Integrative and Comparative Biology

Integrative and Comparative Biology, volume 0, pp. 1–10
https://doi.org/10.1093/icb/icaf083
Society for Integrative and Comparative Biology

SYMPOSIUM ARTICLE

A Conceptual Framework for Integrative Work in Organismal Biology, Bioinspired Design, and Beyond

Jessica L. Tingle[1]

Department of Ecology, Evolution and Organismal Biology, Brown University, Providence, RI 02912, USA

From the symposium "From Evolution to innovation: Bridging biology and engineering through bioinspired design" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7th, 2025.

[1]E-mail: jessica_tingle@brown.edu

Synopsis Crossing traditional disciplinary boundaries can accelerate advances in scientific knowledge, often to the great service of society. However, integrative work entails certain challenges, including the tendency for individual specialization and the difficulty of communication across fields. Tools like the AskNature database and an engineering-to-biology thesaurus partially reduce the barrier to information flow between biology and engineering. These tools would be complemented by a big-picture framework to help researchers and designers conceptually approach conversations with colleagues across disciplines. Here, I synthesize existing ideas to propose a conceptual framework organized around function. The basic framework highlights the contributions of sub-organismal traits (e.g., morphology, physiology, biochemistry, material properties), behavior, and the environment to functional outcomes. I also present several modifications of the framework that researchers and designers can use to make connections to higher levels of biological organization and to understand the influence neural control, development/ontogeny, evolution, and trade-offs in biological systems. The framework can be used within organismal biology to unite subfields, and also to aid the leap from organismal biology to bioinspired design. It provides a means for mapping the often-complex pathways among organismal and environmental characteristics, ultimately guiding us to a deeper understanding of organismal function.

Introduction

Important scientific questions and challenges often require input from multiple fields. Biology, for instance, can benefit from the expertise of engineers, physicists, chemists, mathematicians, and other researchers from outside biology. We can use robotic model organisms to examine the functional effects of varying morphology and behavior, including in ways that would be unfeasible to study in living organisms because those phenotypes do not exist, or because organisms notoriously choose not to behave how experimenters would like them to (Long 2007; Flammang and Porter 2011; Gravish and Lauder 2018; Flammang 2022). Analytical tools from physics and engineering can let us dig into the mechanisms underlying all kinds of biological phenomena. Take the case of finite element analysis, which has yielded insight into form-function relationships in numerous biological systems (Rayfield et al. 2001; Ross 2005; McCullough et al. 2014; Villacís Núñez et al. 2022). Even within biology, different subfields direct their attention to different levels of biological organization, employing a dizzying array of techniques in settings ranging from the field to the bench to computing environments. To answer many of our most interesting and important biological questions, biologists from different subfields must unite their diverse strengths and perspectives.

Engineers, on the other hand, can look towards biology for inspiration to tackle many of the challenges that humans face. Inspiration can come from any level of biological organization, although biomimetic products may particularly draw their inspiration from organism-level observations, perhaps not surprising considering that organisms are more easily observ-

Advance Access publication June 9, 2025

able than smaller- or larger-scale biological phenomena (e.g., molecules, cells, ecosystems) (Bhasin and McAdams 2018). Comparative methods from biology can take bioinspired design to new heights by providing a means to leverage biodiversity (Penick et al. 2022). We might especially reap the benefits of nature's inspiration when biologists are included in the bioinspired design process; yet, bioinspired design teams rarely include biologists, limiting their ability to assimilate biological knowledge (Graeff et al. 2019; Ng et al. 2021; Snell-Rood and Smirnoff 2023; but see the following for pedagogical approaches that involve integrating biologists into bioinspired design teams: Yen et al. 2011; Helms and Goel 2014; Full et al. 2015, 2021).

Despite the clear benefits of integrative work, at least two inherent discipline-bridging challenges pose a barrier to its successful pursuit. First, specialization can lead towards fixation. Individual researchers often struggle to maintain a mile-high view of the context, if we strive to achieve the mile-high view at all. Second, researchers from different fields must grapple with communication barriers, which must be overcome for us to work effectively together. Difficulty communicating stems not only from different vocabularies, but also from different and incomplete perspectives with respect to the huge body of knowledge available for interdisciplinary studies to draw upon.

Due to its inherently integrative nature, bioinspired design has been the focus of several efforts to bridge the gap between fields, specifically engineering and biology. One example, AskNature, provides a database to help designers more easily find inspiration in biology (Deldin and Schuknecht 2014; see also Wanieck et al. 2017 for a review of such tools in biomimetics). Databases provide a helpful start, but they should not be an endpoint for inspiration—literature searches and conversations with biologists can lead to more sources of inspiration and a deeper understanding (Snell-Rood and Smirnoff 2023). An engineering-to-biology thesaurus helps engineers translate their vocabulary into terms useful for searching and interpreting the biology literature, enhancing their ability to integrate biological knowledge into engineering design (Nagel et al. 2010; Nagel 2014). This tool can also reduce the communication barrier between engineers and biologists by helping them navigate vocabulary differences, once they have decided to have a conversation on a particular topic. However, it is often not obvious what to ask or discuss with someone from another discipline in the first place.

Conceptual frameworks in biology and design

Conceptual frameworks can help researchers identify important open questions and determine the most effective (potentially interdisciplinary) approach to answering those questions. Not surprisingly, multiple fields therefore make use of conceptual frameworks, including biology and design. For example, Arnold's morphology-performance-fitness paradigm has had a huge and enduring impact on how we think about organismal biology (Arnold 1983). It made a major analytical contribution by suggesting path analysis as a statistical method for quantifying the impact of morphology on fitness via performance. It prompted (and continues to prompt) functional morphologists and biomechanists to step back and see the bigger picture—it is tempting to tell just-so stories about how particular morphological features must be adaptations, but Arnold's paradigm forces us to assess whether they really are. Much of the paradigm's strength arises from its simplicity, which makes it widely applicable to many study systems, and its specificity, which provides a practical guide on what to study, including how the parts relate. The paradigm is also readily modifiable: Garland and Losos (1994) updated it to explicitly include behavior, an important property in organismal systems.

Design theory has produced various conceptual models to set forth stages of the design process, often with explicit reference to iteration for refining ideas or designs. Gero's function-behavior-structure (FBS) model and subsequent modifications provide one such framework (Gero 1990; Gero and Kannengiesser 2004; Vermaas and Dorst 2007; Galle 2009). In this model, a designer starts with the desired function for their designed artifact. Because a direct leap between function and structure can rarely be achieved, the designer then uses behavior as an intermediate step: they determine what behaviors would contribute to achieving the desired function, and what behaviors result from a candidate structure. To illustrate using the window example from Gero's original paper, a designer might start with a list of functions that includes providing daylight and controlling noise. Relevant behavior variables include light flux transmitted and sound reduction index. Structural considerations follow from the list of behaviors, and might include glaze- and frame-related variables. A process of formulation, synthesis, analysis, evaluation, documentation, and reformulation eventually results in a design prototype.

Several authors have presented frameworks specific to bioinspiration and biomimicry, which commonly fall into problem-driven or solution-driven cognitive

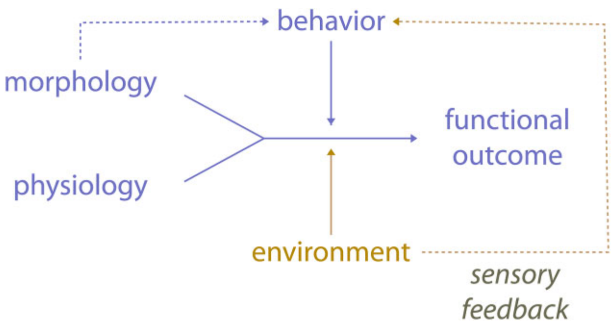

Fig. 1 Main framework. Sub-organismal or sub-device traits, including morphology (physical form) and physiology (processes of lower-level systems) contribute to functional outcomes. Behavior (what the organism or device does) can change the relationship between sub-organismal traits and functional outcomes, but on the flip side, the range of possible behaviors may be constrained by sub-organismal traits. Finally, environment can directly influence functional outcomes, or it can have indirect influence via effects on behavior, which the organism or device can change in response to sensory feedback about the environment.

strategies (Kruger and Cross 2006; Helms et al. 2009). These reference biology as a source of inspiration, but do not often provide explicit instruction for engaging with biologists. Generally lackluster engagement with and from biologists means that engineers usually are not taking full advantage of the potential organisms have to offer (Snell-Rood 2016; Graeff et al. 2019; Ng et al. 2021; Penick et al. 2022; Snell-Rood and Smirnoff 2023). On the flip side, barriers to cross-disciplinary engagement mean biologists often are not getting input from engineers and scientists in other disciplines that could substantially advance our understanding of biology.

A new conceptual framework

The main framework

A conceptual framework uniting big-picture topics can prompt researchers to think about the broader context of their work while also sparking interdisciplinary conversations. Here, I present such a framework, drawing from previous work to synthesize ideas likely to matter across disciplines (Fig. 1).

Function provides a central concept around which to gather biologists from different subfields whose questions require an integrative approach, as well as scientists and engineers interested in biomimicry or bioinspired design (Snell-Rood and Smirnoff 2023). Although we all care about function in some form or another, the term can have different meanings across fields and within them, potentially impeding communication. Biologists and philosophers of evolutionary biology have formulated various definitions of function, which may or may not include criteria related to evolutionary history (Amundson and Lauder 1994). Function in engineering has several different but related meanings, which all "arise from the idea of a machine, system or a person *doing* something or having a property that is *intended* or *desired* by someone" (Chandrasekaran and Josephson 2000). The field of design methodology had struggled with the concept of function for decades, leading to a variety of definitions (Umeda et al. 1990, 1996; Vermaas and Dorst 2007). Moreover, an individual may not explicitly employ a working definition of function, so they may use the term inconsistently. Different iterations of Gero's function-behavior-structure model used different definitions of function over the years, sometimes distinguishing function from purpose and sometimes blurring the line between them (Vermaas and Dorst 2007). Because organisms are not designed, they do not have a purpose. However, we might think of survival and reproduction in place of purpose, since only by survival and reproduction of enough individuals can a species persist. We might then think of function as "the thing the organism or device accomplishes" to ultimately aid survival and reproduction (in the case of organisms) or to achieve a desired purpose (in the case of designed devices or systems). Although I will use this as my working definition of function for the purposes of this paper, I do not mean to exclude other definitions. Indeed, researchers and designers should use the definition best suited to a given situation, including when using the framework presented here. In any case, it improves clarity of thought and communication to ensure that one's working definition is explicit to oneself and to one's collaborators.

When considering a whole-organism function or the function of engineered systems, it helps to begin with the lower-level traits that enable the function. These traits include things like morphology (physical form, structure) and physiology (processes of sub-organismal systems). Note that we often define physiology as "functions" of organisms, but the key difference from my use of "function" in the present framework is the sub-organismal level of physiology. If a system needs to achieve the function of moving quickly through water, the morphology that best serves that function involves a fusiform body shape, whether in dolphins, ichthyosaurs, sharks, or submarines (Fish 2006, 2023). To give a physiological example where an organism must achieve the functional outcome of preventing hypothermia, countercurrent exchange lets birds stand directly on ice without suffering a drop in their core body temperature thanks to regional heterothermy (Mitchell and Myers 1968). Countercurrent exchange has similar utility in cooling towers, and it can also be used in both organismal and engineered systems to maintain regional differences in chemical concentrations rather than temperature. Morphology translates directly from biology to design as structure (Gero 1990; Gero and Kannengiesser 2004; Vermaas and Dorst 2007; Galle 2009; Nagel 2014). Physiology might not be as directly translatable as morphology, but designed systems certainly have analogous traits (e.g., motor properties). We can also consider biochemical, material, bulk, and surface properties among lower-level traits.

Although lower-level traits like morphology and physiology provide a starting point for understanding function, organisms' behavioral choices can lead to very different functional outcomes from expectations based on lower-level traits alone. Garland and Losos (1994) noted a similar role for behavior in the morphology-performance-fitness paradigm. Nature provides many examples where behavior alters form-function relationships in sometimes surprising ways. Thanks to their sinuous body plan, snakes can easily navigate confined and cluttered spaces, like underground burrow systems or dense tangles of branches (Tingle et al. 2024). Their elongate shape seems less suited to functions like flying or floating. Yet, some snakes have evolved behaviors that let them achieve both of these seemingly unlikely feats (Socha 2002; Herault et al. 2020). Similarly, behavioral flexibility means organisms are not completely beholden to their physiology. Sidewinder rattlesnakes inhabit deserts known for brutally high summer temperatures, so one would expect them to have physiological adaptations to withstand the heat. However, this species is not particularly heat tolerant and, in fact, tolerates low temperatures surprisingly well, at least for a reptile (Cowles and Bogert 1944; Moore 1978; Secor and Nagy 1994). Instead of adapting their physiology, they retreat into cool burrows for protection when temperatures rise. As a result, designers who look to sidewinders for inspiration on dealing with heat will likely find themselves misled. Instead, they might be better served by looking to species that cannot hide from the heat, like the saguaro cactus, which inspired the self-shading exterior structure of the building that houses Arizona State University's Walton Center for Planetary Health (Seckel 2022). While behavior can alter the relationships between sub-organismal traits and function, sub-organismal traits can also constrain behavior: even if they wanted to, pigs simply do not have the morphological or physiological capacity to fly.

Behavior, like function, can have many definitions. In this paper's organismal examples, a definition often used in biology applies: the response of an organism to some input or stimulus, which might be conscious or unconscious (Diogo 2017). Behavioral choices arise in cases where an organism has multiple behavioral options plus the agency to pick one over others (Diogo 2017). As an emergent property of autonomous (and often complex) organisms, behavior can have a degree of unpredictability that excites biologists while vexing engineers (Vincent et al. 2006; Diogo 2017). In contrast, the function-structure-behavior model defines behavior in terms of the "physical dispositions of the artefact," or the "the attributes that are derived or expected to be derived from the structure variables of the object," quite different from most biologists' usage of the term (Gero 1990; Gero and Kannengiesser 2004; Vermaas and Dorst 2007; Galle 2009). Although several additional definitions of behavior appear in the engineering and design literature (Chandrasekaran and Josephson 2000), most of them are imbued with greater predictability than the concept of organismal behavior in biology. We might use "what the thing does" as an implicit or explicit working definition of behavior, a simple and ambiguous enough definition to apply in many circumstances. As with function, different definitions may suit different workers and/or situations. That is okay, so long as one is clear about one's meaning. Careful consideration of different possible definitions may be helpful for work that crosses biological subfields, and even more so for work that bridges the gap between biology and design. An organism's behavior in the sense of "what it does" might translate directly to bioinspired robots, but cleverer interpretation (perhaps involving reconciliation between various engineering and biological definitions of behavior) might be required to make the leap from organisms to other bioinspired design applications.

The environment can interact with organismal traits to impact functional outcomes. Environmental effects might be direct, as may often be the case for locomotion. Snakes on firm, rough surfaces can slide gracefully forward by undulating their bodies from side to side, pushing off of objects in the environment, and making good use of their ventral scales' frictional anisotropy (Jayne 1986; Hu et al. 2009; Hu and Shelley 2012; Rieser et al. 2021). However, many snakes struggle to slither on sand and other deformable surfaces, where stout species are prone to slipping; the stoutest fail miserably, pushing the sand from side to side without making any forward progress (Marvi et al. 2014; Schiebel et al. 2020). Same behavior, different substrate, different functional outcome (or lack thereof). On the other hand, the environment can have indirect effects on functional outcomes when an organism uses sensory information to alter its behavior in light of environmental conditions. When faced with sand, some snake species switch their locomotion from lateral undulation to sidewinding, allowing them to make excellent forward progress on this challenging substrate (Gans and Mendelssohn 1971; Jayne 1986; Tingle 2020). Behavioral alterations in light of environmental conditions can also include relatively small adjustments. To stick with the sidewinding example, snakes can make kinematic changes to the sidewinding motion to improve locomotor performance when ascending slopes, which present different challenges from flat sandy surfaces (Marvi et al. 2014). These examples focus on macro-level (visible with the naked eye) effects of the environment, with implications for robotics. The environment can also impact function at different scales, and with implications for bioinspired design applications other than robotics. For example, water salinity impacts sea urchin adhesive performance, presumably due to the effects of altered ion concentrations on chemical (as opposed to mechanical) interactions (Moura et al. 2023; Garner et al. 2024). By examining direct and indirect environmental effects on functional outcomes at a wide range of biological scales, we can not only improve our understanding of biology (e.g., variation in habitat use or energetic requirements), but also the performance and flexibility of bioinspired design applications.

Adding to the main framework

With the main framework in place, we can build upon it to reach a more profound understanding of our study systems, whether we care primarily about the biology or about using the biology to inform design. To illustrate, the organism-level focus of the main framework can be linked to ecology because different functional outcomes in different environments likely influence habitat use and dispersal, which matter not just to the individual organisms but also for community assembly and evolutionary ecology (Fig. 2A). We could also modify the framework to more explicitly consider the role of the nervous system, which can have major implications for behavior, sensory systems, and numerous aspects of physiology (Fig. 2B).

Living systems come about not by design, but by processes of development and evolution (Fig. 2C and D). Biologists, perhaps especially those who do not specialize in evolutionary developmental biology, can more deeply understand our systems by considering the roles of these processes. Far from irrelevant from engineering, the importance of development and evolution should remain clearly in the minds of bioinspired designers and anyone who seeks to use engineering tools to shed light on biological systems (Flammang 2022). Because biological systems are generally subject to developmental and evolutionary constraints that need not apply to engineering design, a lack of awareness about these processes can lead bioinspired designers astray.

We have so far considered only one function at a time. Yet, organisms must adequately accomplish a suite of tasks to survive and reproduce. As a result, many organismal traits evolve in the face of functional conflicts, a type of trade-off that arises when high performance at one task comes at the expense of another (Walker 2007; Bergmann and McElroy 2014; Garland et al. 2022). Functional conflicts can result from mechanical laws. For example, lever systems—common in vertebrate musculoskeletal systems and in engineering design—can be arranged to maximize force, but only at the expense of velocity, and vice versa. Turtle shell shapes can maximize either hydrodynamic performance or strength to resist predators' jaws, not both (Stayton 2011; Polly et al. 2016). Functional conflicts can also result from physiology, as in the case of muscle fiber type composition and its interaction with muscle architecture in mediating trade-offs among power and energetic efficiency (Hill 1950; Pette and Spamer 1986; Schaeffer and Lindstedt 2013; Cooper et al. 2021). In cases where a trait or network of traits contributes to a suite of functions, it likely represents a compromise, meeting several demands adequately rather than a single demand optimally (Fig. 2E).

Even in the absence of trade-offs between functions, a trait's contribution to multiple functions means that not all of its features contribute to every function. For instance, snake skin can possess features to facilitate locomotion (Hazel et al. 1999; Berthé et al. 2009; Rieser et al. 2021), allow renewal via shedding (Landmann 1979; Irish et al. 1988; Tu et al. 2002), shed dirt (Gans and Baic 1977; Gower 2003), provide waterproofing (Chiasson and Lowe 1989; Spinner et al. 2014), harvest water (Phadnis et al. 2019; McIntyre et al. 2025), promote mechanosensation (Crowe-Riddell et al. 2016, 2019, 2021), accommodate large meals via stretching (Jayne 1988; Rivera et al. 2005; Dellinger et al. 2023; Petersen et al. 2024), or alter color for camouflage or thermoregulatory function (Cooper Jr. and Greenberg 1992; Tanaka 2007; Spinner et al. 2013, 2014). As a result, a snake's integument has a complex collection of features, only some of which may be relevant to a particular function of interest. It may therefore be useful to consider the present framework in the context of multifunctionality, improving our understanding of the system even in cases where we wish to focus on one particular function of many.

Beyond functional conflict, other types of trade-offs may also apply. The "ecological circumstances" category of trade-offs reviewed by Garland et al. (2022) emphasizes context dependence, allowing its relation to the present framework via environment and behavior (Fig. 2F). For example, an animal may face a trade-off whereby increasing its foraging effort gives it more energy, but potentially at the cost of increased predation risk. However, the balance of the trade-off will depend on the concentration of predators and on their performance abilities under the present set of environmen-

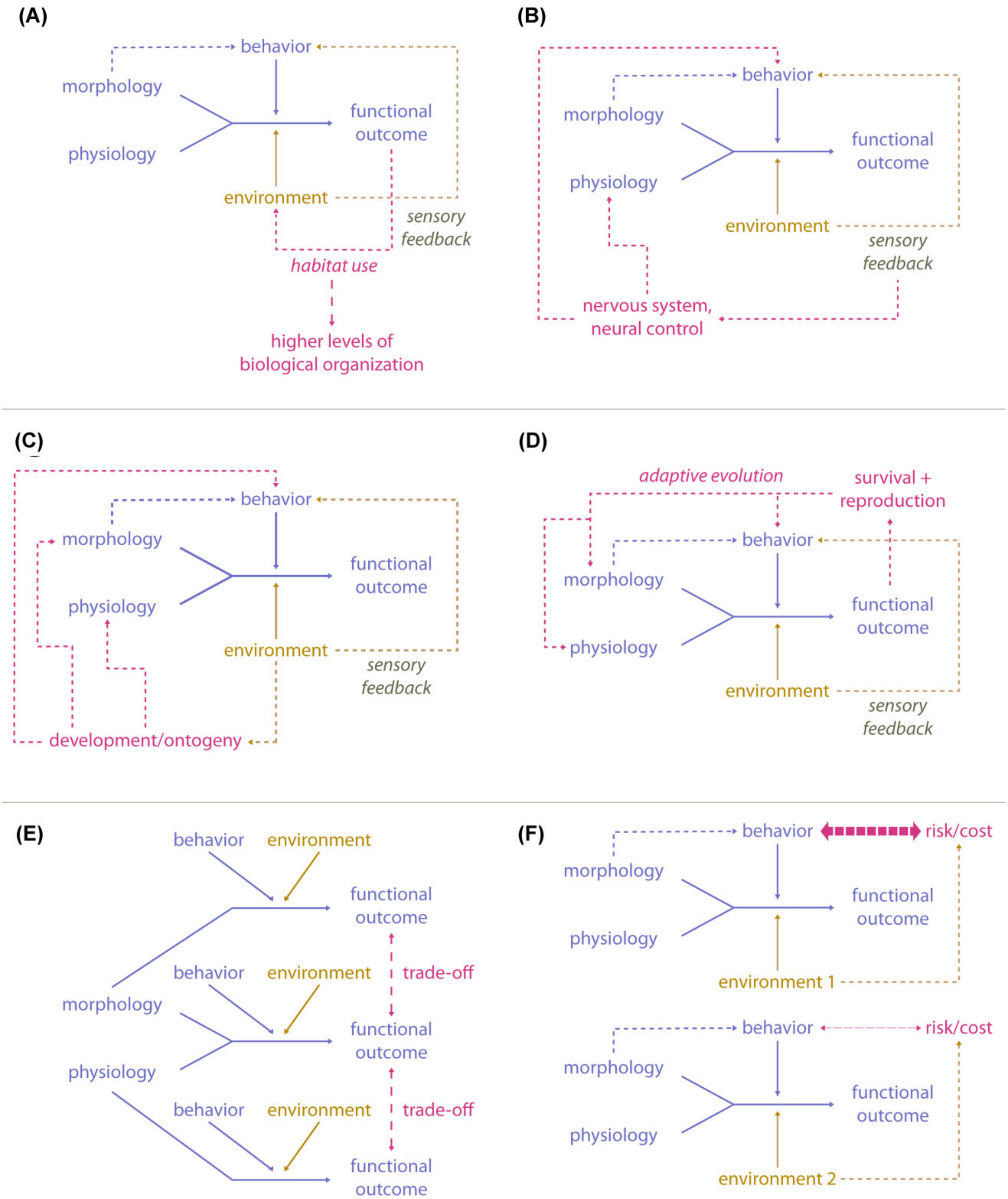

Fig. 2 Modifications to the framework. We can modify the main framework as needed to enhance the main framework. Examples shown here include (A) connection to higher levels of organization via functional effects on ecology; (B) influence of the nervous system on several components of the main framework; (C) the role of development/ontogeny in producing organismal phenotypes, including the potential influence of the environment (in addition to genes) on developmental processes; (D) the role of adaptive evolution in modifying organismal phenotypes (but note that traits also evolve with respect to non-adaptive processes); (E) potential for functional conflicts (a type of trade-off), and (F) potential for context-dependent trade-offs, whereby the risk or cost of a behavior depends on the environment.

tal conditions, hence the context dependence. Context-dependent trade-offs, including allocation constraints, may also matter for engineered systems. As with organisms, increased time or effort allocated towards a given task might help the system achieve a given function, but potentially at some risk, such as incurring damage or running out of fuel. The risk may be increased or diminished in different environments.

A note of caution

This framework's organization of traits around function may introduce a temptation to imagine all organismal features as adaptive. One must resist such temptation. Evolution results not only from natural selection, but also from non-adaptive mechanisms like genetic drift (a random process), mutation (another random process), and gene flow between populations (which can actually thwart adaptation to local conditions). Non-adaptive mechanisms of evolution, combined with phylogenetic inertia and developmental constraint, mean that many organismal features are not adaptive, and also that sub-optimality of a trait for a function it serves can result from many phenomena other than functional trade-offs (Gould and Lewontin 1979). Failure to remember this point can lead to misguided interpretations of biological phenomena, and in the context of bioinspired design, it can cause designers to waste time on false leads.

Conclusion

The present framework can help individual scientists consider aspects of organismal biology beyond our immediate focus, opening the door to interesting and potentially influential integrative research questions. In the context of bioinspired design, the framework can highlight important biological topics to consider during the design process, so that engineers will more readily think to ask biologist colleagues about those topics (Box 1). In addition to aspects of biology that could usefully factor into design, conversations with biologists based on the framework can make designers more aware of aspects of biology that do not factor into design, but that should be considered to avoid potential pitfalls. As previously discussed, organismal traits are shaped not only by functional needs, but also by developmental constraints and evolutionary history. Moreover, organismal traits are often not fixed, manifesting an ability to change in response to environmental conditions, a phenomenon called phenotypic plasticity (West-Eberhard 1989). Organisms also face trade-offs related to phenomena that are not applicable to engineered devices, including shared biochemical pathways, antagonistic pleiotropy, and sexual selection (Garland et al. 2022). A reasonable understanding of these aspects of biology will help designers more effectively sort the organismal features useful to them from those that are not, allowing them to reproduce (probably with modification) the most essential organismal features.

Box 1. Conversation prompts

Engineers connecting with biologists

Use the framework to ask questions, starting with either a function you need to achieve (problem-driven) or some compelling organismal trait or biological phenomenon (solution-driven). Some things to consider asking about:

- Ecological context
- Trade-offs
  - From mechanical laws
  - From balancing multiple functions
- Biodiversity of organisms with similar traits and/or functions
- Evolutionary history
- Developmental constraint
- Non-adaptive evolution

Biologists connecting with engineers

Pitch your cool biological phenomenon in under two minutes. Ask:

- Do you think it might be useful to design?
- What should biologists measure to facilitate design applications?
- Can you think of techniques from your field that might help me understand it?

Biologists connecting with biologists in another subfield, physicists, chemists, mathematicians, etc.

Use the framework to start with something you observed (morphology, behavior, environment, function, etc.) Ask:

- Do you have ideas for what that might have to do with other things in the framework?
- Can you think of techniques from your (sub-)field that might help me understand it?

Wading into biology's vast complexity, one can quickly get bogged down. Scientists and engineers alike might view complexity as an impediment to circumvent or cut through. However, it may sometimes behoove us to sit longer with the complexity of biological systems before deciding on the best approach for simplifying our research or design processes. The conceptual framework presented here can help us map the often-complex pathways among traits and emergent phenomena, ultimately guiding us to a deeper understanding of organismal function.

Author contributions

Jessica L. Tingle conceived of, wrote, and edited the manuscript, and created the figures.

Acknowledgments

Many thanks to Brian Sherman, Peter Niewiarowski, Rachel Olson, and Austin Garner for invaluable conversations during idea development; to University of Akron faculty and students for insightful discussion after a seminar talk; to two anonymous reviewers for helpful feedback on the manuscript draft; to Karley Cohen and Cassandra Donatelli for organizing the symposium; and to the American Association for Anatomy, the Company of Biologists, and the Society for Integrative and Comparative Biology's Division of Comparative Biomechanics for providing funding to participate in the symposium.

Funding

This work was supported by an NSF Postdoctoral Research Fellowship in Biology (Award #2305218).

Conflict of interest

The author has no conflicts of interest to report.

Data availability

No new data were generated or analyzed in support of this work.

References

Amundson R, Lauder GV. 1994. Function without purpose: the uses of causal role function in evolutionary biology. Biol Philos 9:443–69.

Arnold SJ. 1983. Morphology, performance and fitness. Am Zool 23:347–61.

Bergmann PJ, McElroy EJ. 2014. Many-to-many mapping of phenotype to performance: an extension of the F-matrix for studying functional complexity. Evol Biol 41:546–60.

Berthé RA, Westhoff G, Bleckmann H, Gorb SN. 2009. Surface structure and frictional properties of the skin of the Amazon tree boa *Corallus hortulanus* (Squamata, Boidae). J Comp Physiol A 195:311–8.

Bhasin D, McAdams DA. 2018. The characterization of biological organization, abstraction, and novelty in biomimetic design. Designs 2:54.

Chandrasekaran B, Josephson JR. 2000. Function in device representation. EWC 16:162–77.

Chiasson RB, Lowe CH. 1989. Ultrastructural scale patterns in *Nerodia* and *Thamnophis*. J Herpeto 23:109.

Cooper AN, McDermott WJ, Martin JC, Dulaney SO, Carrier DR. 2021. Great power comes at a high (locomotor) cost: the role of muscle fascicle length in the power versus economy performance trade-off. J Exp Biol 224:jeb236679.

Cooper WE, Jr., Greenberg N. 1992. Reptilian coloration and behavior. In: Gans C, Crews D, editors. Biology of the reptilia. Chicago, IL: University of Chicago Press. p. 298–422.

Cowles RB, Bogert CM. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull Am Mus Nat Hist 83:261–96.

Crowe-Riddell JM, Jolly CJ, Goiran C, Sanders KL. 2021. The sex life aquatic: sexually dimorphic scale mechanoreceptors and tactile courtship in a sea snake *Emydocephalus annulatus* (Elapidae: Hydrophiinae). Biol J Linn Soc 134: 154–64.

Crowe-Riddell JM, Snelling EP, Watson AP, Suh AK, Partridge JC, Sanders KL. 2016. The evolution of scale sensilla in the transition from land to sea in elapid snakes. Open Biology 6:160054.

Crowe-Riddell JM, Williams R, Chapuis L, Sanders KL. 2019. Ultrastructural evidence of a mechanosensory function of scale organs (sensilla) in sea snakes (Hydrophiinae). R Soc Open Sci 6:182022.

Deldin J-M, Schuknecht M. 2014. The AskNature Database: enabling solutions in biomimetic design. In:Goel AK, McAdams DA, Stone RB, editors. Biologically inspired design: computational methods and tools. London: Springer. p. 17–27.

Dellinger SB, De Vita R, Vlachos PP, Muñoz MM, Socha JJ. 2023. Material properties of skin in the flying snake *Chrysopelea ornata*. J Exp Zool Pt A 339:269–83.

Diogo R. 2017. Evolution driven by organismal behavior. Cham: Springer International Publishing.

Fish FE. 2006. Limits of nature and advances of technology: what does biomimetics have to offer to aquatic robots? Appl Bionics Biomech 3:49–60.

Fish FE. 2023. Aquatic locomotion: environmental constraints that drive convergent evolution. In: Bels VL, Russell AP, editors. Convergent evolution: animal form and function. Cham: Springer International Publishing. p. 477–522.

Flammang BE. 2022. Bioinspired design in research: evolution as beta-testing. Integr Comp Biol 62:1164–73.

Flammang BE, Porter ME. 2011. Bioinspiration: applying mechanical design to experimental biology. Integr Comp Biol 51:128–32.

Full RJ, Bhatti HA, Jennings P, Ruopp R, Jafar T, Matsui J, Flores LA et al. 2021. Eyes toward Tomorrow program enhancing collaboration, connections, and community using bioinspired design. Integr Comp Biol 61:1966–80.

Full RJ, Dudley R, Koehl MAR, Libby T, Schwab C. 2015. Interdisciplinary laboratory course facilitating knowledge integration, mutualistic teaming, and original discovery. Integr Comp Biol 55:912–25.

Galle P. 2009. The ontology of Gero's FBS model of designing. Design Studies 30:321–39.

Gans C, Baic D. 1977. Regional specialization of reptilian scale surfaces; relation of texture and biologic role. Science 195:1348–50.

Gans C, Mendelssohn H. 1971. Sidewinding and jumping progression of vipers. In: De Vries A, Kochva E, editors. Toxins of animal and plant origin. New York: Gordan and Breach, Science Publishers, Inc. p. 17–38.

Garland T, Downs CJ, Ives AR. 2022. Trade-offs (and constraints) in organismal biology. Physiol Biochem Zool 95:82–112.

Garland T, Losos JB. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Ecological Morphology. Chicago and London: University of Chicago Press. p. 240–302.

Garner AM, Moura AJ, Narvaez CA, Stark AY, Russell MP. 2024. Repeated hyposalinity pulses immediately and persistently impair the sea urchin adhesive system. Integr Comp Biol 64: 257–69.

Gero JS. 1990. Design prototypes: a knowledge representation schema for design. AI Mag 11:26–36.

Gero JS, Kannengiesser U. 2004. The situated function–behaviour–structure framework. Des Stud 25:373–91.

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B 205:581–98.

Gower DJ. 2003. Scale microornamentation of uropeltid snakes. J Morphol 258:249–68.

Graeff E, Maranzana N, Aoussat A. 2019. Biomimetics, where are the biologists? J Eng Des 30:289–310.

Gravish N, Lauder GV. 2018. Robotics-inspired biology. J Exp Biol 221:jeb138438.

Hazel J, Stone M, Grace MS, Tsukruk VV. 1999. Nanoscale design of snake skin for reptation locomotions via friction anisotropy. J Biomech 32:477–84.

Helms M, Goel AK. 2014. The four-box method: problem formulation and analogy evaluation in biologically inspired design. J Mech Des 136:111106.

Helms M, Vattam SS, Goel AK. 2009. Biologically inspired design: process and products. Des Stud 30:606–22.

Herault J, Clement É, Brossillon J, LaGrange S, Lebastard V, Boyer F. 2020. Standing on the water: stability mechanisms of snakes on free surface. In: Vouloutsi V, Mura A, Tauber F, Speck T, Prescott TJ, Verschure PFMJ, editors. Biomimetic and biohybrid systems, lecture notes in computer science. Presented at the 9th International conference, living machines. Freiburg: Springer International Publishing, p. 165–75.

Hill AV. 1950. The dimensions of animals and their muscular dynamics. Sci Prog 38:209–30.

Hu DL, Nirody J, Scott T, Shelley MJ. 2009. The mechanics of slithering locomotion. Proc Natl Acad Sci 106:10081–5.

Hu DL, Shelley MJ. 2012. Slithering locomotion. In: Childress S, Hosoi A, Schultz WW, Wang J, editors. Natural Locomotion in Fluids and on Surfaces, the IMA Volumes in Mathematics and Its Applications. New York, NY: Springer New York. p. 117–35.

Irish FJ, Williams EE, Seling E. 1988. Scanning electron microscopy of changes in epidermal structure occurring during the shedding cycle in squamate reptiles. J Morphol 197: 105–26.

Jayne BC. 1986. Kinematics of terrestrial snake locomotion. Copeia 1986:915–27.

Jayne BC. 1988. Mechanical behaviour of snake skin. J Zool 214:125–40.

Kruger C, Cross N. 2006. Solution driven versus problem driven design: strategies and outcomes. Des Stud 27:527–48.

Landmann L. 1979. Keratin formation and barrier mechanisms in the epidermis of *Natrix natrix* (Reptilia: Serpentes): an ultrastructural study. J Morphol 162:93–125.

Long JH. 2007. Biomimetic robotics: self-propelled physical models test hypotheses about the mechanics and evolution of swimming vertebrates. Proc Inst Mech Eng Part C J Mech Eng Sci 221:1193–200.

Marvi H, Gong C, Gravish N, Astley H, Travers M, Hatton RL, Mendelson JR et al. 2014. Sidewinding with minimal slip: snake and robot ascent of sandy slopes. Science 346:224–9.

McCullough EL, Tobalske BW, Emlen DJ. 2014. Structural adaptations to diverse fighting styles in sexually selected weapons. Proc Natl Acad Sci USA 111:14484–8.

McIntyre MG, Van Mierlo M, Parker MR, Goetz SM, Taylor EN, Boback SM. 2025. Rain-harvesting behavior in free-ranging prairie rattlesnakes (*Crotalus viridis*). Current Zoology 71: 1–13.

Mitchell JW, Myers GE. 1968. An analytical model of the countercurrent heat exchange phenomena. Biophys J 8:897–911.

Moore RG. 1978. Seasonal and daily activity patterns and thermoregulation in the Southwestern Speckled Rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado Desert Sidewinder (*Crotalus cerastes laterorepens*). Copeia 1978:439.

Moura AJ, Garner AM, Narvaez CA, Cucchiara JP, Stark AY, Russell MP. 2023. Hyposalinity reduces coordination and adhesion of sea urchin tube feet. J Exp Biol 226:jeb245750.

Nagel JKS. 2014. A thesaurus for bioinspired engineering design. In: Goel AK, McAdams DA, Stone RB, editors. Biologically inspired design. London: Springer. 63–94.

Nagel JKS, Stone RB, McAdams DA. 2010. An engineering-to-biology thesaurus for engineering design. In: 22nd International Conference on Design Theory and Methodology; Special Conference on Mechanical Vibration and Noise. Presented at the ASME 2010 International Design Engineering Technical Conferences and Computers and Information in Engineering Conference. 5. Montreal, Quebec: ASMEDC. p. 117–28.

Ng L, Elgar MA, Stuart-Fox D. 2021. From bioinspired to bioinformed: benefits of greater engagement from biologists. Front Ecol Evol 9:790270.

Penick CA, Cope G, Morankar S, Mistry Y, Grishin A, Chawla N, Bhate D. 2022. The comparative approach to bio-inspired design: integrating biodiversity and biologists into the design process. Integr Comp Biol 62:1153–63.

Petersen JC, Campbell LC, Jayne BC, Roberts TJ. 2024. Mechanical properties of snake skin vary longitudinally, following large prey ingestion and among species. J Exp Biol 227:jeb248142.

Pette D, Spamer C. 1986. Metabolic properties of muscle fibers. Fed Proc 45:2910–4.

Phadnis A, Manning KC, Schuett GW, Rykaczewski K. 2019. Role of scale wettability on rain-harvesting behavior in a desert-dwelling rattlesnake. ACS Omega 4:21141–7.

Polly PD, Stayton CT, Dumont ER, Pierce SE, Rayfield EJ, Angielczyk KD. 2016. Combining geometric morphometrics and finite element analysis with evolutionary modeling: towards a synthesis. J Vertebr Paleontol 36:e1111225.

Rayfield EJ, Norman DB, Horner CC, Horner JR, Smith PM, Thomason JJ, Upchurch P. 2001. Cranial design and function in a large theropod dinosaur. Nature 409:1033–7.

Rieser JM, Li T-D, Tingle JL, Goldman DI, Mendelson JR, III. 2021. Functional consequences of convergently-evolved microscopic skin features on snake locomotion. Proc Natl Acad Sci 118:e2018264118.

Rivera G, Savitzky AH, Hinkley JA. 2005. Mechanical properties of the integument of the common gartersnake, *Thamnophis sirtalis* (Serpentes: Colubridae). J Exp Biol 208:2913–22.

Ross CF. 2005. Finite element analysis in vertebrate biomechanics. Anat Rec 283A:253–8.
Schaeffer PJ, Lindstedt SL. 2013. How animals move: comparative lessons on animal locomotion. Compr Physiol 3: 289–314.
Schiebel PE, Astley HC, Rieser JM, Agarwal S, Hubicki C, Hubbard AM, Diaz K et al. 2020. Mitigating memory effects during undulatory locomotion on hysteretic materials. eLife 9:e51412.
Seckel S. https://news.asu.edu/20220310-creativity-asu-istb7-architecture-ancient-past-thriving-future 2022. ISTB7: A Building Bridging Our Ancient Past to Our Thriving Future. Arizona State University News. (13 February 2025, date last accessed)
Secor SM, Nagy KA. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. Ecology 75:1600–14.
Snell-Rood E. 2016. Interdisciplinarity: bring biologists into biomimetics. Nature 529:277–8.
Snell-Rood EC, Smirnoff D. 2023. Biology for biomimetics I: function as an interdisciplinary bridge in bio-inspired design. Bioinspir Biomim 18:052001.
Socha JJ. 2002. Gliding flight in the paradise tree snake. Nature 418:603–4.
Spinner M, Gorb SN, Balmert A, Bleckmann H, Westhoff G. 2014. Non-contaminating camouflage: multifunctional skin microornamentation in the West African gaboon viper (*Bitis rhinoceros*). PLoS One 9:e91087.
Spinner M, Kovalev A, Gorb SN, Westhoff G. 2013. Snake velvet black: hierarchical micro- and nanostructure enhances dark colouration in *Bitis rhinoceros*. Sci Rep 3:1846.
Stayton CT. 2011. Biomechanics on the half shell: functional performance influences patterns of morphological variation in the emydid turtle carapace. Zoology 114:213–23.
Tanaka K. 2007. Thermal biology of a colour-dimorphic snake, *Elaphe quadrivirgata*, in a montane forest: do melanistic snakes enjoy thermal advantages? Biol J Linn Soc 92: 309–22.
Tingle JL. 2020. Facultatively sidewinding snakes and the origins of locomotor specialization. Integr Comp Biol 60: 202–14.
Tingle JL, Garner KL, Astley HC. 2024. Functional diversity of snake locomotor behaviors: a review of the biological literature for bioinspiration. Ann NY Acad Sci 1533:16–37.
Tu MC, Lillywhite HB, Menon JG, Menon GK. 2002. Postnatal ecdysis establishes the permeability barrier in snake skin: new insights into barrier lipid structures. J Exp Biol 205: 3019–30.
Umeda Y, Ishii M, Yoshioka M, Shimomura Y, Tomiyama T. 1996. Supporting conceptual design based on the function-behavior-state modeler. AIEDAM 10:275–88.
Umeda Y, Takeda H, Tomiyama T, Yoshikawa H. 1990. Function, behaviour, and structure. Applications of artificial intelligence in engineering V. p. 177–93.
Vermaas PE, Dorst K. 2007. On the conceptual framework of John Gero's FBS-model and the prescriptive aims of design methodology. Design Studies 28:133–57.
Villacís Núñez CN, Ray AP, Cooper KL, Moore TY. 2022. Metatarsal fusion resisted bending as jerboas (Dipodidae) transitioned from quadrupedal to bipedal. Proc R Soc B 289:20221322.
Vincent JFV, Bogatyreva OA, Bogatyrev NR, Bowyer A, Pahl A-K. 2006. Biomimetics: its practice and theory. J R Soc Interface 3:471–82.
Walker JA. 2007. A general model of functional constraints on phenotypic evolution. Am Nat 170:681–9.
Wanieck K, Fayemi P-E, Maranzana N, Zollfrank C, Jacobs S. 2017. Biomimetics and its tools. Bioinspired Biomim Nanobiomaterials 6:53–66.
West-Eberhard MJ. 1989. Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst 20:249–78.
Yen J, Weissburg MJ, Helms M, Goel AK. 2011. Biologically Inspired Design: a Tool for Interdisciplinary Education. Biomimetics: Nature Based Innovation. Boca Raton, FL: CRC Press, Taylor & Francis Group.