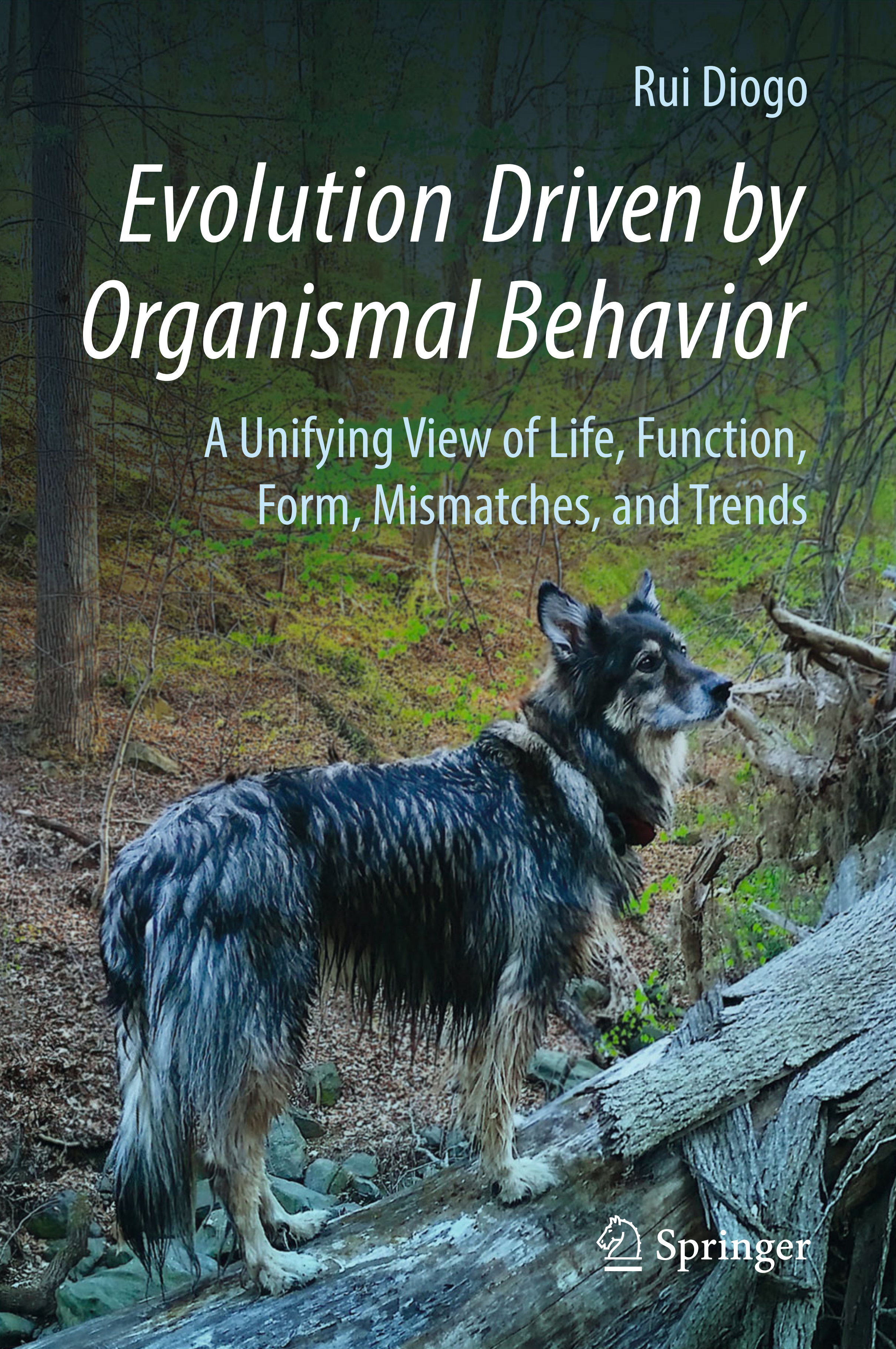

Rui Diogo

Evolution Driven by Organismal Behavior

A Unifying View of Life, Function, Form, Mismatches, and Trends

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Never forget that only dead fish swim with the stream.

Thomas Malcolm Muggeridge (1903–1990)

By displaying, every day, a strikingly diverse range of complex—mostly surprising and often flagrantly non-optimal—behavioral choices, a marvelously fascinating friend has led me to shift my previous, mainly internalist, view of life to recognize the crucial importance of behavioral shifts in evolution. I therefore dedicate the book to Tots, the exceptional member of the species *Canis lupus* shown on the cover.

Preface

There is an important point I want to make clear that is key within my philosophy. I am an avid—if not slightly obsessed—reader. I like to read; I wish I could know everything about everything, but unfortunately there is too much to read and so little time. As in any modern book, most of the ideas I focus on in this monograph were therefore not conceived by me for the first time. Accordingly, I profoundly believe that we should not only clearly mention, but actually pay tribute to, those authors who have influenced our ideas either because we agree with them or because by disagreeing with them we re-think and eventually change our original ideas. My viewpoint is that we should be humble and not pretend that we invented the wheel. Therefore, we should refer to the original works and—particularly for those that do not agree with our opinions—try to change their statements as little as possible so that readers can make a fair judgment about which ideas they agree with. It has occurred too often to me already, and probably to many readers of this book, to see ideas wrongly presented in works by others, either when they agreed or disagreed with them, so I want to make sure I avoid that. Accordingly, when I cite a certain work, I will often use parts of the text written by the original authors. I am aware that in such textbooks one often tends to be more general and to not cite too often directly other works. However, this is against my philosophy, and I think readers will understand, and hopefully appreciate, it as honesty. Having said that, I am fully aware that I could have read more books and papers and added more references to the ones I included in this book because my tendency would naturally be to do so. But because I intend to have the Organic Nonoptimal Constrained Evolution (ONCE) idea proposed in this book read and hopefully discussed by a wide audience, I made the difficult decision to leave out some references. I also tried to reduce the jargon. However, I am conscious that I surely was not completely successful in doing so and that at least some parts of the book will still seem very technical, some sentences too long, and some historical comments unnecessary.

My main aim for this book is to try to provide an integrative, unifying vision about evolution and to help bridge the gap between various theories and lines of thinking that were presented for a long time as if they were conflicting with each other or were even irreconcilable. Thence my emphasis on bringing older ideas to modern discussions. Regarding the recent literature, I combine, for instance, some of the major points defended by the Extended Evolutionary Synthesis with some aspects that are, in my view, not emphasized enough in the books and papers about that synthesis. For example, the fact that the central active players in evolution are in general the organisms themselves and in particular their behavioral shifts and persistence was argued several decades ago by authors such as Baldwin and Piaget but neglected by most current researchers. Or the fact that eco-morphological mismatches are much more frequent than normally assumed. These mismatches are, for instance, related to the highly constrained character of organic evolution including the strong developmental constraints recognized in the Extended Evolutionary Synthesis. However, they are also associated with factors less emphasized in this synthesis such as the importance of behavioral persistence, which can dramatically limit the occurrence of new behavioral shifts and thus the responses to environmental changes often leading to evolutionary dead-ends and eventually to extinctions. In fact, one of the founding fathers of ethology, Niko Tinbergen (1953: 3), has emphasized how even behavior, which is the key driver of evolution according to ONCE and is often seen as highly flexible, is in fact also highly constrained: “Behavior shows wonderful adaptations, but also astonishing limitations.”

Furthermore, ONCE also stresses another crucial point: the N of “Nonoptimal” which could also be the N of “Nonstruggling” because it refers to the fact that evolution is not necessarily a process where organisms are engaged in an incessant, suffocating struggle. Under ONCE, evolution is not simply a desperate, savage competition in which only organisms that have an optimal or almost optimal “match” with the environment that they inhabit can become “winners” and, as the famous Abba song says, “take it all.” That is, within ONCE life is not unavoidably seen as a struggle 100% of the time for 100% of the organisms in 100% of their developmental stages. Life is more diverse and fascinating than that. As recently noted by Gailer and colleagues (2016), more and more studies are emphasizing the large plasticity between the so-called “optimal”morphology of a structure and the potential function of that structure, underscoring the need to appreciate apparently “maladaptive” structures in biological evolution as nevertheless effective functioning units. That is, such structures and the function they perform are “good” enough to allow the organisms displaying them to survive and reproduce, in the nonstruggling view of life defended in ONCE. As long as there is enough time and energy in this planet, there will be behavioral diversity and variation for mistakes, for trial and error, for neutral behaviors, and even for maladaptive behaviors on some occasions, i.e., for both etho-ecological and eco-morphological mismatches and for non-optimality.

Evolution in reality is generally made of mistakes, mismatches, and trial-and-error situations, which lead to new behaviors and that differentiate life and its complexity from the more deterministic existence of inanimate objects. In my opinion, the notion of a “struggle for life” has been blindly accepted for too long. It was mainly fueled by studies that were highly biased, *a priori*, to support this view, and the adaptationist program, e.g., the "just-so stories" mentioned by Stephen Jay Gould. Unfortunately, this view of evolution has led to many wrong ideas in evolutionary biology that unfortunately lead to catastrophic events in human history and that have obstructed, and continue to obstruct, a more comprehensive view of the diversity and complexity of life. An example is extreme adaptationism, which has fortunately been challenged in modern fields such as Evo-Devo but continues to prevail in areas such as evolutionary psychology and behavioral ecology. Currently it is even rising to new levels in recent fields such as evolutionary medicine, a field I particularly admire for its good intentions, but one that has also taken some problematic paths in my opinion.

As an aside, it was mainly a coincidence that the words I choose to express my view of evolution combined to form an acronym that corresponds to the title of one of my favorite movies. In the beautiful and Oscar-winning film *Once* (2007), by director John Carney, the characters played by actors Glen Hansard and Markéta Irglová spend much of their time in both a non-optimal and non-struggling existence, mainly singing and playing deep and powerful songs and being highly constrained by their past. Ultimately, they make a behavioral choice that is surely not the one that most spectators wanted to see them making, what does not mean it was the *wrong* decision, because the diversity, complexity, randomness, and shifts of life can always surprise us. For instance, years after seeing the movie, my girlfriend and now wife, the astonishingly beautiful and intellectually complex Alejandra Hurtado de Mendoza Casaus, with whom I originally saw the film, told me that she chose the main song of the movie for our wedding ceremony. And, years later, here it is, *once* again, now as the subject of the most personal book I have written so far. Because the dedication and cover of the book is dedicated to Tots for obvious reasons related to the main subject of the book, I therefore take the occasion here to thank Alejandra, the "once" of my life.

Washington, DC, USA Rui Diogo

Acknowledgements

Apart from the hundreds of colleagues, students, and friends with whom I had the privilege to collaborate with and/or discuss the numerous topics covered in this book, from broader philosophical questions to specific details about the number of vertebrae in a particular marsupial species, I want to particularly thank the following individuals: Julia Molnar, for doing the very first detailed review of the whole book; Janine M. Ziermann because without her I would probably never have the time to write this book because she literally took care of all things when she was my postdoc and she continues to be a close colleague and friend and extremely helpful even after that; and Alessandro Minelli, Eric Parmentier, Virginia Abdala, Marcelo Sanchez, and Diego Rasskin-Gutman for reading previous drafts of the book and making pertinent and honest comments about it.

I further want to acknowledge, and also dedicate this book to, the advisors of my two doctoral degrees—Michel Chardon and Bernard Wood—who are completely different in many aspects but similar in one crucial one: They are open-minded and always willing to pursue the big questions and, above all, they promote the same type of behavior in their students, which is a true case of behavioral persistence. Moreover, Michel Chardon did a detailed review of a previous draft of the book and, as always, greatly contributed to make the book better. Last, I want to thank my parents, Valter Martins Diogo and Maria de Fatima Boliqueime, because although this might sound cliché, it is a self-evident and powerful, reality: Without them, I would not be here, and this book would not have been written.

Contents

Boxes

Chapter 1
Introduction to Organic Nonoptimal Constrained Evolution (ONCE) and Notes on Terminology

> *Never forget that only dead fish swim with the stream.*
> Thomas Malcolm Muggeridge (1903–1990)

A recent, well-written review by Morris on plasticity-mediated persistence [265: 8] defended the idea that developmental plasticity can allow epigenetic phenomena to "respond in remarkable ways to environmental input." One of the examples given was "the so-called 'two-legged goat effect', named by West-Eberhard after a goat that was forced to walk on two legs due to a congenital limb defect. I italicized the word "forced" to stress the fact that, although Morris is subscribing to a recent tendency within evolutionary developmental biology (Evo-Devo) toward a more organismal and less Neo-Darwinist and gene-centered view of evolution, he still used this word to describe the goat's behavior. Was the goat really forced to walk bipedally? Forced by whom? By a shepherd? By the "external environment"?

What actually happened is that the goat responded to a phenomenon that occurred in its body, i.e. the anomaly of its limbs, with one among many behavioral choices that it could take within the range of its developmental, behavioral, physiological, and/or anatomical plasticity. Of course, that behavioral choice also depended on the external environment in the sense that if, for example, the goat were in an aquatic environment, bipedal walking would not be a possible option. That is, in this case the external environment constrained the number of possible behavioral choices. However, it can hardly be said that the key active player in this example is an external environmental input: instead, it is the goat itself, in particular its behavioral choice. As can be easily seen with a simple Google Images search for "two-legged goat" or "two-legged dog", and as is shown in Fig. 1.1, there is a striking diversity of behavioral choices, postures, and specific types of locomotion that can be assumed by goats and dogs when confronted with a defect/injury of the forelimbs. The box below discusses and compares the chief features that define behaviors, behavioral responses *sensu* most authors, and behavioral choices *sensu* the present work, which are crucial to understand the ideas and empirical data presented/discussed in the present book.

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Fig. 1.1 Selected sample within the strikingly diverse examples of behavioral choices made, and postures and specific types of locomotion assumed, by dogs when confronted with a defect/injury of the forelimbs (modified from public domain internet pages after a simple Google search for "two-legged dog" Google image search, namely from, https://www.gofundme.com/SHHRoo, https://i.vimeocdn.com/video/452201007_1280x720.jpg, https://www.youtube.com/watch?v=w1dVlc_X9yM and http://4.bp.blogspot.com/_LBRxNEgFXaM/SU3djwGRlBI/AAAAAAAAAQ8/y9Ch6Rz-mHU/s320/Chook+The+Two-Legged+Dog.jpg)

Box—Definitions: Behavior, Behavioral Responses, and Behavioral Choices
Unless stated otherwise, terms presented in this book will usually be related to their most commonly accepted, widespread definitions to avoid unnecessary confusion and excessive use of jargon. Accordingly, when I use the term "behavior" I refer to a very simple and broad definition often seen in the literature: behavior is a conscious or unconscious response of an organism to stimuli or inputs, i.e. it applies to all living organisms without exception.

Accordingly, the term "behavioral choice" refers to cases in which at least more than one potential choice is possible: the organism chooses, and then has the drive to undertake, one of the possible choices. This is considered a behavioral choice no matter—again—if the choice and/or drive to undertake it are conscious or not. It is likely that behavioral choices in organisms such as bacteria are often unconscious, whereas in organisms such as humans, chimpanzees and elephants they are usually conscious.

As will be explained and discussed in detail throughout this book, under the definition adopted here, there are three key items for a certain behavior to be considered a behavioral choice. The first is that more than one behavior/outcome is possible, i.e. it is not merely like a rock that falls down from a cliff by "moving" due to the force of gravity, in which the outcome is always the same: the rock will always move downward toward the center of the earth. If we now think about a bird in the air, it experiences the effect of the same force of gravity, but there are many possible outcomes, which are thus behavioral choices. The bird can let itself passively fall downward toward the center of the earth. However, it can instead fly to counterbalance the force of gravity by staying at approximately the same altitude, or it may decide to fly even higher to a greater altitude, and so on. This leads us to the second key item: drive. To undertake a behavioral choice, the bird must have the drive to do so, i.e. the bird is an active agent precisely because there is more than one option and possible outcome, and the bird thus needs to choose and undertake just one of them. Therefore, contrary to inanimate objects, living beings are not automata: rather they are active players. This in turn leads us to the third key item: behavioral choices are always undertaken by the organism as a whole: they are organismal behaviors and cannot refer to the behavior of just parts of the whole, such as for example atoms, cells or tissues.

Therefore, an important point is that behavioral choices, as defined here, are just a subset of the "behavioral responses" *sensu* Sultan [350: 51], which do not need to meet all of the three defining key factors listed previously. In fact, they may even lack all of them at the same time. As explained by Sultan, "a quantitative distinction is sometimes drawn between 'intentional' behavioral responses, which are mediated by a central nervous system, and the kind of growth and movement changes expressed by plants and other non-animal taxa in response to specific environments … this distinction has been challenged by several plant biologists, who have argued that plant evo-devo responses to environmental information constitute behavior and, indeed, intelligence." She then states that "in a broader framework, all types of environmentally mediated phenotypic expression can be viewed as cue and response systems."

However, in my opinion, by following this latter statement, Sultan is missing—as are most Evo-Devoists and biologists in general—the crucial distinction between two types of phenomena with completely different biological and evolutionary meanings. One concerns behavioral responses that are merely physiological and thus sometimes nearly "automatic" responses similar to, e.g. the “response” of my computer when I click the “delete key” while writing this book. The computer does respond to this stimuli (i.e. pressing this specific key) by displaying a “behavior” according to the widely used definition given just above. However, two key defining features of behavioral choices are lacking. First, the computer always responds in the same way to this stimulus: there is only one single possible outcome, which is thus totally predictable. The computer will not surprise us with a different outcome because it lacks the second key item: it has no drive to select a different outcome because it has no drive at all. In a similar way, when I am outside and the temperature reaches 40 °C, my skin will respond always in the same predictable way: I will sweat. That is a behavioral response *sensu* Sultan, but is merely a physiological response that has nothing to do with an organismal behavioral choice because it lacks all three key defining items: there is only one outcome, and it is not a choice, nor does it involve a drive of the organism as a whole because I do not choose—and surely do not have the drive—to sweat. Actually my drive is to avoid sweating, and that is why I normally do not stay outside when the temperature is ≥ 40 °C.

Therefore, the main dichotomy should not be between having “a central nervous system” as animals do versus not having one as in plants. Instead, it is having the capacity to make behavioral choices and the drive to undertake them, and for this organisms do not need to have a central nervous system because all living beings, including plants and bacteria, clearly display behavioral choices, as I will explain in detail throughout this book. A crucial concept—from the field of systems biology—is thus emergence, in which the organism can display a behavioral choice as a single unit, no matter whether or not it has a central nervous system or any type of consciousness. The dichotomy between organismal behavioral choices versus other types of behaviors can thus match the one Sultan referred to, about having or not having “intentionality”. However, this only applies if the term refers to the drive that the whole organisms must undertake to carry out certain behavioral choices, and not necessarily to consciousness nor to any teleological concept related to “evolutionary purpose or goal” (see later text).

Numerous examples of the “behavioral responses” given in Sultan’s [350] excellent book and many other publications cannot thus be considered at all to be behavioral choices sensu the present book. Nor are those examples related to any type of teleological “purpose”, “intentionality” or “goal”, as it is often suggested in the literature. For instance, if a certain lake starts having too many predators, and various salamanders living in that lake start metamorphosing as a “response” to this increase, this is not due to a behavioral choice of the salamanders nor to a drive of the salamanders to do so, and surely not due to any “final goal” of the salamanders. It is instead an epigenetic response that leads to a single possible outcome. As seen in many laboratory experiments, by changing and combining factors—such as the total volume and composition of the water, the number of predators and salamanders, and so on—one can easily predict whether the members of a population of a known species of salamanders will tend to metamorphose or not. The salamanders cannot do anything about it, just as I cannot stop sweating when I am in a sauna, because this is merely a physiological response beyond my control, which I can only avoid by undertaking, for instance, the behavioral choice of leaving the sauna. Accordingly, many other examples of behavioral response provided by Sultan do conform to my definition of behavioral choices, e.g. some of the phenomena she designates as "habitat choice behaviors" in which organisms seek, or avoid, particular climatic conditions. Examples include the behavioral choice of anteaters to switch the foraging activities to nighttime in extremely hot weather, of many reptiles to bask in the sun to increase body temperature during cold weather, and of penguins, mice, bats, marmots, and pigs to aggregate in order to decrease their collective surface-to-volume ratio in cold conditions.

In summary, as Lindholm [232] put it, behavioral choices cannot be reduced to genetics—or, I would add, to mere automatic, physiological, or localized/regional epigenetic reactions to external stimuli or other factors—because this requires a subject to take choices and have the drive to undertake them, which is the whole organism. This capacity and drive to undertake behavioral choices obviously depends on intrinsic genetic or genomic, and epigenetic (e.g. hormonal or physiological), features linked with external factors. However, as noted above the capacity is ultimately mainly related to a phenomenon that is now becoming more and more prominent in biology, particularly due to the rise of systems biology: emergence. That is, a strikingly high number of complex factors, both intrinsic and extrinsic, are combined in a way that an overall outcome that is more than just the sum of the part emerges: the capacity to take a behavioral choice and having the drive to undertake it. Contrary to mechanistic and atomistic views that have prevailed for a long time in the history of biology (see later text), this capacity does not apply to any of the organismal subunits or regional parts/organs. Individual atoms or electrons do not walk bipedally as we do, nor can they choose to do so. This capacity only applies to the whole organism, thence the term "organismal behavior".

The use of the term "forced" in the example of the two-legged goat is even more striking considering that in the very same article, Morris [265] supported Baldwin's idea of organic selection, in which behavioral choices, followed by behavioral persistence across generations by way of social heredity, play a crucial role in evolution. This apparent paradox therefore has nothing to do with a bias of Morris himself. The paradox is instead mainly explained by a historical bias that is ultimately related to a major event in the history of Western science: the so-called "scientific revolution" that occurred in the sixteenth and seventeenth centuries as explained in *Beyond Mechanism—Putting Life Back into Biology* [182].

Box—Definitions: Behavior, Behavioral Responses, and Behavioral Choices
Behavioral persistence refers to cases where the generations that follow those in which a certain behavior was originally acquired continue to respond to the same stimuli or input in a similar way, mainly due to social heredity (e.g. imitation, learning, and/or teaching), as explained below. Regarding epigenetics, I use the term in the *sensu lato* and follow Sultan's [350: 9] statement that "epigenetics effects at the molecular level can be defined as biomechanical mechanisms that shape patterns of gene expression in the absence of any change in nucleotide sequence". Therefore, DNA methylation or histone modification are only specific examples among many other epigenetic phenomena that can be listed, including, e.g. those associated with endocrine activity, as beautifully and extensively reported by Matsuda [245]. An updated list of such other epigenetic phenomena as well as recent experimental and medical studies on the subject—plus a discussion of their evolutionary significance including their links with some (but not all [see Chap. 5]) of Lamarck's ideas—is given in Sultan's [350] book *Organisms & Environment*.

Box—History: The Scientific Revolution and the Historical Context of Darwin's Ideas
The scientific revolution "involved many major changes, including Copernicus's putting the Sun at the center of the universe, Kepler's work on the planets, Galileo's and Descartes' articulation of mechanics, and finally Newton's great synthesis" [320: 409]. As noted by Ruse, contrary to Greeks such as Plato and Aristotle, who "subscribed to an organic view of the world", "after the Scientific Revolution people subscribed to a mechanic view of the world; Robert Boyle saw things clearly—from now on we work in terms of machines, of artifacts: organicists like Aristotle who see living forces directing nature are just plain wrong." In particular, "the concepts of 'function', 'doing', 'purpose' and 'agency' in biology, totally absent in physics where only 'happenings' occur" have become mainly muted in standard biology by a concept expressed by Jacques Monod [207: 4]. This concept explains why many scientists could not resist Darwin's theory and analogies in the nineteenth and twentieth centuries: "when phenotypic variations of a species are interpreted as a state and the selective pressure as a force, exerted by external conditions, a seductive analogy to mechanical operations is obtained" [130: 94–95].

It is surely not a coincidence that Darwin [67] explicitly referred to gravity, and thus to Newton's mechanicism, in the last sentence of his most influential book: "there is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.” As Hoffmeyer [187: 148–152] put it, “Darwin created a perfectly externalist theory, a theory that seeks to explain the internal properties of organisms, their adaptations, exclusively in terms of properties of their external environments, natural selection pressures.” Darwin was a passionate naturalist who observed nature in incredible detail; but because of the historical constraints, particularly the scientific context of his epoch, he tried above all to connect evolution with external forces. However, as noted by Hoffmeyer, although Darwin “managed to construct an externalist explanation for evolution, he was not a fundamentalist in his externalism as were his followers (the Neo-Darwinists) in the twentieth century, who thought they could get rid of organismic agency by enthroning the gene and seeing organisms as passive derivatives of genotypes.” In fact, Darwin did made a crucial distinction between “external” natural selection and selection related to organismal behavioral choices, which broadly corresponds to Baldwin’s organic selection (see Chap. 4), but this was a key point that Neo-Darwinists mainly ignored. Such a Neo-Darwinist view of evolution continues to be followed by many—probably most—biologists as exemplified by Richard Dawkins’s famous quote that organisms are “no more and no less than survival machines” [319: 414]. Even authors such as Edward Wilson—who described insect societies as “emergent” forms of social order that arise through the collective “decision making” of individual insects—at times described the insect colony as a “growth-maximizing machine” composed of “cellular automata” whose operations can be described by the language of physical and computer science [181: 236].

Box—Definitions: Adaptation, Adaptationism, Externalism, Internalism, and Internal Selection

Regarding the definitions of these terms, I will mainly follow the more fluid, engaging style of authors such as Olson [278], focusing more on the ideas and, in particular, on how authors with different views can defend them using similar definitions and data. I will thus begin by using Olson’s [278: 278] very simple definitions: adaptation as “the process by which form comes to reflect function as the result of the action of natural selection”; adaptationism as “thinking of adaptation as the cause of the form-function fit”; internalism as “the view that the dynamics of the developmental system so channel developmental potential that they are the primary directors of the evolutionary process”; and externalism as “the view that developmental potential is so vast that the outstanding directors of evolution are factors external to the organism”. Then, throughout the book, I will show how some of these definitions, or the main ideas on which they are based, are sometimes too simple or even incorrect.

For instance, one of the key ideas defended by Olson, i.e. that cases of developmental internal selection provide support for an adaptationist view of evolution, does not fit in the context of the definitions he provided. The terms "adaptation" and "adaptationism" continue to be mainly associated with the Neo-Darwinian view of evolution, which focused in great part on the fit between adult form and function. As recognized by Olson [278: 283], "one of the most notorious aspects of the modern synthesis has been its elision of development, treating it as a trivial, more or less deterministic black box between the genome and the phenotype." Olson also recognized that within this context, adaptationism was mainly a synonym of externalism with natural selection, in particular the external environment, playing a central role in morphological macroevolution, although Neo-Darwinists also stressed the importance of other factors in evolution, e.g. genetic drift and gene flow. However, as stated in Futuyma's book *Evolution* [136], natural selection has historically been seen as the only mechanism known to cause the evolution of adaptations, i.e. of the processes in which the members of a population become "better" suited to some features of their environment through changes in characteristics that affect their survival or reproduction in that environment.

Ecomorphologists have been, and in a way many continue to be (e.g. [230]), inspired by such views because they are interested in the links between morphological adaptations seen in adults and the ecology/external environment they occupy (a succinct account of the history of adaptationism is given in the first chapter of Wagner's 2014 book *Homology, Genes, and Evolutionary Innovation*). For example, ecomorphologists have stated that a numerical increase in cervical vertebrae is an adaptation to herbivory in theropod dinosaurs [408]. Such ideas may prove to be correct. However, it is too much of a stretch to argue, as Olson [278] did, that Evo-Devo evidence that internal factors play a crucial role in morphological evolution is leading to a renaissance in adaptationism because in many cases unoccupied adult morphospaces can actually be produced early in ontogeny but are then eliminated by internal selection. He correctly cites, as an example of internal selection, the occurrence of eight cervical vertebrae in fetuses/babies/children that is often associated with deleterious conditions that leads to death at an early age [138]. However, this example of internal selection supports the original point made by Galis, which is precisely the opposite of the point that Olson is trying to make. This example emphasizes that internal selection is a subset of internal factors that limit the adult morphospace and that are essentially independent of the external environment, therefore going against an adaptationist/externalist view of evolution. Humans at early developmental stages do not die because of the physical presence of an eighth cervical vertebra that is negatively selected for by the external environment. Instead, having an eighth vertebra is just a byproduct of the collapse of the whole internal developmental homeostasis at a very sensitive ontogenetic period, the so-called "phylotypic stage" ([138]; see Chap. 7). One should thus not confuse the works and ideas of Galis, which inspired the new Evo-Devo subfield of Evolutionary Developmental Pathology and Anthropology [106] with the extreme panselectionist form of adaptationism that is followed by many researchers within the rising field of Evolutionary Medicine [363], to which I surely do not subscribe.

In fact, as pointed out by Schwenk and Wagner [330: 57], it is external (natural) selection that “changes with the external environment, whereas internal selection remains essentially constant because it travels with the organism” and is “imposed by intrinsic, organismal, functional integration, even as the external environment changes.” Or, as put by Wagner and Schwenk [387: 157], internal selection is “independent of external, environmental selection pressures (because the limitations are imposed by intrinsic attributes of the organism); as such, it is the internal coherence and functionality of the system, as a whole, that imposes its own ‘internal selection’ on individual characters, determining which character variants are viable.” Over millions of years, almost all adult mammals in many different external environments and geographical locations had only seven cervical vertebrae because of such internal developmental factors (i.e. constraints [see later text]).

Of course, Darwin’s “external” natural selection exerted over a taxon involves not only purely abiotic factors (e.g. a meteorite affecting our planet, or, an “ice age”) but also biotic factors, which are in turn often related to behavioral choices made by organisms of other taxa. For instance, a major aspect of the “external” natural selection—which corresponds to natural selection *sensu* Baldwin and *sensu* the notion of Organic Nonoptimal Constrained Evolution (ONCE) presented in this book (see Fig. 1.2)—exerted on salmon in rivers in Alaska is related to the behavioral choices of bears to catch and eat them. However, the point of using different terms, as Baldwin did and as done in this book, is precisely to stress the fact that Darwin’s natural (external) selection is the sum of a huge network of abiotic and biotic environmental factors and that those biotic factors are often related to the organic selection, and thus the behavioral choices, of other organisms, therefore emphasizing the crucial role of organismal behavior in evolution. Organisms not only make their own behavioral choices and thus help to construct their own niches, but they also interfere with the selective pressures that will be felt by other organisms and therefore influence the niches that those other organisms help to build. It is a hugely complex and dynamic network that is far from a mechanistic view of evolution and from the idea that evolution is mainly related to “active external forces applied to passive organisms”. Therefore, in this case, if the subjects of our discussion are the salmon, the use of the term “organic selection” by Baldwin and in ONCE is related to the behavioral choices of the salmon themselves, e.g. to go back to the place where they were born, or to the preferences of the females for certain specific features of the males. Then, within the context of the niche/way of life chosen by salmon, natural (external) selection *sensu* Baldwin and ONCE refers to factors that are external to salmon. These include biotic factors such as predation by bears and abiotic factors such as the physical water currents that salmon must face when going back up the river to the place where they were born.

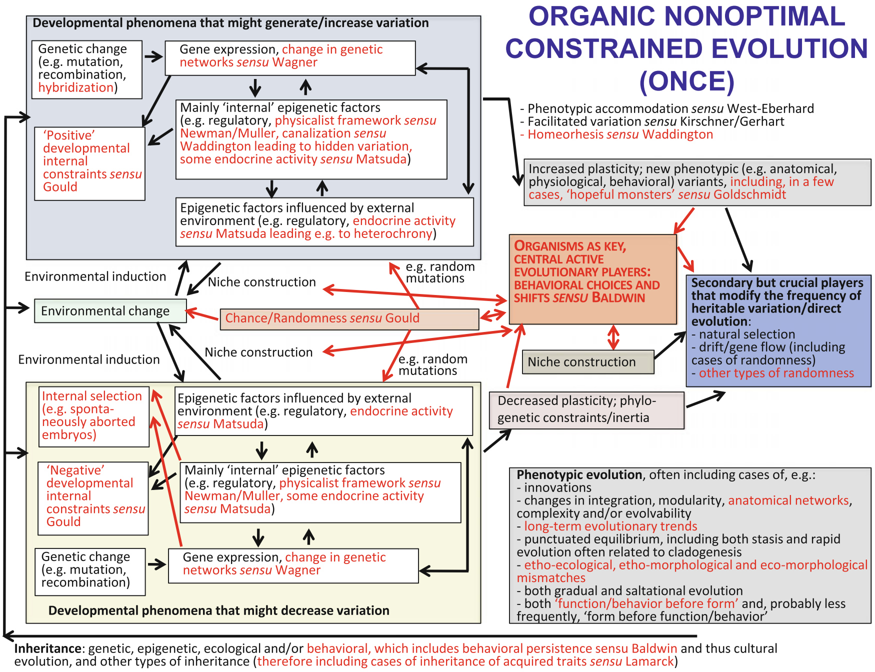

Fig. 1.2 The structure of the idea of Organic Nonoptimal Constrained Evolution (ONCE) presented in this book. Terms and arrows shown in red are those emphasized by ONCE but not in the Extended Evolutionary Synthesis scheme shown in Fig. 1.3. Following the style of that Extended Evolutionary Synthesis scheme shown in Fig. 1.3, arrows represent causal influences (see caption of Fig. 1.3 below for more details). Within the context of the present book, a particularly crucial differences between ONCE and EES, emphasized in a central position of the scheme of this Fig. 1.2 with larger fonts, is the fact that in ONCE organisms, and in particular their behavior (organismal behavior) are seen as the key active players of biological evolution, with Darwinian (external) natural selection playing mainly a secondary—but still crucial—evolutionary role. This "organic" (the "O" of ONCE; based on Baldwin's notion of "Organic selection") view of evolution, together with the "nonoptimal", "nonstruggling" view of evolution also defended in ONCE (its "N"), enables a natural, rational, non-teleological and non-vitalistic explanation for the common occurrence of long-term evolutionary trends, as well as of etho-ecological, etho-morphological and eco-morphological mismatches (for more details, see main text)

Within the context of Baldwin's organic selection and regarding the part of ONCE that refers to that concept (Fig. 1.2), one can thus say that organic selection, i.e. the behavioral shift in salmon to return to their place of birth and their subsequent behavioral persistence to continue doing so for many generations, was an active key player in the evolutionary history of salmon. Natural (external) selection was a secondary, but also hugely important, player because within the niche/way of life that salmon help to construct, advantageous phenotypic features—including morphological (e.g. having fins that allow them to move faster) and/or physiological (e.g. having muscles that can contract faster/more powerfully) ones—were then selected by such an external selection. Of course, regarding the bears, organic selection refers to their behavioral choice to go to the rivers to catch and eat salmon, and natural (external) selection refers to abiotic and biotic factors external to the bears. These may include river currents that might make it easier or more difficult to catch the fish, the way the fish live and move, and so on. Cases of so-called "evolutionary arms races", such as the interaction between bears and salmon, thus involve a very complex interplay between the organic selection of each group of organisms and natural (external) selection. That is, a mix exists between the drive of each group separately to display a certain behavior or to, e.g. select mates in a certain way, and behavioral responses to the behavioral choices of the members of the other group, and/or to other external biotic, and/or to abiotic environmental selective factors.

It is mainly because the mechanistic view has been historically defended by many Neo-Darwinists, as well as its historical background, that terms such as "conscience" and "intelligence"—as well as related discussions on whether or not only humans display a "true" culture—are so controversial and often turn into endless philosophical and/or nomenclatural debates. Even the use of the term "imitation", which at first glance would seem more consensual, has been a major subject of controversy because some researchers cannot admit that "imitation" performed by at least some non-human organisms is really similar to imitation within humans [75]. These controversies explain why even authors such as Morris [265] might feel uneasy referring to or using such terms in the context of non-human animals and thus often opt to simply use more "neutral" terms such as "the goat was forced". However, by using these terms, one risks perpetuating the idea that the role played by non-human animals in their own evolution, and even in their day-a-day life, is necessarily passive. That is, that organisms display certain behaviors only because their genes (e.g. by "random mutation"), the external environment (e.g. "natural selection"), and/or humans (e.g. "artificial selection") forced them to do so. In this view, the organisms themselves seem to have no drive, no options, and no active role: they seem to merely exist, to merely survive. This idea is in fact stressed in the emphasis put on "survival" in the definition of natural selection as "the differential survival and reproduction of individuals due to the differences in phenotype". The idea that organisms as a whole play merely a passive and insignificant role in evolution is even more emphasized in the Neo-Darwinist definition of evolution as "changes in allele frequencies within populations." The specific view that genes are "selfish" replicators, that phenotypes are perishable vehicles, and that life is optimized for genes rather than for organisms, has therefore emerged as particularly persuasive in large subsets of the academic community, as well as the general public and press, since the 1970s [232].

This discussion leads us to the question: Why is this book needed? According to Downes [115: 41], one should not need to invoke explanations other than Neo-Darwinism unless one needs to explain phenomena "that appear to go against what one would expect from an evolutionary (Neo-Darwinist) standpoint." That is why I am writing this book: because there are two major facts, among many others that I will discuss in this work, that go against what would be expected from a purely Neo-Darwinian view of evolution. One has been discussed in several books and specialized papers without any consensus being reached so far: the occurrence of long-term macroevolutionary trends, which is related to the teleological concepts of "purpose" or "progress" in evolution (see box below), and to the difficulty of explaining the origin of morphological novelties. The other has been less discussed because it has only come to be shown to occur consistently in more recent phylogenetic ecomorphological studies: the common occurrence of etho-ecological, eco-morphological, and etho-morphological mismatches. That is, in the last few years, numerous papers—most of them written by ecomorphologists to identify/confirm correlations between ecology and anatomy—consistently reveal eco-morphological mismatches in which form is, for instance, much more strongly related to the phylogeny of a group of organisms than to the current ecological habitats inhabiting by them. The frequent occurrence of such mismatches was not at all expected in the light of the works of Neo-Darwinists, particularly those subscribing to an adaptationist framework—and, for that matter, even of Darwin himself, who for instance stressed how the morphology of the Galapagos finches seems to be beautifully optimized for the specific habitats in which they live.

Box—History: Aristotle, Scala Naturae, Religion, Design, Purpose, Teleology, and Vitalism

Subjects such as the passive versus active role of organisms and related topics as the notion of evolutionary trends, the idea that complexity supposedly increases during evolution, and the form versus function debate, have been crucial within the history of biology since Aristotle and particularly of evolutionary biology since Darwin, Wallace, and others [109]. These subjects are also related to the old concept of scala naturae (ladder of nature from "lower forms" to humans, which supposedly represent the culmination point of a "progression" toward perfection) and to associated teleological topics such as the notion of "design" or "purpose" in evolution [236]. Specifically, such teleological notions are linked to the question "why are organisms constructed so well to perform their functions?" [361: 193].

Reiss' [305] *Not by Design* provides a detailed and well-documented summary of the history of teleological reasoning from the Greeks to modern times. I thus refer the readers to that book for more details on this topic and strongly recommend the book to anyone interested in evolutionary biology in general. According to McShea [255: 665), a major reason why scientists have been so interested in such topics for millennia—which in turn makes discussions on these issues so difficult and often contentious—is that "there has always been an aura of mystery, of magic, around such systems on account of their seeming future directedness." McShea further notes that "the three standard terms of discourse (teleology, goal-directedness, purpose) all imply a future object or event (a telos, a goal, an achieved purpose) that is in some sense explanatory of present behavior." This last sentence also emphasizes the idea that even among those authors who defend the existence of evolutionary trends related/leading to new behaviors/phenotypes, these trends were historically usually seen as driven by other forces, e.g. either vitalistic, or created by an intelligent designer, or selected by the external environment. Within all of these diverse ways of thinking, organisms were once again mainly seen as being passive within the larger scheme of things created by such powerful forces.

Examples of the renewed interest in these issues include the publication of several books about them in the last 25 years (see also, e.g. Johnson et al. 2002; [268, 282, 310]). These include, among many others, *Randomness in Evolution* [45], *Evolution Without Darwinism* [49], *Forms of Becoming* [259], *Modular Evolution—How Natural Selection Produces Biological Complexity* [369], *Not by design—Retiring Darwin's Watchmaker* [305], *Niche Construction – The Neglected Process In Evolution* [276], *Darwin and Design—Does Evolution Have a Purpose?* (319], *Arrival of the Fittest: Solving Evolution's Greatest Puzzle* [385], and *The Music of Life: Biology Beyond the Genome* [272].

A central tenet of ONCE is actually that, contra the notion of "design", in most cases organisms are not so well constructed to do what they do/how they live in their current habitats. Therefore, ONCE also has no connection with a mysterious vitalistic force within living tissues driving organisms in a single direction, or to "perfection", as proposed by some defenders of orthogenesis in the past (see Chap. 4). Instead, a certain behavior choice by an organism/a group of organisms is simply one among many possible choices as emphasized previously. For instance, some organisms are positively phototactic (i.e. tend to move toward the light), whereas others are negatively phototactic because, among the many options available and possible within the context of their own plasticity and constraints, the choices they made were viable in that specific case, time, geographic location, and habitat where they took place. Therefore, there is nothing vitalistic or deterministic here. Instead, ONCE assumes precisely the opposite. That is, ONCE does not hold if there were a simple, unidirectional, constant force guided by simple natural laws, such as gravity making a stone rolling downhill, nor by an internal program or genome into which a deterministic goal of the organism has been "coded" as in a homing torpedo [255]. As noted by McShea [255], apart from plasticity and behavioral persistence, theories such as ONCE require partial independence between the organism and the various forces being exerted on it because this is also part of what makes behavioral plasticity, choices/shifts, and persistence possible. Partial independence gives the entity the capacity to make errors, or to be deflected in arbitrary ways, and to respond with corrections unlike a stone rolling downhill. For McShea, it is the constant error-or-deflection followed by correction that generates their signature, and apparently teleological, persistent behavior.

It is particularly interesting to note that even Darwin's finches, which are often used as a landmark case study for Darwinists and Neo-Darwinists and for the concept of allopatric speciation—i.e. random changes in allelic frequencies allow fitness to vary, which in combination with geographic isolation eventually lead to new species—actually stress the crucial role of behavioral choices and shifts in evolution. This is because the finches and other organisms that colonized the