Bridging Evolutionary Biology and Developmental Psychology:

Towards an Enduring Theoretical Infrastructure

Abstract

Bjorklund synthesizes promising research directions in developmental psychology using an evolutionary framework. In general terms, we agree with Bjorklund: evolutionary theory has the potential to serve as a metatheory for developmental psychology. However, as currently used in psychology, evolutionary theory is far from reaching this potential. In evolutionary biology, formal mathematical models are the norm. In developmental psychology, verbal models are the norm. In order to reach its potential, evolutionary developmental psychology needs to embrace formal modeling.

MAIN TEXT

"I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics; for men thus endowed seem to have an extra sense" – Charles Darwin, 1828-1831, *Autobiography*

Although Bjorklund notes the importance of mathematical modeling, we believe this point deserves more emphasis. A strong, enduring metatheory *requires* mathematical foundations (Shou, Bergstrom, Chakraborty, & Skinner, 2015). In this commentary, we argue that models are essential to building an enduring bridge between evolutionary biology and developmental psychology.

Models are tools for thinking

Natural language is ambiguous. Therefore, ideas stated verbally are often imprecise. Formalizing ideas means describing them in mathematical or logical terms. Doing so often reveals ambiguities in verbal arguments and gaps in our assumptions. Once we clarify our assumptions, we can determine their consequences, including predictions. In some cases, models reveal that our ideas are logically incoherent. That is, our predictions do not follow from our assumptions. In other cases, they show that our predictions are only coherent under specific conditions. Models are tools for thinking. Although we educate ourselves and train students in methodological and statistical tools, we invest less in theoretical ones (e.g., formalizing ideas) (Borsboom, 2013; Farrell & Lewandowsky, 2010; Gigerenzer, 1998; van den Bos & Eppinger, 2016). Why should our field have lower standards for theory than for empirics?

To illustrate: a widespread claim is that natural selection favors the development of fast life histories—characterized by early onset of reproduction, a large number of offspring, high levels of risk taking and impulsivity, and so forth—in harsh and unpredictable environments. Harshness here refers to age-specific rates of death and disability beyond individuals' control (e.g., infectious disease), and unpredictability to random variation in harshness over space and time (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Frankenhuis Panchanathan, & Nettle, 2016). Although certainly thoughtful, such definitions do not do justice to the complexity of biology. For example, modeling shows that spatial vs. temporal environmental variation in harshness can favor the evolution of distinct life histories, as can different rates of temporal variation (i.e., fast vs. slow relative to the lifespan of individuals) (Ellis et al., 2009; Frankenhuis, Panchanathan, & Belsky, 2016). Moreover, different definitions of harshness (e.g., resource scarcity vs. mortality rates) can even favor opposite life-history trajectories (Baldini, 2015). Models further suggest that it is only adaptive to tailor development to some specific 'future' level of harshness in predictable environments. With high or even moderate unpredictability, early life provides a poor 'weather forecast' of future conditions, especially in long-lived organisms such as humans (Nettle, Frankenhuis, & Rickard, 2013; for discussion, see Del Giudice, 2014).

Formal theory in biology

In biology, formal theory tackles such complexity by developing families of models and exploring their consequences. By approaching the same question from different angles, families of models reveal useful generalizations, alongside specific predictions in particular conditions. Evolutionary developmental psychology needs to embrace this complexity by representing the full richness of models from biology and developing its own models of human development. Bjorklund's paper is rife with intriguing ideas that are ready to be modeled. For instance, we can model Geary's (2005) hypothesis that constraints on cognitive mechanisms should be weaker, and the effect of experience greater, in more heterogeneous environments. This would require clarifying concepts such as 'constraint' and 'environmental heterogeneity'. Or we can model how natural selection shapes probabilistic cognitive mechanisms (Bjorklund, Ellis, & Rosenberg, 2007) for solving a specific developmental challenge (e.g., learning about dangerous animals), depending on the statistical structure of the environment. Or we can model the conditions in which natural selection favors a prolonged childhood or cognitive immaturity, as it has in humans (Bjorklund & Green, 1992; Oppenheim, 1981; Piantadosi & Kidd, 2016). Because there has been so little modeling in evolutionary developmental psychology, many of its central ideas still await formalization. We see this as an exciting niche for future research.

Even simple models can provide useful insights. For instance, they reveal that if an environment varies spatially (i.e., each individual is born into one of many possible locations), long-term fitness depends on a sum of fitness across locations. In contrast, if an environment varies temporally (i.e., it cycles through one of many possible states), long-term fitness depends on fitness at time 1 multiplied by fitness at time 2, and so forth. Values of zero have less impact in addition than multiplication, where they collapse the entire series. Therefore, temporal variation is more likely to favor developmental mechanisms that avoid low fitness in 'bad years', even at a cost to fitness accrued in 'good years'. For example, rather than producing offspring that are well-suited to one environmental state, parents might produce offspring that are developmentally plastic, allowing offspring to match their phenotypes to local conditions. Alternatively, parents might produce offspring that have different phenotypes, so that some offspring will always match the current conditions (Frankenhuis et al., 2016). Such basic principles are immediately apparent in simple models, but are not obvious in verbal theorizing.

Formal models come in different flavors. Some models are general: they improve our understanding of qualitative features, but their parameters are not easy to measure and they do not make quantitative predictions. For instance, the Hawk-Dove game (Maynard Smith & Price, 1973), even in its simplest form, has provided deep insights into the logic of animal conflict, and has spurred empirical research in biology, psychology, economics, and other fields. Other models are specific: they are based on the details of a particular system, their parameters are measurable, and they make quantitative predictions (Houston & McNamara, 2005, Parker & Maynard Smith, 1990). Specific models considerably benefit from empirical research by integrating its findings as constraints (e.g., focusing on measured values of a variable instead of exploring all possible values). All models are too simple to accurately represent the real world. Yet, this is no defect. Models are like maps: by leaving out unnecessary detail, they uncover patterns that would otherwise escape our understanding.

Towards synergy

The question remains: *how* can we efficiently move towards synergy with evolutionary theory? Non-modelers need to appreciate the value of modeling, and become savvier consumers of formal models. Modelers, in turn, need to ensure that their work keeps up with new conceptual developments and state-of-the-art empirical knowledge. They should also better explain the value and limitations of their approach. Any verbal idea can be modeled in multiple ways (e.g., environmental variation can be structured on different spatial and temporal scales). Although a single model may serve as a proof of principle (e.g., trait X can evolve in a subset of conditions), it only allows inferences when its assumptions hold. The art of modeling consists in making assumptions that capture key aspects of reality relevant to a particular question, while remaining as simple as possible (Epstein, 2008; Kokko, 2007).

Models can be criticized for failing to capture key aspects of reality, but not for making assumptions precise and explicit (Smaldino, 2017). Although general verbal statements are tempting, the illusion of generality stems from lack of transparency about assumptions. Closer inspection often reveals their inaccuracy across a wide range of conditions (i.e., trait X is only adaptive in conditions Y), and in some cases exposes logical incoherence (i.e., trait X is never favored by natural selection). In this way, models shed light on the plausibility of ideas.

Formalization increases precision and transparency. In this sense, our plea for modeling dovetails with recent efforts towards improving the reliability of psychological science (Chambers, 2017; Morey et al., 2016; Munafo et al., 2017; Nosek & Lakens, 2014). Precise assumptions allow us to transparently deduce predictions. In contrast, reliance on verbal theorizing hinders our ability to know which ideas are worth pursuing. Just as buyers of used cars cannot distinguish between dependable vehicles and lemons when car dealers withhold relevant information (Akerlof, 1970), buyers of informal theory cannot differentiate between empirically plausible ideas and logically incoherent ones (Vazire, 2017, applies the same analogy to lack of transparency in empirical research). As a consequence, ideas that vary in quality receive equal empirical stage-time, hindering the efficiency of science. Formal models provide one solution to these problems by allowing us to 'look under the hood' of ideas. Without them, we are left guessing whether an idea will run reliably for 50,000 miles, wither in the rain, or explode upon one turn of the ignition key.

Concluding remarks

We share Bjorklund's enthusiasm for the future of evolutionary developmental psychology. The field has made progress on many questions and is becoming increasingly integrated with other approaches. Although these accomplishments deserve praise, our field has substantial room for improvement. In the future, we envision a developmental psychology in which evolutionary ideas are formalized and held to the same standards as those in biology (or better still). Achieving this goal will require evolutionary developmental psychologists to embrace formal theory, as well as invest in training the next generation of scholars to use and understand formal modeling tools. For interested readers, we recommend a number of resources that serve as friendly starting points for learning about theory and modeling in evolutionary biology in the suggested reading list at the end of this commentary.

Building a metatheory is a daunting task (Badcock, 2012; Geary & Bjorklund, 2000; Ploeger, Van Der Maas, & Raijmakers, 2008). Over 150 years ago, Charles Darwin (1859) prophesized that psychology would be built on an evolutionary foundation. Bjorklund's article represents another step towards this synthesis. Grounding our metatheory in mathematics will allow us to take the fast lane, avoiding winding roads and dead ends in the process. By doing so, we will do more than build a bridge between developmental and evolutionary psychology. We will build multitudes of bridges, connecting psychology with all fields that have mathematical metatheories. Together, these will constitute a path towards consilience, the integration of all sciences (Wilson, 1998).

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Suggested reading list

Otto, S. P., & Day, T. (2007). *A biologist's guide to mathematical modeling in ecology and evolution* (Vol. 13). Princeton University Press. Marches readers through the modeling process, starting with conceptual models and advancing to cutting-edge formal models.

Kokko, H. (2007). (See References). A gentle introduction to various modeling approaches in evolution and ecology. Provides programming code to facilitate understanding.

McElreath, R., & Boyd, R. (2008). *Mathematical models of social evolution: A guide for the perplexed*. University of Chicago Press. An outstanding primer on mathematical theories of social behavior.

Mangel, M., & Clark, C.W. (1988). *Dynamic modeling in behavioral ecology*. Princeton, NJ: Princeton University Press. A challenging but excellent introduction to state-dependent optimality modeling.

Frankenhuis, W. E., Panchanathan, K., & Barrett, H. C. (2013). Bridging developmental systems theory and evolutionary psychology using dynamic optimization. *Developmental Science*, *16*, 584-598. An accessible introduction to state-dependent optimality modeling tailored to psychologists. DOI: 10.1111/desc.12053

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