

Chapter 2

Baldwin's Organic Selection and the Increasing Awareness of the Evolutionary Importance of Behavioral Shifts

Baldwin's developmental and evolutionary theories of organic selection were developed in the context of passionate debates about a wide range of broader biological and evolutionary topics, approximately 120 years ago (e.g., [23–26]). Baldwin's main aim was to explain how directional evolution could occur without the Lamarckian direct inheritance of acquired characters. It is therefore very interesting to see how the so-called “Baldwin effect” has been increasingly widely discussed in the last decades. In addition, in recent years evolutionary biologists from very different backgrounds—including psychology, ethology, ecology, and developmental biology—have also become increasingly interested in Baldwin's broader idea of “organic selection”. A quick search in Google Scholar shows that, since 2000, at least 735 publications have focused on “organic selection” and up to 4360 works have focused on the “Baldwin effect”. Due to a lack of space, and to not lose the focus on its central message, I will not provide an extensive account of Baldwin's life and work in this chapter. This is beautifully done in many of those thousands of publications, including entire books dedicated to this and related subjects such as *Evolution and Learning—The Baldwin Effect Reconsidered* [390] and *Beyond Mechanism: Putting Life Back Into Biology* [182]. I will simply provide a brief summary of those of Baldwin's key ideas that are particularly relevant to ONCE. Part of this summary will be based on a recent paper by a fascinating and outside-the-box thinker who provides a well-considered introduction to Baldwin's organic selection, its historical context and influences, and the differences between his ideas and those of Lamarck and Darwin: Corning [61].

Corning notes that both Lamarck and Darwin appreciated that functional adaptation to an environment is problematic for organisms. However, Lamarck argued that because the environment is not fixed, when it changes organisms must accommodate themselves or they will not survive/reproduce. Changes in the environment over time can thus lead to new “needs”, which in turn can stimulate the adoption of new “habits”: thus, in theory, changes in habits (function/behavior) would come before changes in structure (form). As noted by Corning, Darwin also valued the role of behavior in evolutionary change but was more cautious, stating

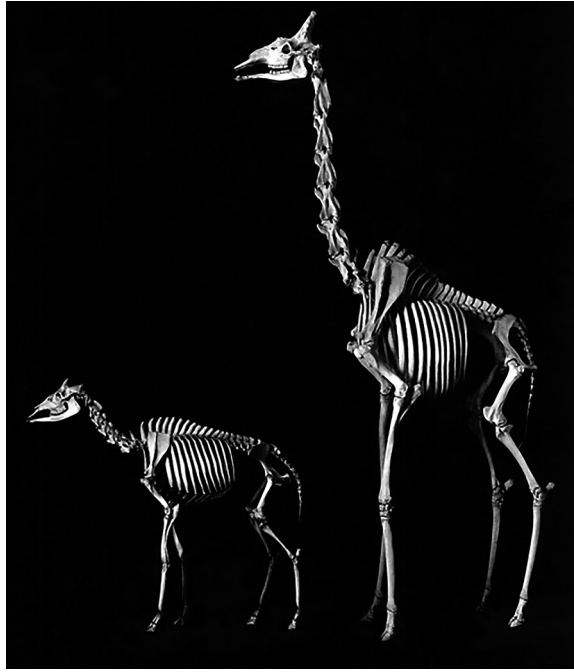
that “it is difficult to tell, and immaterial for us, whether habits generally change first and structure afterwards; or whether slight modifications of structure lead to changed habits; both probably often change almost simultaneously” [67: 215]. Moreover, most of Darwin's followers did not acknowledge an important evolutionary role for behavior, except for some scientists who “Darwinized Lamarckism” at the turn of the twentieth century. These include, among others, Baldwin, Morgan, and Osborn: despite their different individual perspectives, their overall views were generally lumped together under Baldwin's Organic Selection [61].

Corning wisely uses the most common example to differentiate the theories of Lamarck and Darwin, i.e. the size of giraffes and their necks, from Baldwin's organic selection. According to Baldwin's view, naturally occurring variations in the neck lengths of ancestral Giraffidae (i.e., the family that includes extant giraffes) would have become adaptively significant when these animals acquired, probably through behavioral trial-and-error, a new “habit” (eating Acacia leaves) as a way of surviving in the relatively dry environment of the African savanna. As stressed by Corning, we cannot know for sure that this was the case, but some suggestive evidence can be found in another species of the family Giraffidae, the okapi, which occupies woodland environments. As expected within the context of Baldwin's theory, the members of this species have very different feeding habits than giraffes do and accordingly also have a different form: their necks are much shorter than those of giraffes (Fig. 2.1). Paleontological studies in fact suggest that, compared with their last common ancestor, neck length was both dramatically increased in the giraffe lineage and secondarily decreased in okapi lineage [66]. This example therefore illustrates how behavioral choices—such as whether to move elsewhere or continue to live in a savannah environment versus a woodland one, and specifically whether to eat Acacia leaves in the former environment or leaves, buds, and shoots in the latter—can lead to very different evolutionary trends in giraffes compared with okapis (i.e. increase vs. decrease of neck size).

This example also shows how Baldwin's ideas, *Neo-Darwinism*, and Lamarckism share some common points but also have fundamental differences. Neo-Darwinism would mainly argue that the first, and crucial, changes were random mutations that resulted in giraffes having both longer and shorter necks and thus allowed those with longer necks to eat Acacia leaves. That is, that the behavior of the giraffes themselves, per se, was mainly a secondary actor in the story. Baldwin's idea is similar in the sense that mutations are needed to explain the directional evolution leading to a longer neck, but the first key driver was the behavioral choice of the giraffe ancestors to move to, or continue to live in, a dry environment and then to eat certain specific types of plants and ultimately Acacia leaves, among the numerous other plant species existing in the African savanna. Only *subsequently*, within this specific behavioral context and constructed niche, did certain random mutations specifically providing advantages for this mode of life thrive. This view suggests a codependent process between the active behavioral choices of organisms, genetic phenomena such as random mutations, and natural (external) selection.

According to Lamarckism, the first key actors of the story are also the giraffe ancestors and their behavioral choices, as for Baldwin. Lamarck's ideas were also

Fig. 2.1 Skeletons of an okapi (*left*) and a giraffe (*right*), which are both from the family Giraffidae (modified from [74])



similar to those of Baldwin—although, as explained previously, the latter did not recognize this point—in the assumption that acquired traits are inherited, in the sense that the behavioral persistence to eat Acacia leaves is passed down through the generations. That is, it is inherited through teaching, learning, imitation, and so on (social heredity *sensu* Baldwin) and possibly then partially ‘fixed’ in giraffes by way of the Baldwin effect. The main difference is the way in which Lamarck used, his concept of “use-and-disuse” as though a giraffe could, over a lifetime of effort to reach high branches, develop an elongated neck and pass that acquired morphological feature to its descendants. Such an idea is of course essentially wrong, and it is the main factor that has led many authors to even avoid using Lamarck’s name. However, it is clear that Lamarck’s thoughts were much more complex, and in general more accurate, than this caricature. His key idea of inheritance of acquired traits does apply to behavioral and ecological inheritance, for instance, as is now widely recognized (Figs. 1.2 and 1.3) and as will be discussed in more detail in Chap. 5.

Box—History: Baldwin and the debate on preformationism versus epigenesis

As stressed by Kull [215] and Young (2003), Baldwin essentially opposed a strict preformationist position. In a very simplified way, preformationists argued that organisms are preformed, i.e. that they develop from miniature versions of themselves, and therefore that their ontogeny is mainly defined from the beginning by a specific, defined program. Young [413] summarized

a few contrasting tenets of epigenesis versus preformationism. In the former, variations appear in definite directions because they are caused by the interaction of the organic being and its environment, and thus they can be inherited. In the latter, variations are promiscuous, being “congenital” or caused by mixing of male and female germ-plasmas, and thus could not be inherited. Contrary to the suggestion of many authors that attacked him during the first decades of the twentieth century, Baldwin was strongly opposed to a Lamarckian epigenesist position. For Baldwin, the Lamarckian inheritance of acquired characters was too rigid because it would not allow organisms to display behavioral plasticity and accommodate themselves to the external environment and/or conditions in order to alter their behavior in adaptive ways (Young 2003). Baldwin (e.g., [23–26]) argued that plasticity (both behavioral and morphological) is essential for the new behavior to be acquired and performed and for its later imitation and/or learning by other members of the population. This in turn allows social heredity, i.e. the passage of behaviors from one generation to another, which works in concert with external natural selection so that the more useful behaviors/adapted phenotypes are selected across generations.

Baldwin [25: 549–552] stated that “natural selection is too often treated as a positive agency; it is not a positive agency; it is entirely negative... it is simply a statement of what occurs when an organism does not have the qualifications necessary to enable it to survive in given conditions of life; it does not in any way define positively the qualifications which do enable other organisms to survive. He added:” ... assuming the principle of natural selection in any case, and saying that, according to it, if an organism does not have the necessary qualifications it will be killed off, it still remains in that instance to find what the qualifications are which this organism is to have if it is to be kept alive... so we may say that the means of survival is always an additional question to the negative statement of the operation of natural selection.” He explained that the term “organic” in organic selection is related to “the fact that the organism itself cooperates in the formation of the adaptations which are effected, and also from the fact that, in the results, the organism is itself selected; since those organisms which do not secure the adaptations fall by the principle of natural selection” [25]. For him, the word “selection” is “appropriate for just the same two reasons... animals may be kept alive let us say in a given environment by social cooperation only; these transmit this social type of variation to posterity; thus social adaptation sets the direction of physical phylogeny and physical heredity is determined in part by this factor.”

Significantly, the term “social heredity”, as used by Baldwin and in the present work, does not apply only to taxa in which individuals display a highly complex social organization and/or neurobiological skills. “Social heredity” is simply one of the factors that can lead to behavioral persistence—or behavioral inheritance—for Evo-Devoists (Fig. 1.3) through e.g. teaching, learning, or imitation, but this can be

done at a very basic level without necessarily invoking consciousness or any particularly complex type of behavior. As Birkhead and Monaghan [38: 12] stated, in behavioral ecology "animals are viewed as having *choices*", and the use of such terms caused misunderstandings and "provided ammunition for those opposed to behavioral ecology", for whom such terms "implied a conscious decision by an animal - something the behavioral ecologists never intended." Or, as stated by Ydenberg [412: 132], "in behavioral ecology the term *decision* is used whenever one or two (or more) options is/are selected, with no implication that the choice is conscious; the choice need not be cognitive at all, and may not even use neural mechanisms." Basically, any organism can thus make behavioral choices, as I argue in the present book. As will be explained later in the text, in this sense Baldwin's "social heredity" has similarities to factors leading to the so-called "ecological inheritance" of the niche construction theory and thus can be applied to any type of biological organisms from bacteria to modern humans, elephants, dolphins, or octopuses. Another important point is that "plasticity" here refers to different possible alternatives, e.g. as noted previously behavioral choices/shifts will not always "meet the needs" of the organism; they can also go wrong and be subsequently eliminated by natural selection.

As summarized by Kull [215], according to Baldwin's idea, a population might thus first face new conditions (e.g. due to change in their environment either locally or due to migration), and then its organisms *accommodate* to the new conditions by way of physiological adjustment/behavioral changes, possibly due to physiological/behavioral plasticity. Significantly, when a population faces a change in conditions, all of its organisms may respond simultaneously and in a similar way. Second, the new behavior and/or niche built by the organisms can last for generations because of the permanence of the new habitat conditions, the stability of the environmental conditions, the continuation of a newly established ecological link with other organisms or food resources, and/or, very importantly for Baldwin, because of behavioral persistence due to learning/imitation or other factors. Third, natural (external) selection then plays a crucial role because it allows a trial-and-error type of evolution, in which random mutations that lead to behavioral/morphological adaptations within the context of the new behavior/habitat can be selected (while others are not), thus explaining the occurrence of directional evolution/evolutionary trends that last for long geological time periods. Therefore, while abandoning the transmission of acquired characters, Baldwin's organic selection did place individual behavior and adaptation first and random mutations/variations second, as Lamarckians contended, instead of placing survival conditions by fortuitous mutations/variations first and foremost as NeoDarwinists defend.

According to Hoffmeyer and Kull [188: 263–265], a major difference between Neo-Darwinism and Baldwin's organic selection is that in the former "an ability to use sign processes", e.g. in behavioral choices/shifts, may "turn out to be an advantage in the struggle for existence (like many other features, such as an ability to move quickly), but it cannot itself be a factor that is sufficient for *creating* evolutionary adaptations" as proposed by Baldwin. Hoffmeyer and Kull reviewed an illustrative example of a behavioral shift of a population of invertebrates in

which there was no genomic change: “the dreaded locust, which most of the time lives its life as an ordinary, harmless grasshopper”, but which, under certain conditions, changes its behavior. This change leads to “new generations with a markedly changed morphology and behavior, causing these locusts to form enormous flocks flying many kilometers, and devouring every green thing in their path.” For them, such examples stress how behavioral shifts can take place simultaneously in many individuals of a population (as a result of a change in environment or migration to a new environment) in contrast to the difficulty of explaining how random mutations can spread so quickly throughout an entire population. The behavioral shift, and the subsequent phenotypic shifts to which it potentially leads, may be sufficient to decrease the effectiveness of recognition of the original population needed for mating, thus leading to isolation and possibly to subsequent mutations that will fix this separation also at the level of the genome/other type of incompatibility. This idea therefore links behavioral shifts, speciation, and cladogenesis. In fact, as stressed by Larsen [220: 120], the “migratory locust form differs from the solitary form in a variety of ways; not only is behavior modified, but pigmentation and morphology as well; changes in phase do not occur in one generation but require several reinforcing generations in which maternal effects are important, since it appears that maternal juvenile hormone influences juvenile hormone titers of their final instar progeny.”

Many of the previous points were elegantly summarized in Kull’s [215] table, which I use and update here (Table 2.1) to summarize the main differences between ONCE and the views of Baldwin, Neo-Darwinists, Lamarckians, and mutationists such as Morgan. As shown in Table 2.1, a crucial point of Baldwin’s organic selection is that the first event is a plastic/phenotypic change, which is followed by stochastic genetic changes. This view contrasts with (1) Lamarckism (i.e. first event is also a plastic/phenotypic change but is followed by the inheritance of acquired characters), (2) mutationism (i.e. nonrandom mutations with genetic change

Table 2.1 Different views on adaptive evolution

	Nonrandom mutations/epigenetic phenotypical events	Random mutations	Random mutations but also epigenetic phenotypical events selected/influenced by external selection, both being strongly constrained by internal factors
Epigenetic changes (e.g. learning) first	Lamarckian (e.g. exercising/use-disuse)	Baldwinian/semiotic (organic selection)	Organic nonoptimal constrained evolution (ONCE [the view defended here])
Genetic changes (e.g. mutations) first	T. H. Morganian (mutationism)	Neo-Darwinian (natural selection)	–

occurring first), (3) Neo-Darwinism (i.e. the first event is a random genetic change followed by a new phenotype and natural selection), and (4) nonadaptive, neutral, and/or other mechanisms of evolution such as genetic drift. As will be explained later in the text, it also contrasts with ONCE because Baldwin's organic selection is just one of the major points of ONCE. For instance, ONCE also incorporates data from recent Evo-Devo studies stressing the influence of the external environment on multiple aspects of early development through epigenetic factors that were not known in Baldwin's time as well as studies on the links between ecology, morphology, and phylogeny showing that etho-ecological and eco-morphological mismatches are far more frequent than Baldwin's idea would predict (Fig. 1.2). I will also explain, in further chapters, that Baldwin's criticism of Lamarck's inheritance of acquired traits is in fact invalid if one considers that these traits do include behavioral/ecological features. Of course, one can argue that behavioral persistence, in the way Baldwin defined it, might not be the same as the "inheritance of behavioral traits" because those traits are not innate: within the general context of organic selection they must be gained over and over again, during each generation, e.g. through teaching, learning, or imitation. However, within this general context, even Baldwin defined a subset of cases that can in fact lead to innate behavior, which became known as the "Baldwin effect" (see Chap. 1 and later text).

Due to the emergence of genetics, Baldwin's ideas—as well as Lamarckism—became largely ignored, but this downturn was transient. For instance, Simpson [338] renamed, and disseminated, this "Baldwin effect" component of Baldwin's main idea of organic selection [61]. In contrast, Waddington, who published several works in the 1940s and 1950s, strongly criticized the gene-centered Neo-Darwinist view of evolution. He stated: "it is the animal's behavior which to a considerable extent determines the nature of the environment to which it will submit itself and the character of the selective forces with which it will consent to wrestle; this 'feedback' or circularity in a relation between an animal and its environment is rather generally neglected in present-day evolutionary theorizing" [384: 170]. A very interesting point made by Corning [61]—which, in my opinion, is not emphasized enough in the literature—is that a major reassessment of Baldwin's organic selection did occur in the late 1950s. Specifically, this occurred when the American Psychological Association and the Society for the Study of Evolution jointly organized various conferences that resulted in the book *Behavior and Evolution*, edited by Roe and Simpson [311]. The book included the following suggestions: (1) adaptive radiations might be fundamentally behavioral in nature (Simpson), (2) behavior might often serve as an isolating mechanism in the formation of new species (Spieth), and (3) during evolutionary transitions, new behaviors may appear first and genetic changes may follow (Mayr). As noted by Corning, Mayr later wrote, in his influential chapter "The Emergence of Evolutionary Novelties", that behavioral changes are the "pacemaker" of evolution [247], an idea that he also discussed in his 1976 book *Evolution and the Diversity of Life*.

In the late 1950s and 1960s, there was a dramatic increase in the number of publications highlighting the role of learning and behavior in evolution, including Thorpe's [353] *Learning and Instinct in Animals*, Waddington's [380, 383] *The*

Strategy of the Genes and The Nature of Life, Hardy's [174] *The Living Stream*, Whyte's [398] *Internal Factors in Evolution*, Hinde's [184] *Animal Behavior: A Synthesis of Ethology and Comparative Psychology*, and Koestler's [210] *The Ghost in the Machine* (see [61]). Since then, research on learning and innovation in living organisms—from “smart bacteria” to wise apes and playful dolphins—has grown exponentially. This includes empirical data suggesting that *Escherichia coli* bacteria, *Drosophila* flies, ants, bees, flatworms, laboratory mice, pigeons, guppies, cuttlefish, octopuses, dolphins, gorillas, and chimpanzees—among many other taxa—can learn and display novel responses to new conditions by way of, e.g., “classical” and “operant” conditioning. According to Duckworth [117: 414], encompassed within this growing recognition that behavior is crucial in evolution, are two contrasting ideas about how behavioral changes affect evolutionary rates.

On the one hand, behavior can be seen as a constraint in the sense that it could in theory slow the rate of evolutionary change because behavioral plasticity can shield organisms from strong directional selection by allowing them to either exploit new resources or move to a less stressful environment. For instance, Morris [265: 2–3] noted that “plasticity, by slowing the rate of population decline, can overcome this hurdle, providing time for beneficial mutations to arise; this has been confirmed empirically: the likelihood of extinction for great tits increased 500-fold in the absence of plastic responses to climate change... this was largely true in thirteen other bird species, although faster generation times offset the need for plasticity.” Also, “climate change has resulted in population declines of numerous nonplastic species... for instance, rising temperatures shifted flowering time but not West Greenland caribou calving time, producing a trophic mismatch that declined calf production fourfold.” Morris further noted that “in order to successfully invade a new environment, individuals must first disperse to that environment... species with high dispersal rates should also be highly plastic, as dispersal involves encountering spatial heterogeneity... indeed, dispersal of nonplastic organisms can reduce the likelihood of successful colonization by introducing maladaptive alleles to colonizing populations.” He reviews a study that tested the relationship between dispersal and plasticity in 258 species of marine invertebrates and showed that, on average, dispersing species were more plastic than nondispersing ones, i.e., presumably without such plasticity dispersers would fail to colonize the locations to which they disperse. However, he noted, “it is clear that many species have high dispersal rates and low levels of plasticity, so plasticity is again sufficient but not necessary for colonization; rapid generation times, for instance, may allow colonizing populations to rapidly evolve to meet the demands of the new environment.” On the other hand, it can be said that even in such cases behavior would actually drive evolutionary change. A behavioral shift that results in a new way of interacting with the existing environment, or a switch to a new environment, exposes organisms to novel selection pressures resulting in evolution of life history, physiology, and morphology as emphasized by Baldwin and in ONCE (Fig. 1.2). In fact, as stressed by Duckworth [117: 414], the major point is that, be that as it may, these examples “emphasize that the critical novel step in the evolutionary sequence is a behavioral shift.”

Interestingly, in recent years Baldwin's organic selection has become particularly fashionable in the fields of systems biology and complex systems because it is closely related to a term currently very much in vogue: "teleonomy". Within these fields, this term, coined by Pittendrigh in his chapter "Behavior and Evolution" of Roe and Simpson's [311] book, refers to the "internal teleology", i.e. "the fact that the purposefulness found in nature is a product of evolution and not of a grand design" [61: 248]. As Corning explains, there are historical links between this term and not only 'Intelligent Selection' *sensu* Morgan and 'Organic Selection' *sensu* Baldwin but also 'Holistic Selection' *sensu* Smuts and 'Internal Selection' *sensu* Whyte and Koestler in the 1960s and, more recently, with 'Psychological Selection' *sensu* Munding, 'Rational Pre-Selection' and 'Purposive Selection' *sensu* Boehm, 'Baldwinian Selection' *sensu* Deacon, 'Neo-Lamarckian Evolution' *sensu* Jablonka and Lamb, 'Behavioral Selection' *sensu* various authors, 'Selection by Consequences' *sensu* Skinner, and 'Social Selection' *sensu* biological anthropologists. The crucial common link between these concepts is that living beings do the selecting: they have emergent properties that allow problem-solving, innovation, and decision-making so they can—and do—choose among various possible behavioral options.

For Corning, the proximate causes of novel forms of symbiosis—from lichens to such evolutionary turning points as the origin of eukaryotic cells as well as the origin of land plants and animals, the evolution of birds, and even the rise of social organization—were most likely the result of various behavioral 'initiatives.' One emblematic example of organic or "teleonomic" selection he provided is the intense competition among the towering evergreen trees (western hemlock, Sitka spruce, Douglas fir, and western cedar) in a forest canopy of the rainforest of the Olympic National Park in Washington State. Hemlocks produce by far the most seeds and are said to be the best adapted to grow in the park as an outcome of both competition and the weather, especially the low-sunlight conditions. However, the Sitka spruce dominates because the abundant Roosevelt elks in the park feed intensively on young hemlock trees but do not eat Sitka spruces. That is, the food preference of the elk is the *proximate cause* of differential survival between the hemlock and spruce trees. Similarly, the many kinds of artificial selection practiced by humans, including sexual selection, can be seen as behavioral selections by third parties that shape the course of natural selection in other species as noted in Chap. 1. I will discuss sexual selection in some detail in Chap. 4.

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