Adaptability and evolution

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The capacity of organisms to respond in their own lifetimes to new challenges in their environments probably appeared early in biological evolution. At present few studies have shown how such adaptability could influence the inherited characteristics of an organism’s descendants. In part, this has been because organisms have been treated as passive in evolution. Nevertheless, their effects on biological evolution are likely to have been important and, when they occurred, accelerated the pace of evolution. Ways in which this might have happened have been suggested many times since the 1870s. I review these proposals and discuss their relevance to modern thought.

1. Introduction

Darwin’s famous metaphor of natural selection is deeply embedded in the modern language of biologists. It ‘pressurizes’, ‘forces’, ‘scrutinizes’, ‘picks out’, ‘stabilizes’, ‘directs’ and so forth. In other words, natural selection is treated as an agent in much the same way as humans are agents in artificial selection. Natural selection, as Darwin defined it, provided a wonderful mechanism to explain adaptation and, as it happened, to discredit the natural theology of William Paley whose writing had been so popular among educated people during the first part of the nineteenth century [1]. Paley, who was unquestionably an excellent naturalist as well as being a theologian, gave many examples of adaptation of the organism to its environment. He believed that the only explanation for such exquisite adaptations lay in the existence of a designer. Darwin had disposed of the need for such an agent but the metaphor he had used encouraged a belief in one. While Darwin grew increasingly unsympathetic to attempts to couple selection with a conception of design, it was his metaphorical language that has stuck in the minds of many modern biologists [2].

Treating the organism as a passive vehicle in the evolutionary process has led to a substantial area of biology being ignored. Admittedly Darwin himself did not think that it should be. He argued that choice of a mate could drive evolution [3]. He called the evolutionary process ‘sexual selection’. Alfred Russel Wallace, although the co-author with Darwin of the first clear statement about the role of natural selection, did not like the new idea. Indeed, for many years most biologists did not take sexual selection seriously. When I was an undergraduate I was told confidently that, even if it were possible in theory, the process probably played little part in biological evolution. In recent years, however, many experiments have supported Darwin’s thinking. A famous study by Anderson involved lengthening the tail of male long-tailed widowbirds (Euplectes progne) [4]. He found that when the males were given extra-long tails by inserting feathers into their tails with super glue, they attracted more mates.

The growth of interest in sexual selection is apparent in the number of papers about ‘sexual selection’, as indicated in the Web of Science. In 1960 (the year of my graduation), no papers included the words ‘sexual selection’ in their titles, consistent with the scepticism of my teachers. By the year 2000, a total of 762 papers on sexual selection were published in that year alone. In 2010, only a decade later 1427 papers on ‘sexual selection’ were published and the numbers continue to rise year on year.

Another example of active choice is likely to involve predators’ choice of prey. When Thompson’s gazelle (Eudorcas thomsonii) see a predator they jump into the air, a behaviour pattern called ‘stotting’. A suggested evolutionary mechanism is that at
Table 1. The postulated steps in ‘organic selection’ as described by Lloyd Morgan in 1896. The concept of the ‘adaptability driver’ is strongly derived from the proposed steps.

1. Suppose that a group of organisms that are capable of change in their own lifetimes are exposed to new environmental conditions.
2. Those whose ability to change is equal to the occasion survive. They are modified. Those whose ability is not equal to the occasion are eliminated.
3. The modification takes place generation after generation in the changed environmental conditions, but the modification is not inherited. The effects of modification are not transmitted through the genes.
4. Any variation in the ease of expression of the modified character, which is due to genetic differences, is liable to act in favour of those individuals that express the character most readily.
5. As a consequence, an inherited predisposition to express the modifications in question will tend to evolve. The longer the evolutionary process continues, the more marked such a predisposition will be.
6. Thus plastic modification within individuals might lead the process and a change in genes that influence the character would follow; one paves the way for the other.

Central to my argument is the suggestion that the effects of a new set of conditions could lead, at the extremes, either to immediate death or to an appropriate response to the challenge. The coping might be only partial but could be sufficient to ensure survival. Initially, the response need not be inherited, and differential survival of different genotypes may arise from subsequent differences in the ease with which the new character is expressed spontaneously as the result of mutation or genomic reorganization. The evolution of an adaptive response requires multiple changes in regulatory and developmental networks. The likelihood of this happening bit by bit diminishes with the number of components in the networks necessary to produce an adaptive outcome. By contrast, the adaptability of the individuals allows the evolutionary process to occur piecemeal. Adaptability acts both as a buffer and a driver.

Modern thinking about the importance of adaptability in evolution is usually thought to stem from Baldwin [15] in 1896, but in the same year Lloyd Morgan [16] and Osborn [17] independently developed ideas about ‘organic selection’, as the subject was called at the time. However, Spalding [18] had developed the idea more than 20 years before and should be given precedence. Lloyd Morgan’s account of the postulated process was particularly clear and is paraphrased in Table 1.

It is obvious from this outline of the proposed process, that Lloyd Morgan was not suggesting genetic inheritance of acquired characters as a mechanism. The crucial postulate is a cost of operating the original process of phenotypic adaptation, a cost that can be subsequently reduced by genotypic change enabling Darwinian evolution to occur.

Given Spalding’s precedence and the simultaneous appearance in 1896 of the ideas about ‘organic selection’, it seems inappropriate to term the evolutionary process the ‘Baldwin effect’. The trouble is that calling the proposed process the ‘Spalding effect’ is not descriptive of what initiates the hypothetical evolutionary process. I have a strong preference for a term that captures the active role of the organism in the evolutionary process. That is how I came to my preferred

first some gazelle jumped after noticing cheetah (Acinonyx jubatus) [5]. Cheetah learned not to chase jumping gazelle. The next step is that all gazelle jump after noticing cheetah. Some gazelle gain advantage by giving an exaggerated jump—a stott. Darwinian evolution acts on the gazelle but is not necessary on the cheetah because they quickly learn not to waste time chasing the energetic stotting gazelle.

This hypothesis was supported by the empirical evidence that skylarks (Alauda arvensis) sang when attacked by merlins (Falco columbarius) [6]. Those that sang most were least likely to be killed by the bird of prey, suggesting again that the predator learned not to waste effort attacking the strongest individuals. The predators’ choices had driven the evolution of the anti-predator responses of their prey.

The crucial agents necessary for the evolutionary process of adaptation driven by choice will generally be elements of the genome, but this is not always the case. In the past, the fly Rhagoletis pomonella typically laid its eggs on the fruits of hawthorns [7]. Around 150 years ago some flies laid their eggs on apples. Their offspring preferred to lay their eggs on apples and the fly has because become a serious pest in US orchards. The female offspring retain through pupation a ‘memory’ of what they have eaten and, when the new generation of adult flies have mated, they lay eggs on the particular species of plant they had eaten before metamorphosis. In this case, the variation lies in the behaviour of the adult female flies choosing apples on which to lay their eggs, and onward transmission to the next generation is achieved by an imprinting-like mechanism.

The role of learning in evolution has been discussed with increasing frequency [8,9]. West-Eberhard has been particularly influential in emphasizing how, by learning to accommodate to the special needs of its body and the peculiarities of its environment, an animal can generate novelties that provide the basis for further evolution [10]. She called this ‘genetic accommodation’. An animal’s behaviour is likely to have affected the course of evolution of its descendants in at least four ways. First, animals make active choices as Darwin was the first to suggest, and the consequences of their choices are often important. Second, animals change the conditions in which they live by altering the physical or the social environment—the main role of ‘niche construction’ [11]. Third, active animals often expose themselves to new conditions that reveal variability, with some variants more likely to survive than others. Finally, by their adaptability, organisms are able to modify their behaviour in response to novel conditions and thereby make further genetic change possible. I have considered these points elsewhere [12–14] and will focus on the last one here.

2. Adaptability

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term, namely the ‘adaptability driver’ [13]. The notion of a behavioural driver in evolution was introduced by Wyles et al. [19], but they laid primary emphasis on imitation and, of course, other active behavioural processes such as mate choice had already been recognized by Darwin.

3. Simpson’s critique

George Gaylord Simpson [20] and many others who forged the modern synthesis of evolutionary biology did not think that behaviour played an important role in evolution. This view became the standard line of neo-Darwinists. The dispute over whether or not this view is correct is about whether individual adaptability provided the leading edge for evolutionary change or whether it was both unimportant and, if it occurred, involved no new principles. Simpson asked if learning is so useful, why dispose of it? He went on, if the character generated is so important, Darwinian evolution would be sufficient.

The first criticism is based on an impoverished understanding of how behaviour is changed and controlled. The answer to those who think that the proposed evolutionary change would lead to a generalized loss of ability to learn is to state quite simply that it would not in complex organisms. Learning consists of a series of sub-processes [21]. If an array of feature detectors is linked directly to an array of executive mechanisms as well as indirectly through an intermediate layer and all connections are plastic [22], then a particular feature detector can become non-plastically linked to an executive system in the course of evolution without any further loss of plasticity [23]. In less complex organisms, however, evidence from the fruit fly (Drosophila melanogaster) suggests that Simpson could have been right [24].

On Simpson’s second point of criticism, the chances that all the necessary genetic change or reorganization would arise at the same time are small if the new character consists of several elements. What does adaptability add? The existence of an adaptive phenotype, acquired by the organism’s plasticity, sets an endpoint against which phenotypes that develop in other ways must be compared. In the natural world, if a spontaneously expressed phenotype, resulting from a new mutation or genomic reorganization, is not as good as the one acquired by adaptability in the sense that it is not acquired more quickly or at less cost, then nothing will happen. If it is better in terms of survival or reproductive success, evolutionary change is possible. The question is whether the spontaneously expressed phenotype could evolve without adaptability. If learning involves several sub-processes, as well as many opportunities for chaining (the discriminative stimulus for one action becomes the secondary reinforcer that can strengthen another) then the chances against a spontaneously expressed equivalent appearing in one step are small. However, with the learned phenotype as the standard, every small step that cuts out some of the plasticity with a simultaneous increase in efficiency is an improvement.

4. Development of the idea

Alister Hardy [25] stressed that the adaptability process could be of great significance, especially when caused initially by a change in behaviour. He envisaged a cascade of changes flowing from the initial behavioural event. Even without structural change, control of behavioural development would be expected to alter over time. A group of animals might be forced into living in an unusual place after losing their way, but they cope by changing their preferences to suitable foods that are locally abundant. Later, those descendants that did not need to learn so much might be more likely to survive than those that could only show a fully functional phenotype by learning. A cost was incurred in the time taken to learn. As a consequence, what started as a difference between animals of the same species living in different habitats becomes a genotypic difference.

An early example of how the process might work was provided by the child psychologist Jean Piaget, who began his career as a biologist and was much influenced by Baldwin. He studied the freshwater snail Lymnaea and found that in still ponds the coiled shell of the form known as stagnalis was elongated. In lakes where water action could render such a shell disadvantageous, the shell of the form known as lacustris was much shorter and the snail could cling onto the substrate much more firmly. When the lacustris form was reared in a still aquarium, half of the snails developed the shell of the stagnalis form, whereas the other half developed the more compact lacustris form without needing to be exposed to the wave action of a lake. One interpretation of this result is that the population of snails living in the lakes was mid-way through an evolutionary change. On this view the stagnalis form was evolutionarily more primitive, and in the lakes with wave action, some snails developed the lacustris adaptation as a result of developmental plasticity, but the evolutionarily more advanced snails no longer required such plasticity to develop their advantageous shell shape. Although Piaget carried out this work early in his career, it did not come out in book form until the end of his life [26]. In the terms used by Lloyd Morgan, the initial change could involve adaptability by the individual snail; the adaptability is won at some cost so that descendants expressing the character more efficiently would be more likely to survive. Undoubtedly, Piaget’s experiments could be improved upon but they remain of great interest historically.

The Galapagos woodpecker finch (Cactospiza pallida) pokes sharp sticks into holes containing insect larvae. This form of foraging involves two stages: picking up sticks and poking them into holes. Learning makes it possible for them to evolve at different times. Without learning, having one act but not the other has no value. The finch would appear to be half way down the evolutionary road from fully learned to fully spontaneous. Naive birds readily pick up small sticks but then have to learn how to use them [27].

One case of what can happen when an animal is adaptable has been provided by the three-spine stickleback (Gasterosteus aculeatus) first moving from a marine to a freshwater environment and then occupying the deep water of lakes or shallow fresh water. It was able to cope with major changes in its environment and then developed characteristics that distinguished it from its marine ancestors and which were specialized for the environment into which had moved. Shallow water males have striking red bellies involved in territory defence and courtship, whereas those in dark deep water where the colour would be useless do not [28]. The changes could be explained without recourse to the notion of an adaptability driver but the initial moves by the ancestral sticklebacks probably involved considerable adaptability.

An empirical demonstration of adaptability driving evolutionary change is that of the house finch (Carpodacus
This species is endemic in the western parts of the United States. Some individuals were collected and taken east to New York but were quickly released when the collector realized that he might be prosecuted. The birds adapted and spread north to Canada. The same species has spontaneously moved north into Montana where it has been intensively studied. After a period involving a great deal of plasticity in a new environment, the house finch populations spontaneously expressed the physiological characteristics that best fitted them to their new habitats without the need for developmental plasticity. Initially, the adaptive onset of the time of incubation that occurred in colder climates was affected by the new ambient temperature, but as evolution occurred in the population, these behavioural and associated physiological effects were no longer dependent on external cues for their expression. After using their adaptability to respond to the new environmental conditions, the house finch populations spontaneously expressed the characteristics that best fitted them to their new habitats.

The work on the house finch emphasized that adaptability could be physiological as well as behavioural. In humans, most people living at low altitudes can cope with high altitudes by enhancing the oxygen carrying capacity of the blood. However, those who live above 3000 m evolved an inherited response to thin air. Over many generations the initial adaptability was followed by inherited genomic change. This took different forms. In the course of evolution people living in the Andes have developed a different response from those living in the Himalayas.

Another example from human biology is the short stature of people living in equatorial forests. Many people believe that so-called pygmies are very small people who live exclusively in the Congo. If they were right, the pygmies might be thought of as the product of a genetic accident. However, very small people of an average male height of 150 cm occur in the equatorial forests of the Andaman Islands, the Philippines, Malaysia, Papua New Guinea, South America as well as several regions of Africa. These people are not genetically related. The geographical and genetic evidence strongly suggests that becoming very small is an adaptation to the ecological conditions of equatorial forests. That conclusion is strengthened by the underlying physiology. The physiological mechanisms by which small size has been achieved differ from one part of the world to another. In biological evolution, it is the outcome that matters, not the means by which the outcome is achieved. Here again much bigger people can cope in the environment in which the smaller people live but the presumption is that their adaptability preceded the evolution of smaller stature.

5. Models of adaptability

The hypothesis of the adaptability driver has been repeatedly modelled, both analytically [32–38] and by simulation [39–43]. The outcome of this theoretical activity has been variable, sometimes supporting the adaptability driver hypothesis and sometimes not. A general framework could explain both effects [37]. In the cases where the hypothesis has not been supported the costs of adaptability have outweighed its benefits. Spontaneously expressing a behaviour that had been learned in previous generations could be costly if it meant that the animal lost all of its ability to learn. In simpler organisms, the benefits of expressing spontaneously a previously learned behaviour was found to be outweighed by the cost of losing the capacity to learn about other things [24]. The argument is much less cogent when applied to big-brained animals like birds and mammals with multiple parallel pathways involved in learning. In these animals, the loss of capacity to learn in one way has no effect on the capacity to learn in other ways [23].

Inasmuch as it has been taken seriously, the hypothetical adaptability driver was usually supposed to provide a mechanism for the slow accretion of spontaneously expressed phenotypic elements in the course of evolution. Emphasis was placed on how particular behaviour patterns initially acquired by learning could be expressed spontaneously without learning in the course of subsequent evolution. Developments initiated by the work of Hinton & Nowlan [39] have shifted the focus to other issues, such as the way in which plasticity can accelerate the rate at which challenges set by the environment can be met, the advantages of plasticity in a changing environment and the conditions in which plasticity might slow down evolution.

6. Evolutionary ladders

The ramifying effects of adaptability on evolution envisaged by Alister Hardy may have become increasingly powerful as animals, in particular, become more complex [44]. Many examples are given in the recent literature [8,9]. A system that enhances the fitness of an individual depends on a number of elements such as the capacity to use information contained in the energy impinging on a sense organ, specific biochemical reactions and particular effectors that respond adaptively to the stimulation [45]. Elements may be recombined in different ways to perform different functions.

Novel challenges create the conditions for the emergence of new functional systems added to the existing ones either by Darwinian evolution or by an individual’s plasticity. Possible examples are the addition of a face recognition module in primates [46] and the evolution of invasiveness in birds [47]. This evolutionary process could lead to the establishment of increasingly elaborate organization and patterns of behaviour. When such complexity entailed a greater ability to discriminate between different features of the environment or a greater ability to manipulate the environment, the organism would benefit and would be more likely to survive and reproduce in the face of multiple challenges during its lifetime.

A new adaptation was likely to emerge in evolution when the accumulated phenotypic effects of genomic reorganization were added to the existing phenotype. Although these phenotypic effects are specific to the new function, existing parts of the phenotype would have been recruited for this function. Plasticity would promote much more rapid genetic evolution of complex sets of adaptive systems than can be accomplished by mutation or genomic reorganization alone. As elements derived from plastic mechanisms are replaced by inherited elements the organism would have been able to fill by plasticity missing elements in subsequently emerging systems. In general, the proposal is that an ability to cope with complex environmental challenges by means of plasticity opens up ecological niches previously unavailable to the organism. This would inevitably lead to the subsequent evolution of morphological, physiological and biochemical adaptations to those niches and the likelihood of speciation [48]. Where an environmental challenge involved greater processing capacity by the
brain, this organ too would be expected to evolve with greater rapidity. On the assumption that the larger brain relative to body size ensures greater learning capacity, the rate of evolution should correlate positively with the relative brain size. This expectation is given some support by the study suggesting that taxonomic groups evolving most rapidly have the biggest brains relative to body size [19]. The expectation is also supported by the correlation between behavioural innovation and brain size reported for birds [49] and primates [50].

7. Costs of plasticity

Does adaptability have costs? Conrad [51] argued that such a capacity would disappear over time if it were surplus to the requirements of the organism. Bacterial mutants that forego even one biosynthetic function have an advantage on a medium in which the function is not necessary [52]. In a meta-analysis of the costs of plasticity in 27 studies (16 species of plant and seven animals) the costs were found to be low [53]. However, even a low cost could be significant over a long period of time. Mountain chickadees (Poecile gambelli) from a variable high altitude environment were more adaptable and better able to solve novel problems than those from a much more constant low altitude environment [54]. The difference between the populations might not have been inherited and simply reflected the difference in the birds’ developmental histories. A clear link between ecology and adaptability, however, was found by Sultan et al. [55]. They studied two ecologically distinct but closely related species of annual plants, a generalist that could cope well with both dry and moist conditions, and a specialist restricted to moist conditions. They demonstrated that offspring of the generalist species showed adaptive and plastic responses to drought, such as larger root systems, which were not found in the offspring of the species that was specialized to live exclusively in a moist environment.

Bateson & Martin [56] suggested that play affected adaptability later in life. They argued that the generalist species were more playful than the specialist species, supporting the general point made by Sultan and her colleagues and subsequently in a thorough review by Sultan [57] herself. Further argument about the costs of plasticity are provided by Murren et al. [58].

The potential costs of plasticity raise an interesting possibility. The rules governing adaptability may be specific to the evolutionary history of the lineage. So, for example, if every item encountered in individuals’ histories needs to be recognized separately that would have led to a different rule for learning from where different views of the same object needed to be classified together. Classification together is important in the recognition of a parent or mate in which the front view is very different from the back view [59]. The outcome of variation in rules for learning is likely to be important in behavioural adaptability. Therefore, when the rules are relevant in a particular situation, the animal might be perceived to behave intelligently when faced with a new challenge. From a different perspective Watson & Szathmáry [60] arrived at a very similar view. They discuss how the current understanding of learning is helpful in developing a theory of biological evolution. The rules for learning affect the characteristics of the phenotype on which Darwinian evolution acts. As a result apparently intelligent behaviour obtained from an individual’s experience can feed into a lineage’s experience in the course of evolution.

8. Genetic assimilation

When it was not popular to do so, Conrad Waddington [61] argued for the need to establish links between development and evolution. In a classic experiment, he applied heat shock to the larvae of fruit flies (D. melanogaster) [62]. He bred from the flies that had developed a particular character (lack of a cross-vein in the wings) as a result of their larval experience. He continued to apply heat shock in each generation and to breed selectively from the flies with cross-veinless wings. After 14 generations of heat shock and selective breeding, cross-veinless wings developed spontaneously in the absence of the external triggering condition of heat shock. He called this phenomenon ‘genetic assimilation’ and suggested that larval heat shock followed by artificial selection of the flies exhibiting a particular character was due to the expression of genes that were carried in only a part of the population.

Waddington’s fruit fly experiment is just one illustration of innumerable possible scenarios. The generation of fresh variation may provide radically new opportunities for those individuals equipped with the new phenotype. West-Eberhard [10] argued that after developmental disruption, the reorganization of the genome might have a much broader effect than that envisaged by Waddington. She suggested that major changes might evolve as the character in question became more variable; in other words, it became developmentally less robust. The umbrella term that she used for all the heritable changes that might occur in the genetic regulation of development in response to environmental influences was ‘genetic accommodation’. One instance of the broadening effect suggested by West-Eberhard would be the evolution of a variety of distinct developmental trajectories or polyphenisms, expressed under specific conditions. An example of such genetic accommodation was provided by Suzuki & Nijhout [63], who studied tobacco hornworm caterpillars, the larvae of the moth Manduca sexta. These larvae are normally green, but a naturally occurring mutant form is black; both colour forms are heritable, with the black form arising from a sex-linked recessive allele that reduces juvenile hormone secretion, resulting in a black cuticle. When Suzuki & Nijhout heat shocked the black larvae at the fourth larval instar, which is the sensitive period for the effect of juvenile hormone on cuticle coloration, some of the fifth larval instars were greenish. The authors bred from the greenest larvae, as well as those that did not show colour change on heat shock (the persistent black larvae), and monitored in each generation how the larvae appeared after heat shock and after being reared at different temperatures. By the 13th generation, the line selected for blackness developed robustly as black larvae irrespective of the rearing temperature. At high rearing temperatures, the line selected for greenness was more strikingly green than an unselected line that acted as a control group. However, at low rearing temperatures, the green-selected line was mostly black (although not as black as the black-selected line). Thus, the artificial selection process enabled two different phenotypes to evolve at different constant temperatures. The green-to-black colour switch could be seen at a lower temperature, and within a smaller temperature range, compared with the control group. The observed phenotypes were inherited without heat shock.
Table 2. The differences between the adaptability driver (table 1) and genetic assimilation.

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<th>adaptability driver</th>
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<td>initial response</td>
<td>coping</td>
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<td>speed of initial response</td>
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How does what I have called the ‘adaptability driver’ relate to what Waddington called ‘genetic assimilation’? Frequent references are made in the literature to plastic characteristics becoming inherited by genetic assimilation. The claims are made casually and without thought being given to how a usually implicit reference to Waddington might explain what was being proposed. Most of the explanations for Waddington’s results seem either vague or incoherent. How is it supposed that a shake-up of development in one generation leaves the developmental process more likely to be inherited in the next? What is the nature of this cumulative process? Appeals to re-canalization or alterations in threshold do not seem to answer this question precisely.

Evidence provided by Waddington and others for genetic assimilation seems very different from that needed for the evolutionary process of an adaptability driver. The differences are set out in table 2. The adaptability driver involves necessary compensation for the effects of a new set of conditions and immediate response by the individual to the challenge. The accommodation is not inherited and differential survival of different genotypes may arise from subsequent differences in the ease with which the new adaptation is expressed.

The evidence for studies of genetic assimilation also involves expression of a novel character in a new environment, but the character is not necessarily an adaptation to the triggering condition, even though it may confer some advantage on its possessor. Cross-veinless wings of Drosophila adults do not bear any functional relation to the environment that supplied a heat shock when the flies were larvae. All that is required initially is that the environmental conditions trigger the expression of a phenotype that can be repeated generation after generation so long as the environmental conditions persist. The initial response of the adaptable animal is fast whereas the developmental effects of exposing fruit fly larvae to heat shock were not seen until they were adult. In the adaptability process, most individuals will survive in the initial stages. In Waddington’s experiment those expressing the cross-veinless character, a subset of the total population, were artificially selected for further breeding. Finally, in the case of organic selection described by Lloyd Morgan, though not Baldwin, fresh phenotypic variation presumably arises by genomic reorganization which allows the adapted character to be expressed more easily and thence leads to differential survival. In Waddington’s experiment genomic change was to be expressed more easily and thence leads to differential genomic reorganization which allows the adapted character to be expressed more easily and thence leads to differential survival. Waddington would have agreed, but he had some change of heart when he wrote to Alister Hardy as follows: ‘As to the importance of behaviour in evolution, I think I have been moving closer to your position and realizing more fully its central importance’ [64, p. 280]. Although many of the examples about adaptability involve behaviour, adaptability could occur at any of the levels of analysis from the whole organism to the molecular and occur at any stage of development.

9. Conclusion

Adaptability probably appeared very early in biological evolution and is certainly seen in bacteria. It may be costly and in specialist organisms the capacity may have been lost. The most important conclusion is that the adaptability driver, when it occurs, provides a ladder in evolution [65]. Clearly complex structures can develop without such a process, but the driver is important when intermediates provide no benefit and a combination of simultaneous genomic changes needed to provide a functional whole is improbable. Adaptability, as suggested by Lloyd Morgan, can accelerate the rate at which challenges set by the environment can be met. The effect of such plasticity on evolution may have become increasingly powerful as animals, in particular, became more complex. Elements could be recombined in different ways to perform different functions. This evolutionary process could lead to the establishment of increasingly elaborate organization and patterns of behaviour. I contrast the adaptability driver, where the evolutionary process is clear, with genetic assimilation where it is not. Plasticity may be involved in both evolutionary processes but takes a different form. The distinctions between different types of plasticity are described by Bateson & Gluckman [66].

Darwin’s famous metaphor of natural selection is deeply embedded in the modern language of biologists. Natural selection is commonly treated as an agent in much the same way as humans are agents in artificial selection. I appreciate that many biologists use selection to cover exclusively the three points of Darwin’s evolutionary mechanism, namely variation, differential survival and reproductive success, and inheritance. However, his metaphor still exerts a strong influence on the way that evolutionary biology is treated. By replacing ‘selection’ in our writing with ‘Darwinian evolution’ gives honour where it is due and encourages the view that adaptability plays an active role in evolution. The old mantra would have it that evolution is driven by changes in gene frequencies. In many cases, however, changes in gene frequency are likely to be the consequences of an organism’s adaptability.

With the growing acceptance that organisms are not passive in relation to their role in the evolution of their descendants, I hope that much more research will be devoted to the adaptability driver than has previously been the case. It helps to bring together studies of development with those of evolution which is a principal aim of this paper.

Data accessibility. This article has no additional data.

Competing interests. I declare I have no competing interests.

Funding. I received no funding for this study.

Acknowledgements. I am grateful to Richard Watson for discussion. I also thank three anonymous referees who commented extensively on an earlier version of this paper.


58. Murren CJ et al. 2015 Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity 115, 293 – 301. (doi:10.1038/hdy.2015.8)


