Evolution, epigenetics and cooperation

PATRICK BATESON

Sub-Department of Animal Behaviour, University of Cambridge, High Street, Madingley, Cambridge, CB23 8AA, UK

(Email, ppgb@cam.ac.uk)

Explanations for biological evolution in terms of changes in gene frequencies refer to outcomes rather than process. Integrating epigenetic studies with older evolutionary theories has drawn attention to the ways in which evolution occurs. Adaptation at the level of the gene is giving way to adaptation at the level of the organism and higher-order assemblages of organisms. These ideas impact on the theories of how cooperation might have evolved. Two of the theories, i.e. that cooperating individuals, are genetically related or that they cooperate for self-interested reasons have been accepted for a long time. The idea that adaptation takes place at the level of groups is much more controversial. However, bringing together studies of development with those of evolution is taking away much of the heat in the debate about the evolution of group behaviour.

[Bateson P 2013 Evolution, epigenetics and cooperation. *J. Biosci.* **38** 1–10] **DOI** 10.1007/s12038-013-9342-7

1. Introduction

The help that animals give to each other has raised one of the most vexed issues in evolutionary biology. Do animals, including humans, behave in ways that benefit others? Since they often appear to do so, the key question is this: What favoured the evolution of such behaviour and under what conditions is cooperation likely to occur in those animals that show it? Before reviewing the good arguments, one bad theory should be disposed of at once. It runs as follows: if a population is outstripping its resources, then all reproductive individuals stop breeding for the good of the group. The argument is wrongheaded because the individuals who breed while others do not will eventually leave descendants that replace the descendants of all those who failed to breed. Cooperation that is vulnerable to cheating or free-loading will tend to be unstable and not persist over a long period of time.

In this article I shall discuss how the observed cooperation seen between animals may be interpreted in terms of the most widely accepted explanations for biological evolution. I shall begin with a description of the character of neo-Darwinian explanations and ways in which evolutionary theories are themselves evolving in the light of the modern understanding of epigenetics. I shall then deal with three ways in which the observed cooperation between animals (including humans) might have arisen. The first explanation is that, at least in the past, the aided individuals were related genetically; cooperation is like parental care and has evolved for similar reasons. Second, cooperating individuals jointly benefited even though they were not related; the cooperative behaviour has evolved because those who showed it were more likely to survive as individuals and reproduce than those that did not. Third, the cooperative behaviour of individuals in the group generated overall characteristics of the group that, under special conditions, favoured such groups over those that did not cooperate so effectively. The three evolutionary explanations are not mutually exclusive but only the last addresses the challenge posed by the question of emergent properties.

2. Neo-Darwinist theories of evolution

Before discussing the evolution of cooperation, I am going to start with a simple description of Darwin's explanation for the evolutionary origins of adaptations. Despite ongoing disputes, virtually every biologist who cares to think about the subject believes that all living matter has evolved. Existing species were not created in their present form at the beginning of life on this planet. Modern scientific debates are about how the changes came about, not about whether or not they happened. Increasingly, theorists agree that the evolution of life requires several distinctly different

Keywords. Cooperation; epigenetics; evolution; levels of selection

explanations. Stable forms may often arise by chance, for instance; and extinctions and opportunities for further change may result from environmental catastrophe. However, chance and catastrophe are unsatisfying and inadequate as explanations when attempts are made to understand the numerous and exquisite examples of correlations between the characters of organisms and their physical and social environments. For instance, carnivorous and herbivorous mammals have strikingly different types of teeth and the differences are readily related to methods of feeding. To take another dental example, the large canine teeth found in carnivorous mammals are also seen in non-carnivorous species that use them as weapons in fights with members of their own species. Male polygynous primates, which fight with other males for females, have much larger canines than male primates that are characteristically monogamous (Harvey *et al.* 1978). Character–environment correlations of this type are known as adaptations. They grab our attention because they seem so well designed for the job they perform. The most coherent explanation for the evolution of such phenomena is still Darwin's. Indeed, Darwin's proposal is much better seen as a theory about the origin of adaptations than as a theory about the origin of species.

Darwin's proposed evolutionary mechanism depends crucially on two conditions. First, variation in a character must exist at the outset of the evolutionary process. Second, offspring must resemble their parents and related kin with respect to such a character. The initial steps in the process involve some individuals surviving and reproducing more readily than others. If the ones that survive or breed most easily carry a particular version of the character, the character will be more strongly represented in future generations. If the character enabled them to survive or breed more readily, then the long-term consequence is that the character will generally be correlated with the conditions in which it worked. If differences between individuals depend on differences in their mode of inheritance, Darwinian evolution results in changes in the frequency in the population of the particular way in which the successful character is inherited. The orthodox way of expressing this is that evolution involves a change in gene frequency in the population. I have expressed the formulation more cautiously because inheritance may involve inherited events in development that do not involve changes in DNA and are stable across generations (see below).

Darwin used the metaphor of selection to describe the evolutionary process of adaptation because he had in mind the activities of human plant and animal breeders. People who want to produce a strain of pigeons with longer tail feathers than usual pick from their flock those birds that have the longest feathers and exclusively use them for breeding purposes. This is artificial selection of the long-tailed pigeon by animal breeders. By analogy Darwin referred to the differential survival of the characters that adapt an organism to its environment as *natural* selection. The Darwinian formulation emphasizes that the precise way in which a character enables an individual to survive and reproduce is part of the process. Moreover, the evolutionary process does not require the postulation of an unconscious motive for inheritance (let alone a conscious one).

If unconscious motives are unimportant, what about the 'selfishness' that is sometimes claimed for genes? Richard Dawkins (1976, 1982) has argued vividly that individual organisms do not survive from one generation to the next, while on the whole their genes do. He proposed that, therefore, Darwinian evolution has acted on the genes. Dawkins' approach to evolution was presented in characteristically entertaining form when he suggested that the organism is '… a robot vehicle blindly programmed to preserve its selfish genes'.

In order to understand Dawkins' particular brand of teleology, it may be helpful to forget biology for a moment and think about the spread of a new brand of biscuit in supermarkets. Consider it from the perspective of the recipe. While shoppers select biscuits and eat them, it is the recipe for making desirable biscuits that survives and spreads in the long run. A word in the recipe might specify the amount of sugar to be added and makes the difference between a good and a bad biscuit. Because it serves to perpetuate itself, that word is selfish in Dawkins' sense. This novel way of looking at things is unlikely to mislead anyone into believing that what shoppers really do in supermarkets, when they pick a particular brand of biscuit off the shelves, is select a word in the recipe used for making the biscuits. It is odd, then, that the selfish gene approach has encouraged some people to run together the crucial differences between individuals that survive and those that do not with the genetic consequences of differential survival and reproductive success in later generations (Bateson 2006). Dawkins (1982) recognized this problem and made a crucial and valuable distinction between vehicles and replicators. The vehicles included what he called the extended phenotype and the replicators were, of course, the genes

3. Development and evolution

In much discussion of evolution, the ways in which an individual develops has been placed in a blackbox and the importance of these processes sidelined. Laland *et al.* (2011) argued that Mayr's (1961) distinction between ultimate and proximate factors encouraged the dogma that knowledge of development was irrelevant to an understanding of evolution which was solely about changes in gene frequencies. The development of behaviour clearly depends both on inherited factors (primarily but not exclusively genes) and non-inherited factors (primarily environmental influences). However, to look at an individual's behaviour and ask, 'Is it genetic or is it learned?', is to ask the wrong question. All

behaviour patterns require both genes and an environment in order to develop. They emerge as a result of a regulated interplay between the developing individual and the conditions in which it lives. Moreover, like the records in a jukebox, different genes may be expressed in different environmental conditions. For that reason, the individual's behaviour cannot be divided into two types – those patterns caused by internal factors (often referred to as 'genetic' or 'innate' behaviour) and those caused by external factors ('acquired' behaviour). Many actions, such as suckling, are clearly present at birth (the strict meaning of 'innate') and many other behaviour patterns, such as some of the motor patterns used by the cat for catching prey, appear without opportunities for practice or for copying from other individuals. Nonetheless, even such spontaneously expressed patterns of behaviour are often modified by learning and by other forms of experience later in development. And other environmental factors, such as the quantity and quality of nutrition, can have general effects on behavioural development.

Modern understanding of an individual's development goes well beyond accepting that interactions between the organism and its environment are crucial. The conditional character of an individual's development and its implications for post-natal health and survival have emphasized the need to understand the processes of development that underlie the interplay between the individual and its environment. This is what Waddington (1957) termed 'epigenetics' more than half a century ago. More recently, epigenetics has become narrowly and mechanistically defined as the molecular processes by which traits defined by a given profile of gene expression can persist across mitotic cell division, but which do not involve changes in the nucleotide sequence of the DNA. The term has come to describe those molecular mechanisms through which both dynamic and stable changes in gene expression are achieved, and ultimately how variations in environmental experiences can modify this regulation of DNA.

Epigenetically mediated variation in the context of the specific expression of genes is critical in shaping individual differences in phenotype. This is not to say that differences in the copy number or nucleotide polymorphisms leading to altered sequences of particular genes between individuals do not contribute to phenotypic differences, but rather that individuals carrying identical genotypes can diverge in phenotype if they experience separate environmental experiences that differentially and potentially permanently alter gene expression. The molecular processes involved in phenotypic development were initially worked out for the regulation of cellular differentiation and proliferation. All cells within the body contain the same genetic sequence information; yet, each cell lineage has undergone specializations to become a skin cell, hair cell, heart cell and so forth. These phenotypic differences are inherited from mother cells to daughter cells. The process of differentiation involves the expression of particular genes for each cell type in response to cues from neighbouring cells and the extracellular environment, and the suppression of others. Genes that have been silenced at an earlier stage remain silent after each cell division. Such gene silencing provides each cell lineage with its characteristic pattern of gene expression. Since these epigenetic marks are faithfully duplicated across cell division, stable cell differentiation results.

When developmental biologists refer to the complex dynamics of epigenetic change, the response of the mathematically inclined theoreticians has been to point to the differential penetrance of the interacting genes. Those with lower penetrance can be ignored in order to preserve the simplicity of the additive models and ensure tractable computation. This won't do. An interaction is just that. When hydrogen and oxygen interact to form water, no special weight can be given to one or other of the combining molecules.

The dynamics of development have proved much more complicated than has been commonly assumed in much of the theoretical biology concerned with population issues. The point can be illustrated by a game that I once played with Waddington's (1957) famous epigenetic landscape. In order to illustrate the landscape for students, I stretched a sheet of elastic across a wooden framework and then, as in another of Waddington's famous illustrations, tied strings from the undersurface of the elastic to pegs representing genes. Try as I might, it proved impossible to create more than one valley by varying the length of the strings. To create the multiply furrowed landscape I had to have strings attached to hooks above the elastic surface (figure 1). I thought that this made a nice didactic point about the multiple factors, some internal and some external, influencing development. However, an even more interesting point emerged when I experimented with cutting the strings from above or below. Sometimes nothing changed and the surface still retained its original shape. Cutting others of the strings had a dramatic effect and the shape of the surface was radically altered (figure 2).

4. Relevance of epigenetics to understanding of evolution

The first account of how a phenotypic change induced by a change in the environment could lead to a change in the inherited genome was provided by Spalding (1873). Spalding's driver of evolution comprised a sequence of learning followed by differential survival of those individuals that expressed the phenotype more efficiently without learning. The same idea was advanced once again by Baldwin (1896), Lloyd Morgan (1896), and Osborn (1896), all publishing in the same year. It was known at the time as 'organic selection' and is now frequently termed the 'Baldwin effect'. Given Spalding's

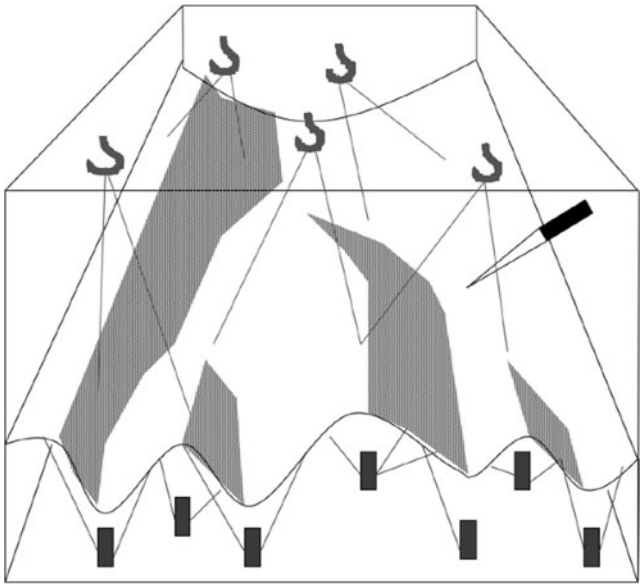

Figure 1. Result of an attempt to construct a working model of Waddington's (1957) epigenetic landscape. The pegs underneath the landscape were depicted by Waddington as being genes that control the shape of the landscape. However, they were not enough to give shape to the landscape and it was necessary to add strings attached to hooks from above the landscape. These hooks could represent factors that had been constant for many generations, such as the acidity of the oceans. The knife poised next to one of the strings represents an imminent change in one of these factors.

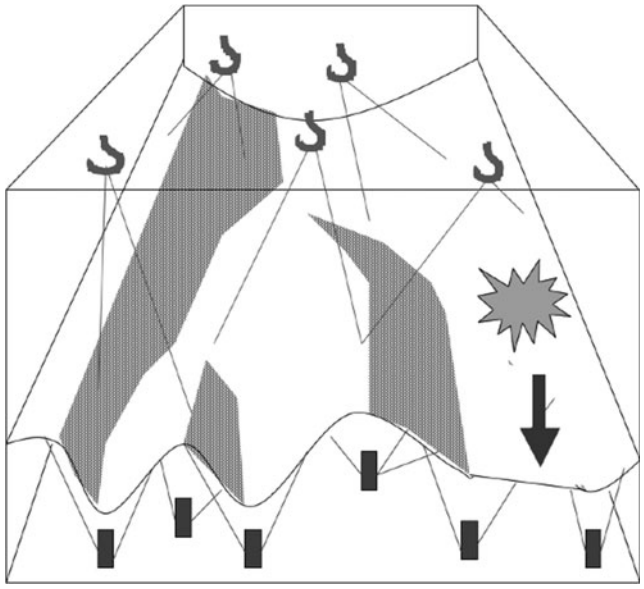

Figure 2. The knife has cut one of the strings and the result is a radical change in the shape of the epigenetic landscape.

precedence and the simultaneous appearance in 1896 of the ideas about 'organic selection', it seems inappropriate to term the evolutionary process the 'Baldwin effect', particularly since it has not been used consistently (Weber and Depew, 2003). Calling the proposed process the 'Spalding effect' is not descriptive of what initiates the hypothetical evolutionary process. It would therefore be more appropriate to employ a term that captures the adaptability of the organism in the evolutionary process, and to this end, I have suggested the term 'adaptability driver' (Bateson 2005).

A clear case of adaptability driving evolutionary change may be that of the house finch (*Carpodacus mexicanus*). In the middle of the 20th century, the finch was introduced to eastern regions of USA, far from where it was originally found on the west coast. It was able to adapt to the new and extremely different climate and spread up into Canada. The finch also extended its western range north into Montana, where it has been extensively studied. After a period involving great deal of plasticity, the house finch populations spontaneously expressed the physiological characteristics that best fitted them to their new habitats without the need for developmental plasticity (Badyaev 2009). Initially, the adaptive onset of incubation and the sex bias in the order of ovulation were affected by ambient temperature in the more northerly climes, but as evolution in the population occurred, these behavioural and physiological effects were no longer dependent on the external cues for their expression.

The question remains: under what circumstances will fixation of a previously plastic phenotype occur? The chances that all the mutations or genetic reorganizations necessary to give rise to genetic fixation would arise at the same time are small. To take a behavioural example, if a phenotype expressed spontaneously without being learned is not as good as the learned one (in the sense that it is not acquired more quickly or at less cost), then nothing will happen and fixation will not occur. If the spontaneously expressed phenotype is better than the learned one, evolutionary change towards fixation is possible. If learning involves several sub-processes, then the chances against a spontaneously expressed equivalent appearing in one step are small. However, with learning processes available to fill in the gaps of a sequence, every step that cuts out the need for a plastic component while providing a simultaneous increase in efficiency is an improvement.

A wide variety of changes in endocrine regulation following developmental stresses are mediated by epigenetic mechanisms in experimental animals (Bateson and Gluckman 2011). Induced epigenetic changes have also been described in naturally occurring plants (Pigliucci and Müller 2010). The evidence for their transmission across generations in both animals and plants continues to grow (Gissis and Jablonka 2011). Epigenetic inheritance over at least eight generations has been reported in the plant *Arabidopsis* (Johannes *et al*. 2009). One research programme on mice examined individuals possessing

a Kitparamutation (a heritable, meiotically stable epigenetic modification resulting from an interaction between alleles in a heterozygous parent) that results in a white-spotted phenotype. Injection of RNA from sperm of heterozygote mice into wild-type embryos led to the white-spotted phenotype in the offspring, which was in turn transmitted to their progeny (Rassoulzadegan 2011). In another study, mouse embryos were injected with a microRNA that targets an important regulator of cardiac growth. In adulthood, these mice developed hypertrophy of the cardiac muscle, which was passed on to descendants through at least three generations without loss of effect (Wagner *et al.* 2007). Furthermore, the microRNA was detected in the sperm of at least the first two generations, thus implicating sperm RNA as the likely means by which the pathology is inherited. The possible involvement of sperm is also supported by observations that transgenerational genetic effects on body weight and appetite can be passed epigenetically through the mouse paternal germline for at least two generations (Yazbek *et al.* 2010).

In most experimental studies, the environmental stimulus producing an epigenetic change is only applied in one generation. This might be sufficient, since work on yeast suggests that an environmental challenge can permanently alter regulation of genes (Braun and David 2011). In natural conditions, the environmental cues that induce epigenetic change may be recurrent and repeat what has happened in previous generations. This recurring effect might stabilize the phenotype until genetic accommodation and fixation have occurred. Alternatively, DNA silencing may be stable as, for example, in the plant *Linaria* (Cubas *et al.* 1999), in which the epigenetically induced phenotype does not change from one generation to the next.

DNA sequences where epigenetic modifications have occurred may be more likely to mutate than other sites. The consequent mutations could then give rise to a range of phenotypes on which Darwinian evolution could act. If epigenetic change could affect and bias mutation rates, such nonrandom mutation would facilitate fixation. Methylated cytosine-guanine sequences are mutational hotspots due to the established propensity of methylated cytosine to undergo spontaneous chemical conversion to thymine (Pfeifer 2006). As these are functional nucleotides, they are not recognized as damaged DNA and excised or corrected by DNA repair mechanisms. Thus, the mutation becomes incorporated in subsequent DNA replications. Further discussion of this possibility is given in Bateson and Gluckman (2011) and Bateson (2012). The general point is that a growing body of evidence links epigenetic processes to biological evolution (Bateson 2010; Shapiro 2011). How do these conceptual advances relate, if at all, to the evolution of cooperation?

Three evolutionary explanations have been proposed for non-manipulative social cooperation: (a) The individuals are closely related; (b) the individuals mutually benefit and groups whose members all cooperate survived better than groups that contain non-cooperating individuals; and (c) the adaptive character of the group is an emergent property of many individuals working together. I shall deal with these explanations in turn before returning to the general issue of how epigenetics relates to the thinking about the different levels of selection.

5. Individuals cooperate because they are related

Individuals will often put themselves at risk and do things that are bad for their health in the production and care of offspring. Hamilton (1964) generalized this point to collateral relatives and in an extensive theoretical argument produced the following much-quoted rule for what is known as 'kin selection':

Self-sacrificial behaviour will tend to evolve when $C < rB$, where C = Fitness cost to actor; r = Genetic relatedness between actor and recipient; B = Fitness benefit to recipient.

The overall fitness of an individual is known as its 'inclusive fitness'. Hamilton's famous argument was preceded by a view of JBS Haldane (1955). After an informal calculation made in a London pub, he declared that he would lay down his life for two brothers or eight first cousins. However, it would have only been sensible for him to lay down his life if he especially wanted to perpetuate the habit of self-sacrifice. And even if he had wanted to do that, he would have needed to be sure that the difference between the presence and the absence of the self-sacrificial tendency was associated with a difference in a single gene. If it were two genes, presumably he would have needed to save at least 4 brothers or 64 first cousins. Some caution is required, therefore, when evolutionary arguments are applied without thought given to developmental biology. Hamilton (1996) recognized that the value of r was not simply based on a genealogical closeness but could depend on overall genetic or phenotypic similarities. Nevertheless, his formalization of inclusive fitness applies to whole organisms when the difference between two types is that one type helps other individuals and the other does not and the types differ in only one gene. The gene-based approach assumes that the products of genes do not interact. If they do, as seems highly likely in many cases, the calculation of genetic similarity (r) is affected and will tend to have a much lower value than would be calculated from a simple measure from, say, knowing that the actor and the recipient were cousins.

Major controversy has been stimulated by some theorists questioning whether kin-selection has ever occurred (Nowak and Highfield 2011; Nowak *et al.* 2010). Their threat to well-established principles evoked a furious rejoinder from a large contingent of evolutionary biologists and behavioural ecologists (Abbot *et al.* 2011). The opponents in this debate have been talking past each other. Birch (in press) suggests that the critics of kin selection have based their argument on a

special version of the theory, derived from game theory, and their adversaries based theirs on a general version derived from the partial regression coefficients for a statistical formulation of the evolutionary process. Instead of chiding each other for being confused, the theorists should start listening to what has been proposed by their opponents. My sense is that while the special version is probably incorrect, the general version does describe what may have happened in evolution, subject to no interactions occurring between the genes necessary for the expression of the cooperative behaviour.

6. Mutual benefits

Two cooperating individuals are not necessarily related and may be of different species, but they are both more likely to survive and reproduce themselves if they help each other. A classic example of a symbiotic relationship between two different species is provided by cleaner wrasse and large predator fish such as a coral cod. The wrasse is strikingly marked and performs a dance in front of the cod. The cod opens its mouth and the wrasse enters and takes pieces of food wedged between the teeth of the predator. After a while the cod jerks its lower jaw and the cleaner fish exits. So long as the cleaner fish does not get eaten or does not damage the fish it cleans, both species benefit from this arrangement and have evolved signals to which the other responds appropriately. Such symbiotic arrangements provide an example of enlightened self-interest. Mutual aid was the theme of Kropotkin's (1915) famous book.

A special case of mutual aid is known as reciprocal altruism. In highly complex animals an action that benefits another may be reciprocated on a subsequent occasion by the original beneficiary (Trivers 1971, 1985). So, if one male baboon helps another to fend off competition for a female today, the favour will be returned at a later date (Packer 1977). Such examples will only tend to evolve in social structures that tend to be stable since they require individual recognition and opportunities to return favours received.

Sometimes, cooperative arrangements that benefit members of a group retain their stability because defecting individuals might be punished by the others in the group (Clutton-Brock and Parker 1995). The argument is much repeated in relation to the fate of deserters in human armies or the treatment of pacifists in times of war. However, animal examples are harder to come by despite the intuitive appeal of the proposal (Raihani *et al*. 2012). Part of the problem is that punishment is often implicit. A remarkable example from humans is provided by the response to eyes. Melissa Bateson and her colleagues found that when members of a laboratory were asked to pay for the coffee and milk on a weekly basis, they contributed three times as much when the request was accompanied by a picture of eyes instead of a picture of flowers (Bateson *et al*. 2006). Remarkably the scientists were unaware that they had been manipulated in this way.

The joint parental care of offspring provides a subtle example where individuals cooperate and thereby benefit themselves. Every type of parental care is found in animals. Maynard Smith (1977) suggested how such diversity might have evolved. A simplified (and slightly modified) version of it is given in table 1. Consider the bottom right-hand case where neither parent cares for the young; herrings are like this. If a mutant male entered the population and by caring for his young was able to have greater reproductive success than deserting males, male parental care should spread through the population. In many fish, such as the stickleback, males care for the young and the females do not. Exactly the same argument would have applied if a mutant female had had a comparable advantage over other females and also applies when such a female enters a population where male care had been the usual practice. If such a female does better than the other females, females will eventually care for the young alongside the males. In mammals females generally care for their young without help from a male. In contrast, biparental care is especially common in the birds.

Even when both parents care for young, their interests do not coincide. They certainly have a common interest in their offspring's survival, but they have diverging interests in as much as each one might be able to increase its reproductive success by spending time seeking extra mates elsewhere. In many species of birds, in which both sexes normally care for the young, if one parent dies or disappears, short of abandoning its young, the remaining mate increases the time and energy it devotes to caring for the young. This frequently observed event raises the question of the extent to which an animal can be a 'free-rider' on the efforts of its mate. Micro-economic models have been borrowed to explain what happens when two animals cooperate but do not share identical interests (Chase 1980; Bateson 1988).

Table 1. The probabilities that offspring will be produced under four arrangements of bi-parental care (simplified from Maynard Smith 1977)

		Female	
Male		Cares	Deserts
Cares	Female gets	P_2	$P_1(1+f)$
	Male gets	P_2	P_1
Deserts	Female gets	P_1	$P_0(1+f)$
	Male gets	$P_1(1+m)$	$P_0(1+m)$

P_0, P_1 and P_2 are the probabilities of survival of young cared for by 0, 1 or 2 parents, respectively, m is the probability that a deserting male will acquire a new mate and f is the probability that a deserting female will acquire a new mate.

If an animal has a fixed amount of energy available, it might use all of that energy on caring for its young. At the other extreme, it might spend all of it on looking for other mates. Since the amount of help an animal gets in caring for its young varies, the best response would also be expected to depend on conditions. Therefore, animals that are capable of taking note of the conditions should have evolved so that they change the amount of time they allocate to care of the young in response to changes in conditions. Free-riders who leave all parental care to their mates will not evolve if the respective amounts of care given by cooperating parents reaches an equilibrium when they both care for the young. Each animal involved in the cooperative care of young has an independent set of conditional rules about what to do if the help provided by its partner changes. These may not be the same for both sexes and will depend on the opportunities available for getting other matings. The rules will be the product of Darwinian evolution in the sense that the animals that had most offspring in the past would be those that most nearly found the optimum for a particular set of conditions. The equilibrium for biparental care is shown in figure 3 where the conditional rules of each parent intersect.

Houston and Davies (l985) have provided an illustration of how such postulated rules might work in a common English garden bird, the Dunnock. Birds are generally but erroneously supposed to be monogamous. In the Dunnock (*Prunella modularis*) only some of the breeding arrangements involve a stable relationship between one male and one female. Some are polygynous, some are polyandrous and, even more remarkably, some breed in combinations of several males and several females (Davies 1985). In all breeding arrangements the amount of effort put into feeding the young increases with the number of young. Taking that into account, in monogamous pairs the female is responsible for slightly more than half of the feeding. However, the female reduces the number of feeds to the brood when she is helped by two males. The feeding rate is about 7% less when she has two mates. Houston and Davies (1985) found that she does reduce her own rate of feeding the young when she has more help, but she certainly does not give up altogether – as might be naively expected if she operated on the principle of unenlightened self-interest.

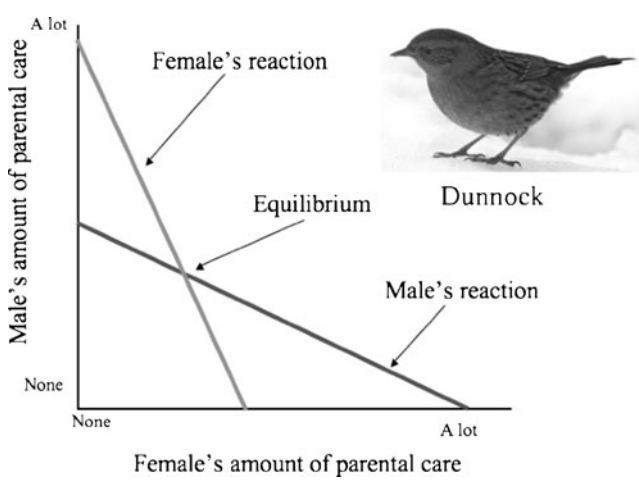

Figure 3. The female's reaction to a given amount of parental care by the male and the male's reaction to the female. Both sexes tend to reduce their parental care if the other increases its care, but the nature of the two individual's reactions to the other is such that if both sexes are present and healthy, the value for the amount of parental care given by each sex stabilises after interplay between the two of them. These values (which need not be the same for the two sexes) represent the separate optima for both of them.

7. Behaviour of groups

The final evolutionary explanation for cooperation is the most controversial. Do assemblages of individuals, through their concerted efforts, generate an outcome that puts their group at an advantage over other groups? The possibility of group characters changing in Darwinian fashion is not in question among serious evolutionary biologists (Okasha 2006). However, the consensus used to be that the conditions for such evolution were too stringent for the group-level explanation to apply, since groups are usually much slower to die off than individuals and individuals can readily move from one group to another (Maynard Smith 1976). Some authors have argued in favour of new group selection theories and suggested that they call into question other explanations for the evolution of cooperative behaviour (e.g. Wilson and Wilson 2007). The debate continues. West *et al*. (2011) referred disparagingly to 16 misconceptions about group selection, and Eldakar and Wilson (2011) replied by listing eight reasons why group selection should not be dismissed.

In the most recent edition of a justifiably famous text book, Davies, Krebs and West (2012) wrote:

> 'The new group selection approach tells us that cooperation is favoured by: increasing group benefits; reducing individual cost; and increasing the proportion of genetic variance that is between-group as opposed to within-group. However, this is mathematically equivalent to the prediction from Hamilton's rule that altruism is favoured by high *B*, low *C* and high *r*.' (p 428)

In one sense they and others before them (e.g. Grafen 1984; Gardner and Grafen 2009) were certainly right in that cooperating groups are likely to be much more closely related to each other than they are to members of groups that do not cooperate so effectively. In another sense, though, they missed the point that the character that makes one group more likely to survive than another is a property

of the whole assemblage and not of the component individuals.

In any event, the opinion of Davies *et al*. (2012) assumes that the assumptions of Hamilton's rule apply. If, as I have already noted, the expression of the behaviour depended on interactions between the products of two or more genes, the value of relatedness with respects to those genes drops and the prediction is unlikely to have any validity. Furthermore, if the adaptation is at the level of the group, then the cost to the individual may be very high.

The case for new theories of group selection becomes more obvious once observed characters are separated conceptually from their effects on gene frequencies found in individuals in subsequent generations (Bateson 1988). The well-adapted character that survives from one generation to the next is not the same as the necessary conditions for its expression. Once these distinctions are made, we can ask: to what does that character belong? The character, which Darwin's metaphorical hand has supposedly selected, may be formed by more than one individual. The characteristics of the whole entity provide the adaptations to the environment. One assemblage of individuals, acting as an organized system can compete with another in the strict Darwinian sense of differential survival.

The essential point is that the outcome of the joint action of individuals could have become a character in its own right. The nature of the argument may be perceived most clearly in the arrangements of different species that are obliged to live together in symbiotic partnership. A good example is provided by the lichens found on virtually every stable and unpolluted surface throughout the world from rocks and tree trunks to paving stones and old roofs. While they look like single organisms, lichens are composed of algae and fungi fused together in obligatory partnership. In Darwinian terms, though, the overall features of a lichen might enable it to survive better in a given environment than a lichen with other characteristics. Even though the character is replicated in an 'offspring' lichen by the independent reproduction of the component algae and fungae, the mechanism of inheritance is irrelevant to the evolutionary process. So long as offspring characteristics are correlated with parental characteristics, it does not matter how they got like that.

To take a specific example, suppose that in one 'individual' lichen, an algal mutation has made the lichen less tasty to reindeer (which are lichen specialists). The less palatable lichens will survive better than those without the mutant algae. This is not because of competition between algae, but because of the effects they have on the entity of which they are a part. In terms of my supermarket analogy, different recipes might be used for the biscuit and its chocolate coating, but the customers select the whole package and by doing so increase the numbers of copies of both types of recipes. Scott Gilbert (in press) argues much more extensively than I have done here about the need think of what have been regarded as individuals as packages of many different organisms.

The general point is that the methodology of focusing on the genetics of individuals merely serves to muddle the issue of what is necessary for differential survival with what is required for replication. Once liberated from the confusion, biologists can, with easier minds, examine the characters generated by the cooperative behaviour of social groups of animals.

If the conditions were right, the outcome of the joint actions of individuals in the social group would have changed as the result of Darwinian evolution. It is important to appreciate that this perfectly straightforward Darwinian argument does not undermine what we know about genetics or return to muddled good-for-the-species thinking. It merely draws attention to a higher level of adaptation. This requires acceptance that the characteristics of social groups are the emergent properties of the participating members, and the logic of Darwinian theory applies as much to these characters as it does to those of individual organisms.

8. Conclusion

In this article I have argued that the understanding of evolutionary biology is aided by rapid developments in epigenetics. The conventional definition of evolution in terms in changes in gene frequency laid the emphasis on outcome. The conclusion was initially fostered by the successes of molecular biology, but by degrees the simplistic notions of genes and how they affect phenotypes have been replaced. Moreover, the dynamics of development at all levels and, together with it, the understanding of the organism's active role in the evolution of its descendants have drawn attention to process as opposed to outcome.

Knowledge of each of the letters in a sentence does not help understanding of the meaning of the sentence until the sequence of letters is also known as well as the spaces between them. The success of the reductionist approach to science has meant that a methodology for putting things back together again has been slow to develop. Yet, the need has become increasingly obvious (Bateson 2005). While the behaviour of whole animals can be informed by knowledge of the underlying mechanisms, the process of reassembly can only be conducted at the level of the whole organism. Except in a small number of cases, the notion of genes, however they are defined, coding for an organism's characteristics has been discredited. Referring to genes as being adapted to the environment no longer makes any sense. Adaptation is at the level of the phenotype. These considerations have profound implications for what should be regarded as the appropriate units for evolutionary biology and how cooperation should be treated.

In this article I have considered various explanations for the evolution of cooperation. My own view is that all of the proposed processes have been important and they may all have been involved in the evolution of some forms of cooperation. Once evolutionary stability of cooperative behaviour was achieved by one or more of the Darwinian processes I have discussed, features that maintained and enhanced the coherence of the highly functional cooperative behaviour would then have tended to evolve. If a given phenotypic character (A) at whatever level of organization has benefit, then other phenotypic characters (B, C, etc.) that stabilize A would also evolve.

The explanations for the origins of cooperative behaviour are not mutually exclusive for any organism. Adopting a pluralistic approach to the evolution of cooperation in humans does impinge on the motivation of somebody who is faced with a decision on how to behave in a particular set of circumstances. That person might weigh up consciously or unconsciously the benefits to themselves of behaving in a particular way. The benefits might include avoiding disapproval of or punishment by other people. However, all these considerations can be overridden sometimes by powerful impulses to act in ways that benefit the group, the tribe or some larger assemblage without any direct benefits to the individual. What the person does on any one occasion is no longer, I would argue, a challenge to explanation in Darwinian terms. Rather, it is a challenge to psychology and behavioural biology to understand how humans and other animals resolve the incessant conflicts with which they are faced throughout their lives.

Acknowledgements

This article grew out of a lecture that I gave at Almora, India, in May 2012. The conference was organized and conducted with gentle wisdom by Vidyanand Nanjundiah. I thank him for his friendship and encouragement. A question that he posed to all those attending the meeting was the following: 'To what extent can one account for group behaviour in terms of the properties of its constituent units as exhibited when they are isolated, and to what extent does one need to invoke group-level, emergent traits?' It is an important challenge. I am grateful to Stuart Newman and Madeleine Beekman for their comments on my earlier attempt to meet the challenge.

References

Abbot P, Abe J, Alcock J, Alizon S, Alpedrinha J, Andersson M, *et al*. 2011 Inclusive fitness theory and eusociality. *Nature* **471** E1–E4

Badyaev AV 2009 Evolutionary significance of phenotypic accommodation in novel environment: An empirical test of the Baldwin effect. *Philos. Trans. R. Soc. London B* **364** 1125–1141

Baldwin JM 1896 A new factor in evolution. *Am. Nat*. **30** 441–**451** 536–553

Bateson M, Nettle D and Roberts G 2006 Cues of being watched enhance cooperation in a real-world setting. *Biol. Lett*. **2** 412–414

Bateson P 1988 The biological evolution of cooperation and trust; in *Trust: Making a breaking cooperative relations* (ed) D Gambetta (Oxford: Blackwell) pp 14–30

Bateson P 2005 The return of the whole organism. *J. Biosci.* **30** 31–39

Bateson P 2006 The nest's tale: a reply to Richard Dawkins. *Biol. Philos.* **21** 553–558

Bateson P 2010 The evolution of evolutionary theory. *Eur. Rev.* **18** 287–296

Bateson P and Gluckman P 2011 *Plasticity, robustness, development and evolution* (Cambridge: Cambridge University Press)

Bateson P 2012 The impact of the organism on its descendants. *Genet. Res. Int.* doi:10.1155/2012/640612

Birch J (in press) Hamilton's rule and its discontents. *Br. J. Philos. Sci.*

Braun E and David L 2011 The role of cellular plasticity in the evolution of regulatory novelty; in *Transformations of Lamarckism: From subtle fluids to molecular biology* (eds) SB Gissis and E Jablonka (Cambridge, MA: MIT Press) pp 181–191

Clutton-Brock TH and Parker GA 1995 Punishment in animal societies. *Nature* **373** 209–216

Chase ID 1980 Cooperative and non-cooperative behaviour in animals. *Am. Nat.* **115** 827–857

Cubas P, Vincent C and Coen E 1999 An epigenetic mutation responsible for natural variation in floral symmetry. *Nature* **401** 157–161

Davies NB 1985 Cooperation and conflict among dunnocks, Prunella modularis, in a variable mating system. *Anim. Behav.* **33** 628–648

Davies NB, Krebs JR, and West SA 2012 *An introduction to behavioural ecology* 4th edition (Oxford: Wiley-Blackwell)

Dawkins R 1976 *The selfish gen*e (Oxford: Oxford University Press)

Dawkins R 1982 *The extended phenotype* (Oxford: Freeman)

Eldakar OT and Wilson DS 2011 Eight criticisms not to make about group selection. *Evolution* **65** 1523–1526

Gissis SB and Jablonka E 2011 *Transformations of Lamarckism: From subtle fluids to molecular biology* (Cambridge, MA: MITPress)

Gardner A and Grafen A 2009 Capturing the superorganism: a formal theory of group adaptation. *J. Evol. Biol.* **22** 659–671

Gilbert SF (in press) Symbiosis as the way of eukaryotic life: the dependent co-origination of the body. *J. Biosci*. **38**

Grafen A 1984 Natural selection, kin selection and group selection; in B*ehavioural ecology: An evolutionary approach* 2nd edition (ed) JR Krebs and NB Davies (Oxford: Blackwell) pp 62–84

Haldane JBS 1955 Population genetics. *New Biol.* **18** 34–51

Hamilton WJ 1964 The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7** 1–52

Hamilton WD 1996 *Narrow roads of gene land: the collected papers of WD Hamilton Volume 1: Evolution of social behaviour* (New York: WH Freeman)

Harvey PH, Kavanagh M and Clutton-Brock TH 1978 Sexual dimorphism in human teeth. *J. Zool.* **186** 475–486

Houston AI and Davies NB 1985 The evolution of cooperation and life history in the dunnock, Prunella modularis; in *Behavioural ecology* (ed) RM Sibly and RH Smith (Oxford: Blackwell) pp 471–487

Johannes F, Porcher E, Teixeira FK, Saliba-Colombani V, Simon M, Agier N, *et al.* 2009 Assessing the Impact of transgenerational epigenetic variation on complex traits. *PloS Genet.* **5** e1000530

Kropotkin P 1915 Mutual aid: a factor in evolution (London: Heinemann)

Laland KN, Sterelny K, Odling-Smee FJ, Hoppitt W, Uller T (2011) Cause and effect in biology revisited: is Mayr's proximate–ultimate dichotomy still useful? *Science* **334** 1512–1516

Lloyd Morgan C 1896 On modification and variation. *Science* **4** 733–740

Mayr E (1961) Cause and effect in biology. *Science* **134** 1501–1506

Maynard Smith J 1976 Group selection. *Quart. Rev. Biol.* **51** 277–283

Maynard Smith J 1977 Parental investment: a prospective analysis. *Anim. Behav.* **25** 1–9

Nowak MA and Highfield R 2011 *SuperCooperators: Evolution, altruism, and why we need each other to succeed* (New York: Free Press)

Nowak MA, Tarnita CE and Wilson EO 2010 The evolution of eusociality. *Nature* **466** pp 1057–62

Okasha S 2006 *Evolution and the levels of selection* (Oxford: Oxford University Press)

Osborn HF 1896 Ontogenic and phylogenic variation. *Science* **4** 786–789

Packer C 1977 Reciprocal altruism in *Papio anubis*. *Nature* **265** 441–443

Pfeifer GP 2006 Mutagenesis at methylated CpG sequences. *Curr. Topics Microbiol. Immunol.* **301** 259–281

Pigliucci M and Müller GB 2010 *Evolution - the extended synthesis* (Cambridge, MA: MIT Press)

Rassoulzadegan M 2011 An evolutionary role for RNA-mediated epigenetic variation? in *Transformation of Lamarckism: From subtle fluids to molecular biology* (eds) SB Gissis and E Jablonka (Cambridge MA: MIT Press) pp 227–235

Raihani NJ, Thornton A and Bshary R 2012 Punishment and cooperation in nature. *Trends Ecol. Evol.* **27** 288–295

Shapiro JA 2011 *Evolution: A view from the 21st century* (Upper Saddle River, NJ: FT Press Science)

Spalding DA 1873 Instinct with original observations on young animals. *Macmillan's Magazine* **27** 282–293

Trivers R 1971 The evolution of reciprocal altruism. *Quart. Rev. Biol.* **46** 35–57

Trivers R 1985 *Social evolution* (Menlo Park: Benjamin/Cummings)

Waddington CH 1957 *The strategy of the genes* (London: Allen and Unwin)

Wagner GP, Pavlicev M and Cheverud JM 2007 The road to modularity. *Nat. Rev. Genet.* **8** 921–931

Weber BH and Depew DJ 2003 *Evolution and learning: The Baldwin effect reconsidered* (Cambridge, MA: MIT Press)

West SA, El Mouden C and Gardner A 2011 Sixteen common misconceptions about the evolution of cooperation in humans. *Evol. Hum. Behav.* **32** 231–262

Wilson DS and Wilson EO 2007 Rethinking the theoretical foundation of sociobiology. *Quart. Rev. Biol.* **82** 327–348

Yazbek SN, Nadeau JH and Buchner DA 2010 Ancestral paternal genotype controls body weight and food intake for multiple generations. *Hum. Mol. Genet.* **19** 4134–4144