberts et al. 2004) and male partners are more attentive (Haselton and Gangestad 2006) and possessive (Gangestad et al. 2002). While fertile, women prefer more masculine males (Penton-Voak, et al. 1999; Gangestad et al. 2005), make more effort to dress attractively (Haselton et al. 2007) and are more flirtatious and sociable (Haselton and Gangestad 2006). Finally, ovulating lap dancers earn, on average, \$30 an hour more than menstruating lap dancers (Miller et al. 2007).

What sets humans apart from all other species is the presence of accumulated cultural knowledge. Culture is defined as information capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or imitation (Richerson and Boyd 2004). Many non-human species, including blue tits (Perrins 1979), chimpanzees (McGrew 2004) and dolphins (Simões-Lopes et al. 1998), have simple systems of cultural transmission where non-genetic, non-species-wide behaviours are passed across the generations. However, only humans have the cognitive capacity to support a cumulative culture where skills are learnt, improved and transmitted to others via teaching or imitation (Boyd and Richerson 1985, 2005a; Henrich 2005, 2008). The positive fitness effect of cumulative culture is evident in even simple human technologies such as a 60,000-year-old stone-tipped spear (Pettit 2005). Its design is the product of multiple innovations to the shaft, hafting and point. No modern human could ever arrive in the Savannah and design such a spear on the

spot. Unlike other animals, humans rely upon the accumulated cultural knowledge of past generations for survival.

Humans show many adaptations for acquiring and using cultural knowledge. We are unusually docile (Simon 1990), highly sensitive to expressions of approval and disapproval by parents and peers (Baum 1994; Henrich and McElreath 2003) and most importantly, we excel at high-fidelity imitation (Tomasello 1999). These imitation skills enable humans to perform social learning via imitation and practice (Whiten and Ham 1992; Heyes and Galef 1996), which ethnographic studies confirm is how we acquire the majority of our skills (as opposed to doing so independently via individual learning, which is what animals typically do; Fiske 1999). Furthermore, our cognition adapts to the local environment as some behaviours learnt during our childhood can become hard-wired in the brain, permanently modifying our minds at the subconscious level (Quartz and Sejnowski 2000; Quartz 2002). This is evidenced by between-cultural variation in susceptibility to optical illusions, hand-eye coordination and male stress and aggression levels (Segall et al. 1966; Cohen et al. 1996; Henrich 2008). It appears that such traits become permanently fixed by about twenty years of age, and remain fixed for life, even if the individual migrates into a new culture (Segall et al. 1966).

Compared with other animals, humans possess cognitive adaptations for problem solving, strategic thought, and behavioural flexibility which are unique. People learn from their life experiences and the experiences of those around them and then use this knowledge to decide how best to seek out happiness and avoid pain. As people have different life experiences, we expect them to behave very differently and to possess widely divergent beliefs about how to fulfill the same evolved preferences. This means that behaviours that appear drastically different may share a common evolutionary foundation. For example, some young men may disrespect their parents, smoke and drive fast cars; other young men may choose to socialize with elder family members, work long hours and avoid contact with girls. Both may be trying to fulfill their desire for social status, but they have learnt to achieve the same goal in very different ways. Similar explanations can sometimes be applied to those that vow to be celibate or to forego material wealth – behaviours often cited as a challenge to evolutionary explanations for human behaviour. (This also ignores the added complication that such ‘maladaptive’ behaviours may benefit familial interests and so could help to increase relatives’ fitness.) Since members of the same family, class, culture or tribal group share many formative experiences in common, it follows that the variation in

beliefs within such groups should be far less than the variation found between them.

Humans, like other group-living vertebrates, show adaptations for sociality. This is evidenced by many elegant behavioural economic experiments, which show that we are often willing to cooperate and to punish those who do not cooperate. Importantly, this includes cooperation or punishment toward strangers in one-shot experimental encounters where there is no way of benefiting from the act (Fehr and Gächter 2002; Fehr and Fischbacher 2003; Gintis et al. 2005). Not surprisingly, such behaviour has a neurological basis: the brain's reward centres (e.g. the striatum; Stanfey 2007) activate and make us feel good when we donate money to charity (Moll et al. 2006), observe charitable behaviour (Harbaugh et al. 2007), engage in reciprocal cooperation (Rilling et al. 2002) and in costly punishment (de Quervain et al. 2004). There are many possible evolutionary explanations for why we are motivated to perform these social behaviours (Figure 2.2) and a detailed discussion is beyond the scope of this chapter (see Sachs et al. 2004; Lehmann and Keller 2006; West et al. 2007b, 2011). The fact that these behaviours are seen as irrational (with respect to an income-maximizing agent) in economic experiments involving positive externalities has generated the false impression that humans are uniquely social organisms. Such an impression feeds from misconceptions about evolutionary theory, the difference between ultimate and proximate questions, and the ways that cooperation evolves (West et al. 2011). Indeed, if the recent history of experimental social sciences had instead tested for income-maximizing behaviour in experiments with negative externalities or direct benefits to cooperation, then the same logic would have resulted in a view of humans as irrationally anti-social (Kümmerli et al. 2010).

To explain the adaptive value of social behaviours, we must understand the evolutionary trade-offs and constraints the individual experienced in the environment where the behaviours were selected for and were maintained (Herre 1987). As we do not know the full details of our ancestral environment, it is not possible to know whether social adaptations we now see were favoured due to direct or indirect benefits. Therefore, we will probably never be able to quantitatively measure the extent to which these adaptations for sociality are (from an evolutionary perspective) mutually beneficial or altruistic. However we can glean insights into the key selective pressures that operated in the past with experiments that utilize implicit cues of key environmental features (Tooby and Cosmides 1990). For example, in experiments

eye-spots have proved to be a salient cue of reputational effects, and people condition their cooperation levels on the presence or absence of such cues (Bateson et al. 2006; Haley and Fessler 2005; Rigdon et al. 2009; Ernest-Jones et al. 2011).

2.5 WHY DO OUR ACTIONS SOMETIME APPEAR NOT TO MAXIMIZE INCLUSIVE FITNESS (OR ANYTHING ELSE)?

Behavioural ecologists commonly use the economic tools of optimization theory and game theory, which assume organisms behave as optimal fitness-maximizing agents (Davies et al. 2012). Constructing such models entails making assumptions about the constraints and trade-offs facing the individual in order to define the available choices (the strategy set) and the potential payoffs (in terms of fitness) they may receive. Crucially, in order to be testable, the model requires feasibly measurable parameters, and because fitness is near impossible to measure, this means that proxies for fitness (e.g. number of offspring, food intake, number of matings or income) and fitness-based payoffs (e.g. cost = time spent on task, calories used or price; benefit = calories gained, matings, change in social rank or profit) must be used (Parker and Maynard Smith 1990). If the data and model match, the model may correctly capture the adaptive purpose of the behaviour being studied. However, often observations do not fit model predictions and it appears that the individuals are not maximizing their inclusive fitness (or anything else). Indeed, while data and models can match well, meta-analyses show that on average, evolutionary or ecological models explain only 2–5% of the variation between natural populations (Møller and Jennions 2002). There are many reasons for this – here we discuss six of them.

First, natural selection acts upon the average consequences of particular traits. This means that a particular trait may entail some costs, but as long as the cost/benefit analysis is favourable (i.e. on average it increases inclusive fitness over the individual's lifetime), the trait can be favoured. For example, in hedge sparrows (*Prunella modularis*), females often mate with multiple males, so a male cannot be sure which eggs he sired (Davies et al. 1992). As the males invest in parental care, they must estimate their paternity. This potentially difficult task is achieved via a simple approximation: the amount of uninterrupted access they had with the female (Burke et al. 1989). This rule is favoured despite the fact that about 15% of males estimate their paternity incorrectly and raise chicks of another male (Burke et al. 1989). This fitness cost is carried, as it seems the males

are unable to achieve any better with the information they have. As we mentioned above, humans react to a subconscious cue of being watched by behaving more cooperatively. While the cues we respond to usually correlate with being watched, we do make mistakes. For example, if pictures of eyes, or stylized eye-like drawings are displayed, we will contribute more to public goods games, donate more to honesty boxes or litter less (Haley and Fessler 2005; Bateson et al. 2006; Burnham and Hare 2007; Ernest-Jones et al. 2011). Even seeing three dots configured as a down-pointing triangle (resembling two eyes and a mouth), instead of an up-pointing triangle, is enough to make males offer significantly more in a dictator game (Rigdon et al. 2009).

The lesson here is that if a few individuals in a population act irrationally, it does not automatically imply that their behaviour is maladaptive or that it needs a specific evolutionary explanation. We expect natural selection to minimize the average cost of errors, but we do not expect it to eliminate them. This may mean an odd individual makes a very costly error, or that everyone who performs the behaviour may incur occasional costs. Psychologists refer to this idea as ‘error management theory’ (Funder 1987; Haselton and Buss 2000; Haselton et al. 2005; McKay and Efferson 2010). As these errors in themselves are not adaptive, to seek an explanation for them in isolation is not possible.

Second, natural selection prefers cheap solutions. In response to the varied constraints organisms face, natural selection tends to favour traits of sundial-like design, by which we mean adaptations that are quick and cheap, but do the job, rather than are time-consuming, costly and precise. Biologists call these rules of thumb; psychologists and social scientists refer to them as heuristic biases (Kahneman and Tversky 1972; Tversky and Kahneman 1974; Gilovich et al. 2002; Gigerenzer and Gaissmaier 2011). For example, the parasitoid wasp *Trichogramma* uses a rule of thumb to estimate the volume of a sphere. This sphere is the egg of its host species. Its estimate must be accurate so that it lays the right number of its own eggs inside – too many and the larvae will run out of food, too few and it reduces its reproductive success. The wasp has reduced this complex calculation to a single proxy measure, the angle her head makes with her front leg when balanced on the egg (Wehner 1987). Since the 1970s, psychologists have discovered that humans rely on a diverse array of heuristic biases in many aspects of our decision making (Gilovich et al. 2002; Pohl 2004; Haselton et al. 2005). For example, we use heuristics to make estimates of relatedness, which allows us to avoid incest and to direct cooperative behaviours

toward those we share genes with. Specifically, individuals are treated as closer relatives if there was a longer period of association during their childhood (Westermarck 1921; Lieberman et al. 2003; Corriveau and Harris 2009), if they bear a facial resemblance (DeBruine et al. 2008), if they speak the same dialect (Shutts et al. 2009) or if they smell familiar (Russel 1976; Russel et al. 1983; Porter and Cernoch 1983; Olsson et al. 2006).

Heuristics are cheap, but they are only adapted to maximize an aspect of fitness in a particular situation. They enable fast decision making and are reliable in commonly encountered situations (such as the example above of childhood association with close relatives), but they can cause us to behave in irrational ways, particularly when faced with novel situations. For this reason, the approximation used by the *Trichogramma* wasp is only accurate over the natural range of egg sizes she encounters; if presented with an abnormally small or large host egg, her rule of thumb fails and she would lay too many or too few eggs (Wehner 1987). In humans, the approximations for relatedness we use for incest avoidance cause problems in China and Taiwan where occasionally parents adopt a female infant and rear her with their son, whom she will eventually marry. Compared with marriages where spouses were raised apart, such marriages result in lower fertility and higher divorce rates (Wolf 1995). There is a vast and growing literature detailing how heuristic biases cause humans to make irrational decisions, particularly when faced with complex calculations or unfamiliar environments (Gilovich et al. 2002; Pohl 2004; Haselton et al. 2005).

Third, the solution to fitness trade-offs can change across time and circumstances. Behaviours may not appear to maximize anything, because different fitness components are traded off against each other and, as our circumstances and life stages change, these different components will change in importance (Stearns 1992). For example, we may be risk prone as adolescents, when our desire for social status outweighs our desire to avoid danger, and become risk averse once we have children, as our desire to keep our children and ourselves from harm outweighs any desire to be 'cool' (Steinberg 2008). Similarly, an old lung- or skin-cancer patient will probably wish they had not taken up smoking or used sunbeds when young. To an economist, such remorsefulness may appear irrational due to the inconsistency of preferences, but we are not designed to behave consistently, but to make the best of the situations we find ourselves in, continually altering our preferences throughout our lives in response to what gives us pleasure.

Fourth, novel environments produce non-optimal behaviour. Even behaviourally flexible organisms can only be expected to respond optimally within the range of natural variation they or their species have encountered before. Therefore in unfamiliar environments (such as a laboratory) organisms will make mistakes. In humans, this source of error is variously known as the ‘mismatch hypothesis’ (Hagen and Hammerstein 2006), artifact biases (Haselton et al. 2005) or, in cooperation research, the ‘big mistake hypothesis’ (Boyd and Richerson 2005b). As the physical and cultural environment humans live in is radically different from the one we evolved in, we may exhibit traits that are not adapted for our current environment. For example, in our ancestral environment, individuals with strong preferences for sugary, fatty and salty foods were favoured, as they sought out higher-quality diets. Today in developed countries, these evolved preferences are contributing to obesity and heart disease (Birch 1999). Similarly, strong sexual desires drove males to find the best mates and more willing mates. Now they also maintain a multibillion-dollar-a-year porn industry. It is not immediately clear whether suffering from heart disease or spending income on pornography is maladaptive or not, but this is not the point; and attempts to find out are often misguided. The point is that if these behaviours are not offset by other benefits then they will be selected against, providing the environment remains stable for a sufficiently long evolutionary time. For example, it is possible that the factors contributing to heart disease may have inclusive fitness benefits in early life, and that an attraction towards pornography may be a relatively harmless side effect of a beneficial sex drive. This idea is particularly relevant when studying cooperation because of the importance that demography and population structure have in the origin and maintenance of sociality.

Fifth, it is hard to measure fitness. Even when a behaviour is adaptive, the parameters being measured may be unable to detect the relationship. For example, behavioural ecologists use proxies of fitness, such as number of offspring, number of mates, longevity, food intake, body size or antler length. Better proxies (i.e. those more closely correlated with inclusive fitness) are expected to result in a better fit between the model prediction and the observed behaviours. Models that assume people are designed to maximize their income or social status suffer from the same problem as models that assume a stag is designed to maximize its antler length or a bee its nectar intake; they will only be accurate insofar as income, social status, antler length or nectar intake are accurate proxies for inclusive fitness. Furthermore (due to the four reasons highlighted

above), behaviours are more likely to appear mistaken (i.e. the adaptive relationship will be missed) if observed for only a short time, in isolation, in a single individual, or when the individual is in an unfamiliar environment.

Sixth, and finally, not all traits are the target of selection. This means that the existence of such traits, which may be genetically or culturally inherited, cannot be understood with economic tools. For example, a genetic trait of interest may be a by-product of selection for another gene; this applies to fleece colour of Soay sheep (*Ovis aries*; Gratten et al. 2007) and red hair colour in humans (Valverde et al. 1995). In Soay sheep, the gene for dark fleeces is favoured as it is tightly linked (i.e. physically close on the chromosome) to a gene that is essential for cell protein function (Gratten et al. 2007). Similarly in humans, red hair has no adaptive value; however, the gene for red hair also causes pale skin, which is selected for when there is little sunshine, as it increases vitamin D synthesis from UVB radiation, which prevents rickets (Jablonski and Chaplin 2000). Adaptive explanations may help explain the fundamental desires that drive our culturally inherited behaviours. However, they say little about the cultural activities such as music, literature, sport, fashion and art that we undertake to fulfill those desires. In other words, much of what we value does not have an adaptive explanation so we do not believe that the minutiae of human behaviour can be studied using economic tools.

2.6 IS MEASURABLY OPTIMAL BEHAVIOUR EVER EXPECTED?

As optimal behaviour is not to be expected in the natural world, behavioural ecologists do not use economic tools to test whether animals behave optimally. Instead, they use them to make testable predictions that can help them understand why animals show the adaptations they do. Behavioural ecology is typically a *qualitative* science, where evolutionary explanations are established by comparative studies across different conditions or between species (Davies et al. 2012). Having said that, in the natural world, there are very rare cases where optimality models do accurately predict *quantitative* differences. The best-known case of such 'as-if' optimization is that of sex ratios, where very simple models can make accurate quantitative predictions (Charnov 1982; West 2009). For example, there is a tight fit between observed sex ratios in the fig-pollinating wasps and those predicted by theory, which says that as the

number of females laying eggs in a fruit increases, the sex ratios in the broods should become less female biased (West et al. 2000).

Why do the models and data match so well in the case of sex ratios? The first reason is that sex allocation represents a very basic trade-off (male vs female), so it's easy to construct models that accurately reflect the constraints and choices available to the organism. Second, the traits can be measured precisely, as it is relatively easy to sex offspring and count the number of surviving grandchildren. Third, the sex ratio is very strongly tied to fitness, so it is strongly selected for, meaning that natural selection will be the dominant evolutionary force, allowing the trait to get close to the goal of optimality. Finally, the sex ratio is a neat quantitative trait, with the expectation that mutations of small effect can readily arise that will nudge the sex ratio by a small amount, allowing a great precision of adaptation even in a very simple organism such as the fig wasp. The example of sex-ratio research indicates when as-if optimality is most likely to be observed: when there is a simple set of choices, where decisions can be precisely quantified, when there are high stakes and where the individual can control their choice. However it should be noted that even in the case of sex ratios, deviations from predictions are observed, but these deviations are not random. In fact, as predicted, they negatively correlate with the strength of selection and with the reliability of environmental cues (West et al. 2002). Other instances of as-if optimization in animals are found in clutch sizes and various aspects of foraging behaviour (Davies et al. 2012).

The human capacity for learning, reasoning and behavioural flexibility means that, despite the mistakes we sometimes make, in a wide range of cases we do behave in ways that match the predictions of optimality models. Indeed, we are so good at fine-tuning our real-time behaviour toward achieving specific goals that it is typically studied using rational choice models. The maximand for a rational choice model is an individual's utility. Utility is maximized over short timescales and correlates to desires or wants (Marshall 1920) so can be related to inclusive fitness (Grafen 1998). It is a numerical representation of a preference ranking over a set of alternatives. Given money's properties as a universal exchange rate, it is no surprise that in today's world so many people have decided that making money is an effective way to be happy. This justifies the oft-made simplifying assumption that utility represents a single preference for income maximization.

So long as we carefully model the constraints and choices humans face, rational choice models can accurately describe human behaviour, i.e. we do

achieve as-if optimization of utility in real time in many situations (Tversky and Kahneman 1986). Learning from the example of as-if optimality in nature, we predict that human behaviour is more likely to quantitatively match the predictions of rational choice models when the decision can be precisely measured (as is the case for market behaviour), the choices are simple or routine (so there is a clear optimal decision and we do not need to rely on heuristics), the stakes are high (so the individual is motivated to 'care' about the outcome), and the individual is in total control of their choice. It is often hard to give economic explanations for our actions, particularly when they affect others or have other far-reaching consequences. When attempting to model such behaviour, care is needed to avoid unrealistic assumptions, for example by only specifying cognitively feasible concerns. Furthermore, parsimonious explanations are often possible with simpler models that only focus on personal costs and benefits. For example, an experimental participant that acts in a way that benefits or harms others may not be motivated beyond personal concerns; such externalities may be a by-product of experimental design (Kümmerli et al. 2010).

Humans are so capable of achieving as-if optimization of utility in the way rational choice models predict, it is no surprise that most economic theories assume we behave in this way. However, we do not match the predictions of rational choice models all the time (Sen 1977). This is especially true for non-market behaviour. In the previous section, we discussed why our behaviour will often not appear to maximize anything; economists will be familiar with many of these reasons. In addition to these reasons, however, the predictions about human behaviour arising from the expectation that individuals will strive to maximize their inclusive fitness will not always match the predictions of models which assume we strive for real-time utility maximization. This is because income and happiness are similar to body mass and antler length, in that they are only proxies for inclusive fitness, and actual inclusive fitness is the only maximand that the average lifetime consequences of a person's actions might be consistent with. Furthermore humans are not expected to have consistent preferences during their lives (as rational choice theory assumes). Instead, preferences vary in importance and will shift over time as an individual's personal circumstances and knowledge changes. These preference changes may seem irrational from an economic perspective, but they can make sense from an inclusive fitness point of view. Most importantly, whether we appear to solve a particular problem in an economically rational way will depend on the time frame of the problem. Over short time frames, we do maximize our pleasure. However, we are not designed to maximize

pleasure in the same way over our lifetime, as what gives us pleasure will continually change. Finally, optimization models, no matter how sophisticated or complex, cannot describe all our behaviour as we are a product of evolution, not just natural selection. In other words, we may be good, but we are not optimally designed.

2.7 CONCLUSION

How would an alien biologist that was capable of observing our behaviours and reading our minds sum up what humans maximize? They would probably say that, intentionally, humans do not aim to maximize any one thing over their lifetimes, but do generally try to maximize their pleasure and minimize their pain over short time frames. The alien may note that we receive pleasure and pain from adaptively sensible sources, and that we are very good at learning or inventing new ways to increase our pleasure. They may also note that the happiest people are those whose lives have improved constantly, rather than those who started at the top and just had to stay there. Finally, while realizing that humans engage in many instances of cooperation, their energies appear to be mostly directed towards benefiting themselves, their reproductive opportunities, and the wellbeing of their relatives. While finding them fascinating for many reasons, the alien would conclude that humans, along with all other organisms, are best described as striving to maximize their inclusive fitness over their lifetimes, yet in imperfect and non-optimal, but often predictable, ways.

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