

## CHAPTER 2

# The Evolutionary Context of Personality Development

Marco Del Giudice

Studying the development of personality means grappling with some of the deepest and most fundamental questions about human nature. Why are we so different from one another? Where do our desires, goals, and values come from? Is our development shaped by external forces or guided by internal dispositions? And what does it mean to be an individual in the first place? To answer these questions we need the most powerful tools we can find, and when the goal is to understand biological organisms like ourselves, no single tool has proven more powerful than evolutionary theory.

Traditionally, psychology has sought to describe the neural and mental mechanisms that control behavior, understand how they work, and track their development across the life course. Questions that focus on mechanism and development are of the *proximate* kind—they describe organisms as we see them in the present, and deal with the immediate causes and consequences of behavior. While the proximate view is extremely important, it fails to address another, equally important question: *Why* do those mechanisms work and develop the way they do? Or, why did the version we observe today win out in the perpetual game of variation and selection that drives evolutionary change? Evolutionary theory provides an “ultimate” perspective on psychological mechanisms by focusing on their *adaptive* function, that is,

their eventual contribution to genetic replication (see below). In addition, *phylogenetic* questions address the emergence and transformation of those mechanisms over deep evolutionary time, including their variation between closely and distantly related species. The ultimate level of analysis complements and illuminates the proximate one; the four questions of biology—mechanism, development, adaptation, and phylogeny—must be asked in combination if we seek to fully explain a biological system (Scott-Phillips, Dickins, & West, 2011).

The application of evolutionary concepts to the human mind and behavior is the domain of *evolutionary psychology* (see Buss, 2015a, for an introduction and Buss, 2015b, for an in-depth account). Properly understood, evolutionary psychology is a general framework for the study of behavior rather than a specific set of models and hypotheses. If one accepts the idea that humans and their brains are biological entities produced by natural selection, then any realistic science of behavior *has* to be grounded in evolutionary principles. This is why evolutionary psychology is not just another item in the familiar menu of psychological “schools,” but a genuine *metatheory* for the discipline as a whole (Durrant & Ellis, 2012; Tooby & Cosmides, 2015).

Unfortunately, the two subdisciplines of personality and developmental psychology—the

main tributaries of personality development—have been particularly reluctant to embrace evolutionary thinking, as compared, for example, with social and cognitive psychology. To compound the problem, evolutionary psychology throughout the 1990s had a strong emphasis on universal mechanisms—the invariant “design specs” of the human mind—and a tendency to neglect individual differences or regard them as relatively unimportant. In addition, most researchers paid relatively little attention to developmental issues and focused on the adaptive problems of adult individuals, such as foraging and mate selection. The good news is that things have changed rapidly and dramatically over the last two decades. The evolution of personality has become a major focus of interest in both biology and psychology (Buss & Hawley, 2011; Carere & Maestriperi, 2013). At the same time, more researchers have started to integrate the evolutionary and developmental levels of analysis, and evolutionary–developmental psychology is now a thriving subfield (Bjorklund & Ellis, 2014; Ellis & Bjorklund, 2005). While there is still much work to do, the foundation is solid enough to support a biologically informed science of personality development.

In this chapter, I set the development of personality in the broader context of human evolution, and show how an evolutionary approach illuminates important questions and helps integrate findings across disciplines and levels of analysis. In doing so, I aim to convey a sense of the big picture, stimulate reflection, and provide pointers to the literature for the interested reader. I begin the chapter by introducing key evolutionary concepts and outlining some important aspects of the ecology of our species, the ape *Homo sapiens*. I then apply those concepts to three foundational issues: the nature of motivation, the nature of variation, and the nature of development. For each of these topics I present a selection of notable contributions and insights, and discuss their implications for the study of personality development.

## Key Evolutionary Concepts

### *Natural Selection and Adaptation*

The concept of natural selection lies at the core of evolutionary biology. Simply stated, Darwin’s insight was that organisms compete for reproduction in a world of limited resources, so that the traits of those organisms who leave

more descendants spread in the population and eventually replace other variants. As long as new variation is produced (e.g., by genetic mutations), this selection process results in organisms that are increasingly better adapted to their environment—for example, more capable of surviving (at least until reproduction); harvesting energy; and outcompeting other organisms, including conspecifics, prey, predators, and pathogens. Evolution never stops because the environment does not remain static and includes other organisms that also keep changing via selection. A trait can be *adaptive*, *maladaptive*, or *neutral* depending on whether its net effect on an individual’s relative reproductive success (*fitness*) is positive, negative, or null. Over many generations, natural selection results in the gradual evolution of complex mechanisms—organs such as the eye or the liver, behaviors such as predation strategies and mating rituals. In this way, biological mechanisms acquire the appearance of being designed in order to serve specific functions (e.g., pumping blood is the key function of the heart), even though they have been produced by a fundamentally blind and impersonal process. Mechanisms that evolved because of their positive effects on fitness are labeled *adaptations* (Durrant & Ellis, 2012; Tooby & Cosmides, 2015).

The ultimate currency of Darwinian selection is an organism’s number of descendants (relative to others in the population): thus, the function of traits and adaptations can be ultimately linked—even if indirectly—to the organism’s reproduction. Survival is often emphasized in popular discussions of evolution; however, surviving is only useful insofar it leads to reproduction, and many organisms forgo survival in exchange for reproductive opportunities (the male praying mantis offers a memorable example). In organisms that reproduce sexually, there is strong selection for traits that increase mating success by making individuals more attractive or more able to compete with rivals (*sexual selection*). Sexual selection may produce traits that are costly and extravagant (e.g., the peacock’s tail), and often drives the evolution of morphological and behavioral differences between males and females (Stanyon & Bigoni, 2014).

### *Adaptations, Byproducts, and Noise*

While selection is the main driver of evolution and adaptation is ubiquitous in nature, it is im-

portant to stress that not all traits are adaptive. Many traits are byproducts of adaptations—for example, the white color of bones is not an adaptive feature but a byproduct of the chemical composition of bone tissue. Other traits may be neutral or arise from random “noise.” Under certain conditions, even maladaptive traits can spread, especially in small populations. Finally, selection always interacts with all sorts of constraints, from the laws of physics and chemistry to trade-offs between competing functions and adaptations (e.g., lighter bones help an animal move faster but are also more fragile).

### ***Inclusive Fitness***

The classic Darwinian account of natural selection is based on an individual’s relative number of descendants. While this approach can explain a lot about the design of organisms, it cannot explain the evolution of altruistic behaviors that reduce an individual’s reproductive success while increasing that of another. From the standpoint of individual fitness, true altruism of the fitness-reducing kind should never evolve, although there is still room for cooperation and *reciprocal altruism*—that is, behaviors that ultimately increase the fitness of both actors involved (e.g., teaming up to hunt bigger prey; exchanging favors). The solution to this thorny problem was provided by William Hamilton (1964), whose crucial insight was that individuals do not replicate across generations—instead, what is ultimately replicated is their *genes*, defined broadly as units of inheritance rather than segments of DNA. Genes within an individual can maximize their own replication (i.e., their share of *descendants* in the population gene pool) by improving not only the reproductive success of that particular individual but also that of other individuals who are likely to carry the same genes. The probability of carrying the same genes is instantiated by the *relatedness* between two individuals, which is highest between close relatives but can vary systematically across different groups of people within a population (e.g., one’s own tribe vs. neighboring tribes).

The implication of Hamilton’s work is that natural selection does not maximize individual fitness, but a more complex quantity called *inclusive fitness*. Inclusive fitness reflects the joint effects of an organism’s behavior on its own reproduction *and* the reproduction of related individuals. The framework of inclusive

fitness accommodates all sorts of social interactions between individuals: selfishness and competition, reciprocal cooperation, altruism, and even *spite*—actions that reduce one’s reproductive success but impose an even larger penalty on that of other, negatively related individuals. Selection can favor any of these social patterns depending on the exact balance of costs, benefits, and relatedness that applies to a given situation (Bourke, 2011). Inclusive fitness theory (also known by the less accurate label of *kin selection*) lies at the foundation of the modern understanding of social evolution. When populations include multiple groups that compete with one another for resources and (ultimately) reproduction, another way to understand the logic of social evolution is to separate the individual consequences of behavior from those that impact the entire group. In general, selection between groups favors altruism between group members, but this force is opposed by selection for individual selfishness within each group. This approach is known as *multilevel* or *group selection*. Since inclusive fitness theory centers on the individual and does not explicitly consider the hierarchical structure of the population, multilevel selection is often presented as an alternative theory of evolution. In fact, inclusive fitness and multilevel selection are two equivalent ways to describe the same underlying theory—a theory that provides an elegant, powerful explanation of the interplay between cooperation and competition in the biological world (West & Gardner, 2013).

### ***Parent–Offspring Conflict***

An especially striking illustration of this interplay is *parent-offspring conflict* (Trivers, 1974), which arises because siblings in sexual species are only moderately related (i.e., genetically similar) to one another. This basic fact limits the optimal degree of biological altruism between siblings; each offspring should try to obtain a larger share of the parents’ investment of food, protection, and other resources, whereas parents benefit by distributing their investment equally among their offspring (all else being equal). As a result, the amount of investment in each offspring that would maximize the parents’ inclusive fitness is lower than the amount that would maximize the offspring’s fitness. Selection then acts on offspring so they will try to obtain more investment for themselves, and on parents, so that they will curtail their altruistic

investment to some extent. These divergent selection pressures create a cascade of systematic tensions in family relations and counter their inherently altruistic quality. Parent–offspring conflict has far-reaching implications for many aspects of development, from physiological interactions between mother and fetus during pregnancy to differences between parents and adult offspring in the characteristics they value most in the offspring’s romantic partners (see Schlomer, Del Giudice, & Ellis, 2011).

### ***The Gene’s-Eye View of Evolution***

Arguably, the most important implication of inclusive fitness theory is that selection favors traits that maximize the replication of an organism’s genes (Grafen, 2007). This makes it possible to understand the evolution of individual and social behavior by taking the “gene’s-eye view,” that is, by considering the impact of behavior on the replication of genes rather than on the reproduction of individuals. This hugely counterintuitive perspective shift is the rationale for Richard Dawkins’s much misunderstood point that genuinely altruistic behavior between *individuals* can emerge from the competition between *genetic variants* that are selected to replicate as much as possible within the population, and for this reason can be figuratively described as “selfish” (Dawkins, 1976).

### ***Intragenomic Conflict***

The ramifications of the gene’s-eye view of evolution extend beyond social interactions. As a rule, genes within an individual have the same biological interest because they share a common destiny—that is, they have the same chance of ending up in that individual’s offspring. This rule is sufficiently valid that one can calculate a single fitness for the individual as a whole; however, this approximation hides a lot of interesting detail and some important exceptions. Sex chromosomes, for instance, replicate at different rates depending on the sex of the offspring. Moreover, some genes are expressed only (or at higher rates) if they are inherited from a specific parent, the father or the mother. Differential expression is achieved through an epigenetic mechanism known as *genomic imprinting*. Imprinted genes have different coefficients of relatedness with paternal versus maternal relatives, and their interest may diverge quite a bit from that of the individual. For example, pater-

nal genes (or, more precisely, imprinted genes that are expressed when they are inherited from one’s father) are predicted to “side” with the offspring and against the mother in parent–offspring conflict, whereas maternal genes should evolve so as to counteract this effect (Kramer & Bressan, 2015; Schlomer et al., 2011). These and other cases of *intragenomic conflict* make it clear that from the standpoint of natural selection, individuals are not unitary but represent a compromise among a multitude of genetic factions engaged in various forms of cooperation and conflict. What’s more, conflicts within the genome are likely to translate into conflicts for the control of the individual’s behavior—and, not coincidentally, many imprinted genes are highly expressed in the brain.

In total, the picture painted by modern evolutionary theory is one in which conflict, cooperation, and altruism evolve in a complex and shifting interplay, which can be ultimately understood through the lens of genetic replication. With few and unusual exceptions, evolution does not lead to purely cooperative relationships; conflicts of interest easily creep in—even between parents and their offspring, and even between cells and genes of the same individual.

### ***Testing Evolutionary Hypotheses***

When researchers formulate hypotheses about the adaptive function of a trait (or the lack thereof), they inevitably make inferences about the past history of that trait and its contribution to fitness—often in environments that have long disappeared. It follows that, generally speaking, evolutionary hypotheses cannot be tested directly but only through the accumulation of convergent indirect evidence from multiple sources. This does not mean that adaptive hypotheses are unfalsifiable. To begin, they can be used to derive novel predictions that can then be tested with standard psychological methods. In addition, researchers can use mathematical models of the evolutionary process to gain insight into the plausibility of alternative hypotheses and work out their assumptions and implications. Other common sources of evidence employed by evolutionary scholars include cross-cultural research (including studies of forager populations), phylogenetic comparisons with other species, and genetic studies. Researchers may also attempt to measure the fitness contribution of a trait, although past effects on survival and reproduction may be obscured

by recent social and technological changes (e.g., contraception). The methodology of evolutionary psychology is a complex topic that defies a short summary; for more in-depth discussion, see Andrews, Gangestad, and Matthews (2002), Schmitt and Pilcher (2004), and Simpson and Campbell (2015).

### Human Ecology

Humans separated from the lineage of chimpanzees 5–7 million years ago and evolved as hunters and gatherers for the past few million years, until the invention of agriculture around 12,000 years ago. Our distant ancestors migrated out of Africa in multiple waves, adapting to a striking range of environments and ultimately settling the entire planet. The behavioral flexibility of our species and its capacity to generate complex, divergent cultural traditions clearly played a major role throughout its evolutionary history. Without any pretense of completeness, in this section, I introduce two related ideas that illuminate important aspects of human nature and are particularly relevant to personality development: the concept of the *human adaptive complex* and that of the *cognitive niche*.

#### *The Human Adaptive Complex*

The human adaptive complex, shorthand for a unique set of interlocking traits that evolved in our species (Kaplan, Gurven, & Lancaster, 2007; Kaplan, Hill, Lancaster, & Hurtado, 2000), is founded on the sophisticated foraging techniques that enabled us to exploit high-quality, energy-rich food sources such as large game, shellfish, and roots. These techniques involve the use of manufactured tools (cutting and excavation tools, bows and arrows, fishing nets, etc.), learning-intensive skills, and sustained cooperation between group members. The key requirements for such intensive learning are a large brain and a long, slow developmental trajectory, with an extended phase of dependence before sexual maturity. At the same time, large, slow-developing brains require massive amounts of energy, which is provided by high-quality food items and buffered by a multigeneration system in which resources flow from grandparents to parents to children. The economics of human development is also highly dependent on the shared contribution of mothers and fathers, which in turn is supported by long-term bonds between sexual partners (typi-

cally in the form of marriage). Finally, protection by parents and food sharing between kin and cooperative partners contribute to substantially reduce child mortality, thus making slow development and extended dependency viable options. The traits that make up this complex enable and reinforce each other, and could not have evolved in isolation.

The human adaptive complex paints a picture of unusually high cooperation at multiple levels, from parental couples to extended kin networks to broader social groups (Bowles & Gintis, 2011). Indeed, the social organization of our species for the last 200,000 years—and before the demographic explosion kickstarted by agriculture—was defined by a hierarchy of social units nested within each other, from small bands of 30–50 people to tribes of perhaps 1,000 or 2,000 individuals with various degrees of relatedness (Dunbar, 1993). The scale and quality of human cooperation have far-reaching implications for psychological evolution. To begin, our social life involves a delicate and complex balance between “getting ahead” and “getting along”—between gaining individual power and advantages on the one hand, and avoiding rejection and ostracism on the other. Also, getting to the top of social hierarchies—whether peacefully or by force—is rarely possible without building alliances and reciprocal exchanges. This dynamic tension between cooperation and competition sets the stage for the evolution of our sophisticated social intelligence, which in turn depends on a multitude of psychological processes and adaptations, from empathy and “theory of mind” to Machiavellian strategizing (Dunbar & Schultz, 2007).

#### *Dual-Status Hierarchies and Social Selection for Altruism*

The ubiquity of reciprocity and cooperation also explains the dual nature of human competition for status. In many animals, status is mainly determined by *dominance*—the ability to control others with the threat of physical force. In cooperative species, however, status can also be gained by possessing skills, abilities, and knowledge that make one a valuable social partner. This kind of freely conferred status based on admiration rather than fear is captured by the term *prestige* (Henrich & Gil-White, 2001). The duality of dominance and prestige means that human groups allow for multiple kinds of potentially successful social roles. In turn, a multiplicity of social roles creates divergent

selection pressures for a broad range of personalities, as well as different combinations of prosocial and coercive strategies for competition (Hawley, 2014). The evolutionary dynamics set in motion by extended cooperation include the possibility of self-reinforcing *social selection* for altruistic traits. Social selection, a process analogous to sexual selection, depends on being chosen as a social partner rather than a sexual one. If people rely on credible displays of altruism and generosity when they select their cooperation partners, these traits will spread in the population and become more common, in spite of their costs for the individual. Social selection likely contributes to explain our partial but still remarkable disposition to behave altruistically toward other group members (Nesse, 2007). It also provides another striking illustration of how selfish selection processes can drive the evolution of genuinely altruistic behaviors. Finally, one should not neglect the dark side of cooperation and altruism: Aggression and war between enemy groups—which are sustained by extensive cooperation and even self-sacrifice within each group—have been a constant of human societies since the dawn of time (Pinker, 2011).

### ***The Cognitive Niche***

The evolution of language—another defining adaptation of our species—permits the exchange and transmission of information on an unprecedented scale. Language and the cooperative exchange of information have entrenched humans in the cognitive niche: a unique foraging niche in which problem solving based on cause–effect reasoning, transmitted information, and social coordination are used to overcome other organisms’ defenses in order to feed on them (e.g., building traps and weapons for hunting; cooking and processing plants to detoxify them; Pinker, 2010). As inhabitants of the cognitive niche, we depend critically on the transmission and accumulation of massive amounts of information and know-how. Over time, we have evolved a truly amazing range of information-sharing devices, from innate mechanisms, such as imitation, to recent technological innovations, such as drawing and writing. These devices sustain the creation of cultures—cumulative repositories of knowledge, behavioral rules, norms, and institutions. In traditional societies, a great deal of this transmission work is accomplished by storytelling, a biologically based ability whose importance is

hard to overstate (Scalise Sugiyama, 2011). As discussed in Part IV of this volume, our propensity to organize the world into memorable narratives has wide-ranging implications for the way we think about our own lives and present ourselves to others.

### ***Recent Social Evolution***

The evolutionary dynamics that accompanied our entrance in the cognitive niche have undergone a sudden acceleration with the invention of agriculture and the emergence of large-scale, stratified societies over the past few thousand years. Among the many consequences of the agricultural revolution, one is especially important from the standpoint of personality development: the explosive increase in the number of highly specialized social, technological, and cognitive roles within a society—farmers, herders, merchants, soldiers, priests, artists, builders, teachers, and so forth. Each social niche in this ever-expanding menu entails not only a particular set of skills but also a best-fitting range of interests and personality traits. The demands of farming have likely amplified selection for average levels of conscientiousness and self-control (Cochran & Harpending, 2009). However, our recent social evolution may have had an even more important outcome, namely, a marked increase in the *diversification* of individual personalities (Figueredo et al., 2005). Intriguingly, the only detailed study of personality in a population of foragers who practice low-level agriculture—the Tsimane of Bolivia—has found evidence of two broad personality factors of “prosociality” and “industriousness” instead of the customary Big Five. These factors are largely composed of agreeableness and conscientiousness items, mixed with facets of extraversion and openness to experience (Gurven, von Rueden, Massenkov, Kaplan, & Lero Vie, 2013). There is also cross-cultural evidence that correlations among the Big Five decrease as societies become more complex, consistent with the idea that individual personalities become more diversified (Lukaszewski, Gurven, von Rueden, & Schmitt, 2017).

### **The Nature of Motivation**

#### ***Functional Specialization***

While maximizing inclusive fitness can be legitimately described as the ultimate biological goal of all organisms, it is impossible for

individuals to *directly* increase their fitness. Instead, what organisms face is a set of basic tasks—surviving, growing, reproducing—that in turn have to be met by successfully solving a host of narrower problems: finding and choosing food, avoiding parasites and pathogens, securing suitable sexual partners, feeding and protecting the offspring, and so on. In highly social species, these problems are compounded by other unique challenges—for example, improving and defending one’s status, finding and choosing cooperation partners, and avoiding exploitation by other individuals. Living in the cognitive niche, humans must deal with still other tasks that have to do with gathering and transmitting information, learning and teaching one’s culture, and negotiating the difficult balance between conformity and innovation.

Each of the adaptive problems I just listed implies a different set of goals and requires a different type of solution. A good food item and a good partner have totally different characteristics; the behavioral strategies that work best to become a dominant individual are not helpful in avoiding infectious diseases. Whereas some domains (e.g., mating and courtship) admit a large amount of trial-and-error learning, others (e.g., avoiding toxic foods and deadly predators) are much less forgiving of mistakes. For all these reasons, selection tends to favor the evolution of multiple mechanisms for the control of behavior—much like distinct mental “organs,” each specialized for dealing with a certain kind of domain. Functional specialization (often discussed as *modularity* or *domain specificity*) promotes efficiency in dealing with the environment, confers robustness on the mind as a whole, and allows selection to fine-tune each mechanism without affecting the functionality of the others (Barrett, 2015; Tooby & Cosmides, 2015). While some general-purpose processes such as reinforcement learning or working memory can be shared or reused by multiple psychological mechanisms, each mechanism is specifically attuned to a certain kind of input (e.g., potential sexual partners) and employs criteria and rules of operation that are at least in part innate. From another perspective, evolved mechanisms incorporate implicit knowledge that has been accumulated over millions of years, and that in many cases would be too hard, too costly, or too dangerous to relearn from scratch in each new generation. Of course, innate predisposition are often supplemented, refined, and modified by learning: Infants react

automatically to bitter flavors (i.e., potentially toxic foods) with intense disgust, even if later on they learn to enjoy many of the same flavors. Specialization and learning are not antithetical—on the contrary, they are both the product of natural selection and represent two sides of successful adaptation.

### *Motivational Systems*

*Motivational systems* are the specialized systems that regulate goal-directed behavior. A vital motivational system is the one that controls the intake of energy and nutrients through hunger and eating; other systems of this kind regulate water intake (thirst and drinking), body temperature (seeking colder or warmer places), and so on. Survival-related motivations include *fear* and *aggression* systems designed to escape imminent threats and/or fight back against attackers; *behavioral inhibition* and *security* systems designed to deal with potential danger, with anxiety rather than fear as their core emotion; and a *disgust* system, whose main goal is avoidance of pathogens and toxic substances (Corr, DeYoung, & McNaughton, 2013; Curtis, 2011; Woody & Szechtman, 2011). Each of these systems is defined by not only a set of goals but also specific inputs that assess the organism’s state (e.g., blood glucose, stomach fullness), sensations and emotions that signal success or failure (e.g., satiety vs. hunger), and specific physiological and behavioral outputs designed to reach the system’s goals and overcome potential obstacles. Motivational systems depend on specialized neural circuits; however, the neural pathways that serve different systems often overlap to some extent (e.g., sensors of stomach fullness provide inputs to both the hunger and thirst systems). Crucially, biological goals do not have to be consciously represented for the system to work. A person disgusted by rotten food does not need to know anything about microbes; a distressed infant does not need to know in any conscious sense that the function of crying is to maintain proximity with the mother. In this sense, the implicit goals of motivational systems are distinct from the deliberate, planful goals emphasized in McAdams’s model of personality development (McAdams, 2015, and Chapter 1, this volume).

The logic of functional specialization applies just as well to social adaptive problems. Evolutionary psychologists and neurobiologists have described a variety of motivational systems that

regulate social interactions. These include an *attachment* system that promotes contact with (and availability of) one's caregivers and a complementary *caregiving* system that promotes nurturance and protection of one's offspring; a *mating* system that regulates sexual attraction and courtship; a *status* system that mediates interactions based on dominance and prestige; a *reciprocity* system that deals with reciprocal exchanges and the risk of cheating; and *affiliation* and *pair-bonding* systems that underlie close relationships with long-term sexual partners, friends, and select group members. Other likely candidates for autonomous motivations are *play*, *curiosity*, and *acquisition* (Aunger & Curtis, 2013; Del Giudice, 2018; Toronchuk & Ellis, 2013).

Note that different authors in this area may use somewhat different labels to describe the same system; also, there are often multiple ways to draw the boundaries between functionally related systems, as their behavioral and neural correlates overlap to a significant degree. For example, one can legitimately distinguish between a fear and aggression system, but also frame them as part of a unitary "fight-or-flight" system. Similarly, attachment, affiliation, and pair-bonding share many of the same emotions, behaviors, and neurobiological substrates (e.g., molecules such as oxytocin, dopamine, and endogenous opioids) (Feldman, 2017; Machin & Dunbar, 2011). This is not a limitation of the model but a predictable consequence of the evolutionary process—new mechanisms are not built from scratch but emerge as modified and differentiated versions of existing ones (Barrett, 2015). For example, affiliative behaviors seem to ultimately originate from mother–infant bonds but have been adapted and differentiated over time to serve a multiplicity of relationships with other social partners. The result is an organic network of partially overlapping systems rather than a rigid division between independent, self-contained units.

The model of motivation I just sketched is remarkably rich, especially compared with alternative accounts that depend on domain-general processes (e.g., reinforcement learning) or focus on a small set of abstract, general goals. A notable example of the latter is *self-determination theory* (Deci & Ryan, 2000; Sheldon & Schuler, Chapter 16, this volume), a model that explains psychological motivation in terms of three universal needs—competence, autonomy, and relatedness—and frames the ultimate goal of be-

havior in terms of subjective well-being rather than biological fitness. While concepts such as autonomy and self-determination are psychologically meaningful, one can debate whether they represent specific evolved goals, or rather emerge from more fundamental biological motivations (e.g., status, mating) in combination with the human capacity for deliberate self-regulation and self-representation—including the ability to mentally simulate oneself in future scenarios (see Kenrick, Griskevicius, Neuberg, & Schaller, 2010). Clearly, there is still much work to do before we fully understand how motivational systems interact with other psychological mechanisms to construct our multifaceted sense of identity. Still, analyzing human motivation from the standpoint of multiple fitness-relevant goals can yield many fascinating insights, as illustrated by Kenrick and colleagues' evolutionary revision of Maslow's classic "pyramid of needs."

#### *Motivation, Values, and Self-Esteem*

An important implication of adopting a rich model of motivation is that moral values can be framed naturally as extensions of basic motivational goals. When people reason about moral problems they typically rely not on abstract principles, but on a set of emotionally charged intuitions that revolve around a small number of fundamental themes (Haidt, 2007). For example, Jonathan Haidt (2012) has identified six such themes: fairness, avoidance of harm and pain, respect of authority, loyalty to the ingroup, and spiritual purity. It is easy to see how moral themes are rooted in particular motivational systems—reciprocity for fairness-based morality, caregiving for harm prevention, status for authority, affiliation for ingroup loyalty, and disgust for purity concerns. These functional links bring the study of motivation and that of morality under the same theoretical framework. Even more importantly, they suggest ways in which considerations of fitness costs and benefits can be used to illuminate the deeper logic of moral behavior. (For a detailed example, see Baumard, André, & Sperber's [2013] analysis of the evolution of fairness.)

From a similar perspective, self-esteem can be understood as the output of evolved assessment mechanisms that gauge the person's effectiveness in achieving key goals such as affiliation, status, mating, and reproduction (Kavanagh, Robins, & Ellis, 2010; Kirkpat-



rick & Ellis, 2001). By extending the sociometer theory (Leary, 2005) in light of functional specialization, this approach explains not only the multidimensional nature of self-esteem but also the existence of a global sense of value that may summarize the individual's overall fitness prospects (necessarily estimated from his or her success in pursuing narrow biological tasks). On this point, it is crucial to remember that selection maximizes *inclusive* fitness, and that inclusive fitness can be increased by helping relatives, providing benefits to group members, and so on. The fact that altruistic pursuits can boost self-esteem is definitely not in contrast with a sophisticated biological view of motivation.

### ***Cooperation and Conflict***

The interplay of cooperation and conflict pervades motivation at all levels of analysis. To begin, cooperation and conflict with social partners shape the design of motivational systems and associated cognitive processes. For example, evolutionary psychologists have documented how successful reciprocal exchanges require the ability to detect, avoid, and remember cheaters, and how these tasks rely on specialized mechanisms (Cosmides & Tooby, 2015). Different settings of these mechanisms carry different costs and benefits: A suspicious individual who responds to the slightest sign of exploitation will effectively avoid cheaters but also miss many opportunities for fruitful cooperation. Individual differences in the settings of motivational systems contribute to define broad personality traits such as the Big Five—for example, high trust and forgiving responses to exploitation are key aspects of agreeableness (Denissen & Penke, 2008). Motivational systems should also respond to differences in relatedness, systematically tilting the cost–benefit balance in favor of more closely related individuals. The same variables can be expected to indirectly influence moral judgments and decisions. Patterns of nepotism and ingroup favoritism are well documented in human societies; more subtly, our sensitivity to indicators of relatedness is revealed in the tendency to behave more altruistically with people who physically resemble us (e.g., DeBruine, Jones, Little, & Perrett, 2008). On an even broader scale, some evolutionary scholars have argued that morality itself can be understood as an evolved mechanism of conflict resolution and group coordination. Specifically, moral judg-

ments allow people to choose sides in disputes without forming rigid alliances and compromising the integrity of the group (DeScioli & Kurzban, 2013).

An evolutionary perspective highlights the fact that conflict plays a role not only in interactions with strangers, but also in the context of close family relationships. In particular, parent-offspring conflict inevitably shapes the functioning of the attachment and caregiving systems. Insecure attachment styles (Simpson & Jones, Chapter 15, this volume) are typically understood as responses to parents' sensitivity and emotional availability. From a complementary perspective, the behaviors of insecure children (e.g., clinginess, controlling aggression) can be seen as attempts to obtain more investment and care, even against the parent's best interest (see Simpson & Belsky, 2016).

In the model of motivation I sketched earlier, behavior is energized and controlled by a large number of goal-directed mechanisms, each with its own rules and priorities; this leads to the problem of how to manage the resulting patterns of cooperation and competition between different motivational systems. In many ways, how the brain arbitrates between multiple and often contradictory goals is still an open question. Motivational systems can achieve a certain degree of self-regulation by directly activating or inhibiting one another; for example, sexual arousal temporarily suppresses hunger, whereas extreme fear can trigger explosive aggression. However, the complexity of human behavior requires more sophisticated mechanisms of top-down control, including those known as *executive functions*, which range from relatively simple processes such as motor inhibition to high-level abilities such as planning and mental simulation. Executive functions play a crucial role in both cooperation and competition. For example, the ability to suppress immediate impulses is a requisite for all kinds of long-term cooperation; at the same time, inhibition is extremely useful to successfully manipulate others and avoid being manipulated (Barkley, 2012).

Conflict shapes motivational systems not only from the outside but also from within. Because of intragenomic conflicts, different sets of genes (e.g., maternal vs. paternal) may have divergent interests when it comes to the regulation of behavior. Hunger provides a simple but striking example of this dynamics. Since a hungry infant extracts more energy and nutrients

from the mother, one can predict that paternal genes expressed in the infant should evolve so as to increase hunger, whereas maternal genes should suppress it. This invisible tug-of-war should be played within the brain mechanisms that control the motivation to eat and the relevant behaviors (e.g., suckling). And indeed, infants who lack paternal genes because of chromosomal abnormalities (e.g., Prader–Willi syndrome) have very little appetite and are often unable to suckle (Haig & Wharton, 2003). We still know little about the ways in which genomic conflicts affect other motivational systems such as attachment and mating, but their impact is likely to be profound and extend well beyond infancy and childhood (Kramer & Bresnan, 2015; Úbeda & Gardner, 2011).

## The Nature of Variation

### *The Origin of Individual Differences*

#### *Genetic Variation*

A century of twin studies has shown conclusively that personality traits and attitudes are strongly influenced by a person's genotype. Genetic factors account for about 50% of the variance in adult personality, and likely contribute to the remaining variation through genotype-by-environment ( $G \times E$ ) interactions (Knopik, Neiderhiser, DeFries, & Plomin, 2017; see Tucker-Drob & Briley, Chapter 3, this volume). For the most part, this genetic component consists of extremely small effects distributed across thousands of DNA regions (Chabris, Lee, Cesarini, Benjamin, & Laibson, 2015; Penke & Jokela, 2016).

From an evolutionary point of view, there are three main explanations for the existence of genetic differences in personality (Gangestad, 2011). The simplest possibility is that such differences are neutral with respect to fitness and are maintained in the population by fundamentally random processes (*genetic drift*). This hypothesis is not very likely given that personality traits systematically predict key biological outcomes such as mating, reproduction, and mortality (see Ashton, 2013). It is also possible for selection to favor a particular level of a personality trait, for example, an intermediate level of neuroticism or a high level of extraversion. In this scenario, random mutations typically cause maladaptive deviations from the optimal trait level. Selection can take

a long time to eliminate deleterious mutations from the gene pool; the equilibrium between the constant generation of new mutations and their elimination (*mutation–selection balance*) can maintain a considerable amount of genetic variation in a population. While mutation–selection balance is probably not a major source of variation for personality as a whole, there is some evidence that it may play a role in extraversion. High extraversion in men predicts enhanced reproductive success across cultures and is associated with indicators of low “mutation load” (e.g., Alvergne, Jokela, & Lummaa, 2010; Berg, Lummaa, Lahdenperä, Rotkirch, & Jokela, 2014; Gangestad, 2011). Importantly, the genetic variants that influence extraversion need not act directly on brain functioning. An intriguing possibility—for which there is mixed evidence—is that extraversion is calibrated to one's physical characteristics, so that stronger and more attractive individuals tend to become more extraverted as a result (Lukaszewski & von Rueden, 2015; Zietsch, 2016).

While neutral variants and deleterious mutations may contribute to individual differences in some personality traits, the evidence so far is most consistent with a third type of process, namely, *balancing selection* (Penke & Jokela, 2016), which occurs when the fitness contribution of a certain genetic variant is not fixed but changes across different times, places, or individuals. Each personality profile has both benefits and costs: For example, highly extraverted people not only tend to be more successful in social and mating competition but are also at higher risk of accidents and sexually transmitted diseases. Stable social arrangements may select for lower extraversion, dangerous and unpredictable environments may select for higher neuroticism, and so on (Denissen & Penke, 2008; Nettle, 2011). Many different aspects of the social environment can drive balancing selection, including some nonobvious candidates. For example, the proportion of males to females in a population, or *sex ratio*, has a cascade of remarkable consequences for social behavior. When men are scarce relative to women, and thus in higher demand in the mating “market,” the dynamics of sexual competition shift toward the (average) male preference for short-term sexual relations and delayed commitment. As a result, aggressive sexual competition becomes more intense, violent crime increases, and couple relationships become less stable. In contrast, a preponderance of men shifts compe-

tion toward long-term commitment, monogamous relationships, and earlier marriage. As sex ratios fluctuate across time and place, they create the opportunity for variable selection on multiple personality traits at once (see Del Giudice, 2012). Finally, some genetic variation in personality may arise as a side effect of intragenomic conflicts—as, for example, when maternal and paternal imprinted genes “pull” behavioral traits in opposite directions. This type of genetic effect is adaptive from the perspective of individual genes but can be quite maladaptive for the person as a whole.

### *The Role of the Environment*

All in all, the effects of the environment (including potential  $G \times E$  interactions) account for about as much variation in personality as those of the genotype. In biological terms, the fact that the same genotype may give rise to different behavioral profiles depending on the environmental context is an example of *developmental plasticity* (West-Eberhard, 2003). Plastic organisms can adapt to rapid fluctuations in the environment, which would be impossible through genetic evolution alone. In order to be biologically adaptive, developmental plasticity cannot be unconstrained or arbitrarily flexible; on the contrary, natural selection often produces finely tuned plastic responses that attempt to “match” present or future conditions so as to maximize the organism’s fitness. In addition to learning processes, organisms possess evolved *epigenetic* mechanisms that regulate genetic expression based on inputs and cues from the external environment (Ledón-Rettig, Richards, & Martin, 2013; Meaney, 2010). Epigenetic mechanisms are likely to be involved in the long-term development of personality, even though the details of how they operate are still mostly unknown.

Twin studies consistently show that environmental effects on personality are largely or completely nonshared; that is, they act independently on siblings within the same family (Knopik et al., 2017). The predominance of nonshared effects is a developmental and evolutionary puzzle, since many aspects of the environment that may plausibly affect the development of personality—from adversity and socioeconomic status to the quality of family relationships—are shared between siblings. In principle, a child’s personality could be shaped by his or her particular niche within the family, as

determined, for example, by birth order; however, the existence of systematic birth order effects is not supported by the evidence (see Ashton, 2013). Experiences with peers are another plausible source of nonshared environmental influences, but they are hard to disentangle from the indirect influence of genetic factors. In general, a person’s activities and experiences are influenced by his or her preexisting personality; in many cases, those activities and experiences reinforce the initial personality traits and stabilize them even further (Specht et al., 2014). Another possible explanation for the predominance of nonshared effects is the existence of pervasive  $G \times E$  interactions. In this scenario, genetic differences between siblings moderate the effects of shared experiences, so that the same event may have different consequences for the development of personality in different siblings (Duncan, Pollastri, & Smoller, 2014; Knopik et al., 2017; see Tucker-Drob & Briley, Chapter 3, this volume).

### *Differential Susceptibility*

A particularly interesting model of  $G \times E$  interactions is the theory of *differential susceptibility* (Belsky, 1997; Belsky & Pluess, 2009; Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2011). According to this theory, the same genetic variants that make children more susceptible to negative aspects of the environment, such as stress and harsh parenting (and would be traditionally regarded as vulnerability factors), also make them more open to positive aspects such as safety, social support, and positive interactions with parents. In other words, some children are more plastic in response to both types of environmental input (“for better and for worse”). The evolutionary rationale is that the early environment is an imperfect predictor of what will happen later in life; children who are shaped by early experiences not only benefit from enhanced plasticity when cues correctly predict the future but also risk developing maladaptive (mismatched) traits when early cues are misleading. Differences in susceptibility between offspring evolve as a form of “insurance” against such prediction errors. Another version of this idea focuses less strongly on genetic factors and postulates that early experiences shape subsequent plasticity, increasing susceptibility in both adverse and protected environments and giving rise to a U-shaped curve (Boyce & Ellis, 2005).

There is some evidence that infants and young children who are more irritable and higher in negative emotionality are also more susceptible to environmental influences (Slagt, Dubas, Deković, & van Aken, 2016). Other candidate plasticity factors are elevated physiological reactivity to stress and individual differences in various neurotransmitter systems, including serotonin, dopamine, and oxytocin (see Moore & Depue, 2016). However, the role of specific genetic variants is still difficult to assess because of the formidable methodological challenges in this type of study (Del Giudice, 2017; Duncan et al., 2014; Ellis & Del Giudice, in press). Another limitation of current models of differential susceptibility is that they do not consider the possible effects of parent–offspring conflict. Given that highly susceptible offspring are also easier to influence, it is reasonable to expect that the optimal level of plasticity will differ between parents and offspring. This additional layer of conflict might contribute to shape the development of individual differences in plasticity (Del Giudice, 2015c).

### *Life History Strategies*

Individual differences in behavior can be described at various levels of detail and potentially comprise hundreds or even thousands of specific traits and dispositions. Models of personality organize those traits into a manageable hierarchy, with a few broad factors at the top and dozens of narrow facets at the bottom. Crucially, behavioral traits are not independent from one another but tend to covary in clusters. There are also correlations between behavioral traits and individual differences in physiology (e.g., sex and stress hormones), physical and sexual maturation (e.g., timing of puberty), health, and so on. To understand these large-scale patterns from a functional perspective, evolutionary researchers have increasingly drawn on *life history theory* (see Del Giudice, Gangestad, & Kaplan, 2015; Ellis, Figueredo, Brumbach, & Schlomer, 2009). Life history theory is a branch of biology that seeks to understand how organisms allocate time and energy to the various activities that comprise their life cycle—chiefly growth, bodily maintenance, and reproduction. Since all these activities ultimately contribute to fitness, organisms face a number of inevitable trade-offs: for instance, there is a general trade-off between growth and reproduction, as

both require substantial energetic investment. When resources are directed toward reproduction, devoting more time and energy to parenting (e.g., by maintaining stable pair-bonds) leaves one with fewer opportunities for mating (e.g., in the form of short-term sexual relations).

Natural selection favors organisms that schedule developmental tasks and activities so as to optimize resource allocation; this chain of resource allocation decisions—expressed in the development of an integrated suite of physiological and behavioral traits—constitutes the individual’s life history strategy. At the level of behavior, individual differences in life history strategy are reflected in patterns of self-regulation and motivation, with implications for aggression, cooperation, sexuality, and pair-bonding (among others). While life history strategies are partly determined by genetic factors, they also show a degree of plasticity in response to key dimensions of the environment that include danger, unpredictability, and availability of adequate nutritional resources. In a nutshell, dangerous and unpredictable environments tend to favor “fast” strategies characterized by early maturation and reproduction (especially in females), sexual promiscuity, relationship instability, impulsivity, risk taking, aggression, and exploitative tendencies. Safe and predictable environments tend to entrain “slow” strategies characterized by late reproduction, stable pair-bonds, high self-control and future orientation, risk aversion, and prosociality. Slow strategies are also favored by nutritional scarcity in the absence of high levels of danger (Del Giudice et al., 2015; Ellis et al., 2009).

Life history theory can inform the study of personality development in two ways. First, life history models point to broader patterns of covariation—not only among personality traits but also with maturation and physiology—and help make sense of their functional underpinnings. Second, they single out some aspects of the environment (e.g., unpredictability) as potentially important for the coordinated development of individual differences. Note that different authors approach the relations between life history strategies and personality in somewhat different ways. Some focus on specific traits such as agreeableness, conscientiousness, and impulsivity (e.g., Del Giudice, 2014a, 2018; Del Giudice et al., 2015), whereas others look for superfactors that may be as broad as a “general factor of personality” (e.g., Figueredo, Woodley of Menie, & Jacobs, 2015; Olderbak, Gladden,

Wolf, & Figueredo, 2014). Beyond the Big Five, life history concepts have been used to explain the evolution of “dark” traits such as psychopathy and narcissism, autistic-like traits, and other dimensions of personality at the interface with psychopathology (e.g., Del Giudice, Klimczuk, Traficante, & Maestripieri, 2014; Jonason, Koenig, & Tost, 2010).

### ***Sex Differences in Personality***

Throughout our evolutionary history, males and females have faced different challenges in their quest for survival and reproduction. Because of childbearing and lactation, women are the default caregivers for infants and children; from a fitness standpoint, they have more to lose from physical damage, which can severely reduce their ability to bear offspring. Women also depend more on family ties and social networks for successful reproduction, and female competition focuses heavily on exclusion and less on overt dominance. In contrast, men have been engaging in more physical aggression and violence for millions of years, both within their group (dominance contests) and between rival groups. Sexual selection also follows different criteria when males and females choose their mates. Men universally prefer cues of youth and fertility, and can increase their fitness by having children from multiple partners. While women can get some benefits from multiple sexual relationships, they can only bear one child at a time (barring twin pregnancies); moreover, they benefit more from choosing higher-status partners than younger ones given that male fertility decreases much less steeply with age. Historically, most human societies have been polygynous to various degrees—socially imposed monogamy is a recent cultural innovation that originated in ancient Greece and Rome and began to spread during the Middle Ages (see Benenson, 2014; Geary, 2010).

In short, human males and females differ in their mating and social strategies, have engaged in sexual division of labor for millions of years (e.g., hunting and fighting vs. caregiving), and experience different costs and benefits from a wide range of behaviors and life history decisions. In light of all these facts, it would be truly surprising if men and women had not evolved some robust differences in their typical personalities. Yet the consensus view in psychology since the 1970s has been that sex differences in personality are small and inconsequential—the

main exception being that men show moderately higher levels of physical and verbal aggression (Hyde, 2014). As it turns out, this view is vitiated by two methodological problems: (1) a focus on broad personality traits when sex differences mainly emerge at the level of narrower facets and (2) a failure to aggregate differences across multiple traits (Del Giudice, 2015b).

When men and women are compared on Big Five domains, differences tend to be small—from less than 0.1 standard deviations in conscientiousness and openness to about 0.4 standard deviations in agreeableness and neuroticism (both higher in women). However, this is probably not the best level of analysis for sex differences. Natural and sexual selection should lead to sexually differentiated patterns of motivation (e.g., mating, affiliation, caregiving) and self-regulation (e.g., risk taking). While motivational tendencies do not map in a straightforward fashion on broad, multifaceted traits such as the Big Five, they can often be recovered more directly by zooming in to the level of narrower traits such as dominance and trust. This is also where sex differences become stronger and more meaningful. For example, some facets of neuroticism (e.g., anxiety and vulnerability) show much larger effects than others (e.g., angry hostility). Not infrequently, sex differences of opposite sign cancel each other out when one only considers the broader level of analysis: Despite scoring similar to women in overall extraversion, men are lower in sociability but higher in dominance and sensation seeking. Other narrow traits that are not well represented in the five-factor model show extremely large differences; in particular, women score more than two standard deviations higher than men on the personality dimension of *sensitivity* (aesthetic, intuitive, and tender-minded vs. utilitarian, objective, and tough-minded; Del Giudice, Booth, & Irwing, 2012). On top of these average differences, personality traits tend to be somewhat more variable in men than in women (Del Giudice, 2015b). This is a common outcome of sexual selection when males compete more strongly than females for mating and reproductive success (Archer & Mehdikhani, 2003).

When sex differences across multiple traits are combined using multivariate statistical methods and corrected for measurement error, the global difference between the average profiles of men and women is remarkably large (2.7 standard deviations in Del Giudice et al., 2012). This means that the personality distributions of

males and females overlap by about 10%, which is close to the anatomical overlap between male and female faces (Del Giudice, 2013). The comparison between faces and personality profiles is illuminating: While the sexes look fairly similar if one considers one anatomical feature at a time (e.g., the size of the eyes, the length of the nose), the difference becomes obvious as soon as one starts looking at whole faces of men and women.

### *Common Misconceptions*

An evolutionary approach to sex differences in personality tends to evoke two kinds of misconceptions. The first is that large differences imply a categorical, all-or-none separation between males and females and a disregard for the variability that exist *within* each sex. This is definitely not the case. Both males and females exhibit an enormous variety of personalities and combinations of traits; moreover, about 10% of men have a personality profile that is more typical of women (and vice versa). Again, the analogy with faces can be helpful: While each person has a unique face with a peculiar combination of features, there is still a clear-cut difference between the average face of a woman and that of a man. The second misconception concerns developmental timing and holds that evolved traits should already be present at birth or in early infancy. When differences appear later in development, they are often explained with socialization and regarded as not “biological.” It is true that many sex differences in personality emerge or intensify between middle childhood and late adolescence (Soto, John, Gosling, & Potter, 2011); however, this is irrelevant to the question of their evolutionary origin and biological basis. It is quite possible for sex-specific adaptations to be absent at birth and only develop when they become useful to the organism. To cite just one example, breasts in girls do not develop until puberty, but it would be absurd to argue that they are a product of learning or socialization.

### **The Nature of Development**

Evolution and development are more than deeply connected—they are inseparable. Organs and behaviors do not just appear from nowhere but develop over time, ultimately from a single cell; indeed, selection can only modify the traits

of an organism by acting on the developmental processes that build them. At the same time, developmental mechanisms are shaped by selection as adaptations in their own right (West-Eberhard, 2003). An evolutionary perspective can illuminate human development in myriad different ways (see Bjorklund & Ellis, 2014; Ellis & Bjorklund, 2005). In addition to models of  $G \times E$  interactions and differential susceptibility, the last few years have seen tremendous progress in our understanding of sensitive periods and functionally specialized learning processes (Barrett, 2015; Frankenhuis & Fraley, 2017). In this section, I briefly focus on the stages and transitions that make up the life cycle.

### *Human Life Stages*

The trajectory of human development can be segmented into a small number of relatively well-defined stages: fetal life, infancy, early childhood (about 3–7 years), middle childhood (about 7–11 years in modern societies), adolescence, and adulthood. In women, postmenopausal life can also be regarded as a distinct stage. Life stages are characterized by clusters of physical, cognitive, and behavioral features, and are joined to one another by phases of rapid change (transitions), usually mediated by specific hormonal mechanisms. The key biological function of stages is to organize life history tasks into an optimal sequence. Most organisms go through at least two stages: An initial phase of growth is followed by the transition to reproductive maturity, after which energy is diverted from growth and used to produce offspring. From the standpoint of motivation, each life stage corresponds to the activation of particular biological goals and a rearrangement of the organism’s priorities (Del Giudice et al., 2015).

To illustrate these concepts, consider the critical but often neglected stage of middle childhood (Del Giudice, 2014b), which roughly corresponds to *juvenility*, a life stage found in primates and other mammals in which the young are still sexually immature, yet no longer dependent on adults for feeding and protection. Middle childhood starts around age 6–8 years with the eruption of the first permanent teeth and the awakening of the adrenal gland (*adrenarche*), which begins to secrete increasing amounts of androgens. Adrenal androgens promote neural plasticity, and shift the allocation of energy away from the brain and toward the accumulation of muscle and fat in preparation

for puberty. They can also be converted to testosterone and estrogens in the brain, activating sexually differentiated pathways and regulating brain development in a sex-specific manner (Campbell, 2011; Del Giudice, 2014b; Del Giudice, Angeleri, & Manera, 2009). The changes of middle childhood include dramatic increases in self-control and motor skills, enabling juveniles to help with domestic tasks—foraging, preparing food, taking care of younger siblings, and so on. Overall, middle childhood combines intensive social learning and *integration* into one's group and culture with the emergence of social *competition* for status among peers.

Middle childhood is marked by the onset or intensification of sex differences in aggression, social play, attachment styles, and some personality traits (mainly agreeableness and facets of conscientiousness and openness; Soto et al., 2011). The mating system also becomes activated, as reflected in the first sexual and/or romantic attractions. The initial activation of mating and status goals not only prepares children for competition in adolescence but also provides them with important feedback on their attractiveness, competence, dominance, and overall desirability as social partners. Not coincidentally, individual differences in self-esteem are virtually absent in young children but emerge rapidly with the transition to middle childhood (Harter, 2012). With the eruption of permanent teeth and the maturation of fine motor skills, children become capable of feeding themselves; this exposes them to new threats from rotten or poisonous food, and likely explain the sudden increase in disgust sensitivity that is observed at this age (see Del Giudice, 2014b).

The middle childhood stage ends with the transition to adolescence, marked by a characteristic growth spurt and the onset of sex hormones production by the gonads (*gonadarche*). Adolescence completes physical growth and transform children into sexually mature adults. Predictably, sexual and competitive motivations become even more salient to adolescents; this motivational shift is paralleled by enhanced sensitivity to social cues and social evaluation, and by a dramatic increase in risk-taking behavior (especially in boys; Ellis et al., 2012). During adolescence, sex differences in conscientiousness and agreeableness show a temporary decline, whereas those in neuroticism and extraversion appear for the first time (Soto et al., 2011). This pattern of sex differences matches the different social styles of males and females,

and reflects the changing cost–benefit balance of physical aggression, social exclusion, and so on (Benenson, 2014; Del Giudice, 2015b).

### ***Developmental Switch Points***

The nature of transitions between life stages can be illuminated by the concept of developmental switch points, a modern extension of the classic idea of sensitive periods (West-Eberhard, 2003). A *developmental switch* is a regulatory mechanism that activates at a specific point in development, collects input from the external environment and/or the internal state of the organism, and shifts the individual along alternative pathways that result in different outcomes. For example, a switch may regulate the development of aggressive behavior so that safe conditions entrain the development of low levels of aggression, whereas threatening environments trigger high levels of aggression. Developmental switches are often implemented through hormonal signals; their activation controls the coordinated expression of multiple sets of genes—both those involved in the regulatory mechanism itself and those involved in the expression of the new traits. The transition to middle childhood and the onset of puberty are two crucial switch points in human development; they are mediated by the hormonal mechanisms of adrenarche and gonadarche, respectively (Del Giudice et al., 2009; Ellis, 2013). Other, less studied but potentially critical switch points are pregnancy and birth—which trigger hormonal changes in both mothers and fathers—and the onset of menopause (Del Giudice & Belsky, 2011).

A key feature of developmental switches is that they integrate environmental information with variation in the genes that regulate the switch; for example, genetic factors may partly determine the threshold for switching between alternative developmental pathways. The embodied effects of past experiences may also modulate the switch (e.g., via epigenetic mechanisms), allowing the organism to integrate information over time and across life stages. Like a sensitive period, a developmental switch point implies heightened sensitivity to the environment, but with a crucial difference: Since genetic and environmental inputs converge in the same regulatory mechanism, a developmental switch can not only amplify the individual's susceptibility to some aspects of the environment but also reveal the effects of genetic fac-

tors that were previously hidden from view. Accordingly, twin studies of traits as disparate as aggression, prosociality, and language skills consistently show the emergence of substantial new genetic factors during the transition from early to middle childhood (see Del Giudice, 2014b).

### ***Ontogenetic and Deferred Adaptations***

Looking at developmental stages through the lens of biological function suggests a useful distinction between two kinds of adaptations that are often observed in early life. *Ontogenetic adaptations* are designed to serve their fitness-enhancing function at a specific time in development, and often disappear as soon as they are no longer needed. Examples include the placenta (a fetal organ that provides nourishment and other vital functions during the fetal stage and is discarded immediately after birth) and infantile reflexes, such as the suckling reflex. *Deferred adaptations* are traits that appear in childhood but function—at least in part—to prepare children for adult behavior (Bjorklund & Ellis, 2014). Play is a paramount example of a deferred adaptation; in humans and other mammals, playing trains youngsters to deal with unexpected events and, at the same time, paves the way to the acquisition of specialized adult skills (e.g., foraging, fighting, parenting) (Geary, 2010; Spinka, Newberry, & Bekoff, 2001).

The concept of an ontogenetic adaptation is particularly useful to understand the limits of early experiences in shaping adult personality. Some behavioral traits expressed in childhood serve important functions in the context of family life but may cease to be useful as the child turns into an independent adult. These traits may either disappear or get repurposed in a different form in the service of new developmental goals. For example, attachment styles in infancy are largely determined by the parents' caregiving styles and show negligible genetic effects. In middle childhood, attachment styles start to become differentiated by sex, possibly under the influence of adrenal androgens; adults' attachment styles to romantic partners are only weakly correlated with those of infancy, and reflect a sizable contribution of genetic factors (Barbaro, Boutwell, Barnes, & Shackelford, 2017; Del Giudice, 2009, 2015a). At an even deeper level, the existence of parent-offspring conflict implies that the parents' behavior is not *completely* in the best interest of their children.

For this reason, children should not passively accept the influence of parents; instead, they should show a certain amount of developmental “resistance” to parental shaping. While it is difficult to directly test this hypothesis, parent-offspring conflict may well contribute to explain why family experiences have only small and inconsistent effects on the development of adult personality.

### **Conclusion**

At the beginning of this chapter, I argued that evolutionary psychology offers an integrative theoretical framework for personality development and a wealth of insights into the nature of motivation, variation, and developmental processes. On the one hand, the evolutionary approach solidifies some long-standing, even commonsense intuitions—for example, about the ubiquity of social conflicts and the importance of sex differences. On the other hand, it drastically restructures previously familiar ideas, and introduces notions that are often counterintuitive and sometimes unsettling. Philosopher Daniel Dennett (1995) likened this effect of evolutionary theory to that of a “universal acid”—it eats through every traditional concept it touches and leaves in its wake something that is still recognizable but transformed in fundamental ways. In addition to summarizing basic ideas and findings, I hope I have succeeded in conveying some of the excitement that permeates the field, and sparked the reader's curiosity about what lies ahead.

### **REFERENCES**

- Alvergne, A., Jokela, M., & Lummaa, V. (2010). Personality and reproductive success in a high-fertility human population. *Proceedings of the National Academy of Sciences of the USA*, *107*, 11745–11750.
- Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism—how to carry out an exaptationist program. *Behavioral and Brain Sciences*, *25*, 489–504.
- Archer, J., & Mehdi khani, M. (2003). Variability among males in sexually selected attributes. *Review of General Psychology*, *7*, 219–236.
- Ashton, M. C. (2013). *Individual differences and personality* (2nd ed.). New York: Academic Press.
- Auger, R., & Curtis, V. (2013). The anatomy of motivation: An evolutionary-ecological approach. *Biological Theory*, *8*, 49–63.



- Barbaro, N., Boutwell, B. B., Barnes, J. C., & Shackelford, T. K. (2017). Rethinking the transmission gap: What behavioral genetics and evolutionary psychology mean for attachment theory: A comment on Verhage et al. (2016). *Psychological Bulletin*, *143*, 107–113.
- Barkley, R. A. (2012). *Executive functions: What they are, how they work, and why they evolved*. New York: Guilford Press.
- Barrett, H. C. (2015). *The shape of thought: How mental adaptations evolve*. New York: Oxford University Press.
- Baumard, N., André, J.-B., & Sperber, D. (2013). A mutualistic approach to morality: The evolution of fairness by partner choice. *Behavioral and Brain Sciences*, *36*, 59–122.
- Belsky, J. (1997). Variation in susceptibility to rearing influences: An evolutionary argument. *Psychological Inquiry*, *8*, 182–186.
- Belsky, J., & Pluess, M. (2009). Beyond diathesis–stress: Differential susceptibility to environmental influences. *Psychological Bulletin*, *135*, 885–908.
- Benenson, J. F. (2014). *Warriors and worriers: The survival of the sexes*. New York: Oxford University Press.
- Berg, V., Lummaa, V., Lahdenperä, M., Rotkirch, A., & Jokela, M. (2014). Personality and long-term reproductive success measured by the number of grandchildren. *Evolution and Human Behavior*, *35*, 533–539.
- Bjorklund, D. F., & Ellis, B. J. (2014). Children, childhood, and development in evolutionary perspective. *Developmental Review*, *34*, 225–264.
- Bourke, A. F. G. (2011). *Principles of social evolution*. New York: Oxford University Press.
- Bowles, S., & Gintis, H. (2011). *A cooperative species: Human reciprocity and its evolution*. Princeton, NJ: Princeton University Press.
- Boyce, W. T., & Ellis, B. J. (2005). Biological sensitivity to context: I. An evolutionary–developmental theory of the origins and functions of stress reactivity. *Development and Psychopathology*, *17*, 271–301.
- Buss, D. M. (2015a). *Evolutionary psychology: The new science of the mind* (5th ed.). New York: Routledge.
- Buss, D. M. (Ed.). (2015b). *The handbook of evolutionary psychology* (2nd ed.). New York: Wiley.
- Buss, D. M., & Hawley, P. H. (2011). *The evolution of personality and individual differences*. New York: Oxford University Press.
- Campbell, B. C. (2011). Adrenarche and middle childhood. *Human Nature*, *22*, 327–349.
- Carere, C., & Maestripieri, D. (2013). *Animal personalities: Behavior, physiology, and evolution*. Chicago: University of Chicago Press.
- Chabris, C. F., Lee, J. J., Cesarini, D., Benjamin, D. J., & Laibson, D. I. (2015). The fourth law of behavior genetics. *Current Directions in Psychological Science*, *24*, 304–312.
- Cochran, G., & Harpending, H. (2009). *The 10,000 year explosion: How civilization accelerated human evolution*. New York: Basic Books.
- Corr, P. J., DeYoung, C. G., & McNaughton, N. (2013). Motivation and personality: A neuropsychological perspective. *Social and Personality Psychology Compass*, *7*, 158–175.
- Cosmides, L., & Tooby, J. (2015). Adaptations for reasoning about social exchange. In D. M. Buss (Ed.), *The handbook of evolutionary psychology: Vol. 2. Integrations* (2nd ed., pp. 625–668). New York: Wiley.
- Curtis, V. (2011). Why disgust matters. *Philosophical Transactions of the Royal Society of London B*, *366*, 3478–3490.
- Dawkins, R. (1976). *The selfish gene*. Oxford, UK: Oxford University Press.
- DeBruine, L. M., Jones, B. C., Little, A. C., & Perrett, D. I. (2008). Social perception of facial resemblance in humans. *Archives of Sexual Behavior*, *37*, 64–77.
- Deci, E. L., & Ryan, R. M. (2000). The “what” and “why” of goal pursuits: Human needs and the self-determination of behavior. *Psychological Inquiry*, *11*, 227–268.
- Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral and Brain Sciences*, *32*, 1–21.
- Del Giudice, M. (2012). Sex ratio dynamics and fluctuating selection on personality. *Journal of Theoretical Biology*, *297*, 48–60.
- Del Giudice, M. (2013). Multivariate misgivings: Is D a valid measure of group and sex differences? *Evolutionary Psychology*, *11*, 1067–1076.
- Del Giudice, M. (2014a). An evolutionary life history framework for psychopathology. *Psychological Inquiry*, *25*, 261–300.
- Del Giudice, M. (2014b). Middle childhood: An evolutionary–developmental synthesis. *Child Development Perspectives*, *8*, 193–200.
- Del Giudice, M. (2015a). Attachment in middle childhood: An evolutionary–developmental perspective. *New Directions for Child and Adolescent Development*, *148*, 15–30.
- Del Giudice, M. (2015b). Gender differences in personality and social behavior. In J. D. Wright (Ed.), *International encyclopedia of the social and behavioral sciences* (2nd ed., pp. 750–756). New York: Elsevier.
- Del Giudice, M. (2015c). Plasticity as a developing trait: Exploring the implications. *Frontiers in Zoology*, *12*(Suppl. 1), S4.
- Del Giudice, M. (2017). Statistical tests of differential susceptibility: Performance, limitations, and improvements. *Development and Psychopathology*, *29*(4), 1267–1278.
- Del Giudice, M. (2018). *Evolutionary psychopathology: A unified approach*. New York: Oxford University Press.
- Del Giudice, M., Angeleri, R., & Manera, V. (2009). The juvenile transition: A developmental switch point in human life history. *Developmental Review*, *29*, 1–31.
- Del Giudice, M., & Belsky, J. (2011). The development of life history strategies: Toward a multi-stage theory. In D. M. Buss & P. H. Hawley (Eds.), *The*

- evolution of personality and individual differences* (pp. 154–176). New York: Oxford University Press.
- Del Giudice, M., Booth, T., & Irwing, P. (2012). The distance between Mars and Venus: Measuring global sex differences in personality. *PLOS ONE*, *7*, e29265.
- Del Giudice, M., Gangestad, S. W., & Kaplan, H. S. (2015). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology: Vol 1. Foundations* (2nd ed., pp. 88–114). Hoboken, NJ: Wiley.
- Del Giudice, M., Klimczuk, A. C. E., Traficante, D. M., & Maestripieri, D. (2014). Autistic-like and schizotypal traits in a life history perspective: Diametrical associations with impulsivity, sensation seeking, and sociosexual behavior. *Evolution and Human Behavior*, *35*, 415–424.
- Denissen, J. J., & Penke, L. (2008). Motivational individual reaction norms underlying the Five-Factor model of personality: First steps towards a theory-based conceptual framework. *Journal of Research in Personality*, *42*, 1285–1302.
- Dennett, D. C. (1995). *Darwin's dangerous idea: Evolution and the meanings of life*. New York: Simon & Schuster.
- DeScioli, P., & Kurzban, R. (2013). A solution to the mysteries of morality. *Psychological Bulletin*, *139*, 477–496.
- Dunbar, R. I. M. (1993). Co-evolution of neocortex size, group size and language in humans. *Behavioral and Brain Sciences*, *16*, 681–735.
- Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*, 1344–1347.
- Duncan, L. E., Pollastri, A. R., & Smoller, J. W. (2014). Mind the gap: Why many geneticists and psychological scientists have discrepant views about gene–environment interaction (G×E) research. *American Psychologist*, *69*, 249–268.
- Durrant, R., & Ellis, B. J. (2012). Evolutionary psychology. In I. B. Weiner, R. J. Nelson, & S. Mizumori (Eds.), *Handbook of psychology: Vol. 3. Behavioral neuroscience* (2nd ed., pp. 26–51). Hoboken, NJ: Wiley.
- Ellis, B. J. (2013). The hypothalamic–pituitary–gonadal axis: A switch-controlled, condition-sensitive system in the regulation of life history strategies. *Hormones and Behavior*, *64*, 215–225.
- Ellis, B. J., & Bjorklund, D. F. (Eds.). (2005). *Origins of the social mind: Evolutionary psychology and child development*. New York: Guilford Press.
- Ellis, B. J., Boyce, W. T., Belsky, J., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2011). Differential susceptibility to the environment: An evolutionary–neurodevelopmental theory. *Development and Psychopathology*, *23*, 7–28.
- Ellis, B. J., & Del Giudice, M. (in press). Developmental adaptation to stress: An evolutionary perspective. *Annual Review of Psychology*.
- Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., et al. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. *Developmental Psychology*, *48*, 598–623.
- Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. *Human Nature*, *20*, 204–268.
- Feldman, R. (2017). The neurobiology of human attachments. *Trends in Cognitive Sciences*, *21*, 80–99.
- Figueredo, A. J., Sefcek, J. A., Vasquez, G., Brumbach, B. H., King, J. E., & Jacobs, W. J. (2005). Evolutionary personality psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 851–877). Hoboken, NJ: Wiley.
- Figueredo, A. J., Woodley of Menie, M. A., & Jacobs, J. (2015). The General Factor of Personality: A hierarchical life history model. In D. M. Buss (Ed.), *The handbook of evolutionary psychology: Vol 2. Integrations* (2nd ed., pp. 943–967). Hoboken, NJ: Wiley.
- Frankenhuis, W. E., & Fraley, R. C. (2017). What do evolutionary models teach us about sensitive periods in psychological development? *European Psychologist*, *22*, 141–150.
- Gangestad, S. W. (2011). Evolutionary processes explaining the genetic variance in personality: An exploration of scenarios. In D. M. Buss & P. H. Hawley (Eds.), *The evolution of personality and individual differences* (pp. 338–375). New York: Oxford University Press.
- Geary, D. C. (2010). *Male, female: The evolution of human sex differences* (2nd ed.). Washington, DC: APA Press.
- Grafen, A. (2007). The formal Darwinism project: A mid-term report. *Journal of Evolutionary Biology*, *20*, 1243–1254.
- Gurven, M., von Rueden, C., Massenkoff, M., Kaplan, H., & Lero Vie, M. (2013). How universal is the Big Five?: Testing the five-factor model of personality variation among forager-farmers in the Bolivian Amazon. *Journal of Personality and Social Psychology*, *104*, 354–370.
- Haidt, J. (2007). The new synthesis in moral psychology. *Science*, *316*, 998–1002.
- Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York: Pantheon.
- Haig, D., & Wharton, R. (2003). Prader–Willi syndrome and the evolution of human childhood. *American Journal of Human Biology*, *15*, 320–329.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, *7*, 1–52.
- Harter, S. (2012). *The construction of the self: Developmental and sociocultural foundations*. New York: Guilford Press.
- Hawley, P. H. (2014). Ontogeny and social dominance: A developmental view of human power patterns. *Evolutionary Psychology*, *12*, 318–342.
- Henrich, J., & Gil-White, F. J. (2001). The evolution of

- prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22, 165–196.
- Hyde, J. S. (2014). Gender similarities and differences. *Annual Review of Psychology*, 65, 373–398.
- Jonason, P. K., Koenig, B. L., & Tost, J. (2010). Living a fast life: The Dark Triad and life history theory. *Human Nature*, 21, 428–442.
- Kaplan, H. S., Gurven, M., & Lancaster, J. B. (2007). Brain evolution and the human adaptive complex: An ecological and social theory. In S. W. Gangestad & J. A. Simpson (Eds.), *The evolution of mind: Fundamental questions and controversies* (pp. 269–279). New York: Guilford Press.
- Kaplan, H. S., Hill, K., Lancaster, J. B., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, 9, 156–185.
- Kavanagh, P. S., Robins, S. C., & Ellis, B. J. (2010). The mating sociometer: A regulatory mechanism for mating aspirations. *Journal of Personality and Social Psychology*, 99, 120–132.
- Kenrick, D. T., Griskevicius, V., Neuberg, S. L., & Schaller, M. (2010). Renovating the pyramid of needs: Contemporary extensions built upon ancient foundations. *Perspectives on Psychological Science*, 5, 292–314.
- Kirkpatrick, L. A., & Ellis, B. J. (2001). An evolutionary–psychological approach to self-esteem: Multiple domains and multiple functions. In G. Fletcher & M. Clark (Eds.), *The Blackwell handbook of social psychology: Vol. 2. Interpersonal processes* (pp. 411–436). Oxford, UK: Blackwell.
- Knopik, V. S., Neiderhiser, J. M., DeFries, J. C., & Plomin, R. (2017). *Behavioral genetics* (7th ed.). New York: Worth.
- Kramer, P., & Bressan, P. (2015). Humans as superorganisms: How microbes, viruses, imprinted genes, and other selfish entities shape our behavior. *Perspectives on Psychological Science*, 10, 464–481.
- Leary, M. R. (2005). Sociometer theory and the pursuit of relational value: Getting to the root of self-esteem. *European Review of Social Psychology*, 16, 75–111.
- Ledón-Rettig, C. C., Richards, C. L., & Martin, L. B. (2013). Epigenetics for behavioral ecologists. *Behavioral Ecology*, 24, 311–324.
- Lukaszewski, A. W., Gurven, M., von Rueden, C. R., & Schmitt, D. P. (2017). What explains personality covariation?: A test of the socioecological complexity hypothesis. *Social Psychological and Personality Science*, 18, 943–952.
- Lukaszewski, A. W., & von Rueden, C. R. (2015). The extraversion continuum in evolutionary perspective: A review of recent theory and evidence. *Personality and Individual Differences*, 77, 186–192.
- Machin, A. J., & Dunbar, R. I. (2011). The brain opioid theory of social attachment: A review of the evidence. *Behaviour*, 148, 985–1025.
- McAdams, D. P. (2015). *The art and science of personality development*. New York: Guilford Press.
- Meaney, M. J. (2010). Epigenetics and the biological definition of gene  $\times$  environment interactions. *Child Development*, 81, 41–79.
- Moore, S. R., & Depue, R. A. (2016). Neurobehavioral foundations of environmental reactivity. *Psychological Bulletin*, 142, 107–164.
- Nesse, R. M. (2007). Runaway social selection for displays of partner value and altruism. *Biological Theory*, 2, 143–155.
- Nettle, D. (2011). Evolutionary perspectives on the Five Factor model of personality. In D. M. Buss & P. H. Hawley (Eds.), *The evolution of personality and individual differences* (pp. 5–28). New York: Oxford University Press.
- Olderbak, S., Gladden, P., Wolf, P. S. A., & Figueredo, A. J. (2014). Comparison of life history strategy measures. *Personality and Individual Differences*, 58, 82–88.
- Penke, L., & Jokela, M. (2016). The evolutionary genetics of personality revisited. *Current Opinion in Psychology*, 7, 104–109.
- Pinker, S. (2010). The cognitive niche: Coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences of the USA*, 107, 8993–8999.
- Pinker, S. (2011). *The better angels of our nature: Why violence has declined*. New York: Viking.
- Scalise Sugiyama, M. (2011). The forager oral tradition and the evolution of prolonged juvenility. *Frontiers in Psychology*, 2, 133.
- Schlomer, G. L., Del Giudice, M., & Ellis, B. J. (2011). Parent–offspring conflict theory: An evolutionary framework for understanding conflict within human families. *Psychological Review*, 118, 496–521.
- Schmitt, D. P., & Pilcher, J. J. (2004). Evaluating evidence of psychological adaptation: How do we know one when we see one? *Psychological Science*, 15, 643–649.
- Scott-Phillips, T. C., Dickins, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate–proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, 6, 38–47.
- Simpson, J. A., & Belsky, J. (2016). Attachment theory within a modern evolutionary framework. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (3rd ed., pp. 91–116). New York: Guilford Press.
- Simpson, J. A., & Campbell, L. (2015). Methods of evolutionary sciences. In D. M. Buss (Ed.), *The handbook of evolutionary psychology: Vol 1. Foundations* (2nd ed., pp. 115–135). Hoboken, NJ: Wiley.
- Slagt, M., Dubas, J. S., Deković, M., & van Aken, M. A. G. (2016). Differences in sensitivity to parenting depending on child temperament: A meta-analysis. *Psychological Bulletin*, 142, 1068–1110.
- Soto, C. J., John, O. P., Gosling, S. D., & Potter, J. (2011). Age differences in personality traits from 10 to 65: Big Five domains and facets in a large cross-sectional sample. *Journal of Personality and Social Psychology*, 100, 330–348.

- Specht, J., Bleidorn, W., Denissen, J. J., Hennecke, M., Hutteman, R., Kandler, C., et al. (2014). What drives adult personality development?: A comparison of theoretical perspectives and empirical evidence. *European Journal of Personality, 28*, 216–230.
- Spinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology, 76*, 141–168.
- Stanyon, R., & Bigoni, F. (2014). Sexual selection and the evolution of behavior, morphology, neuroanatomy and genes in humans and other primates. *Neuroscience and Biobehavioral Reviews, 46*, 579–590.
- Tooby, J., & Cosmides, L. (2015). The theoretical foundations of evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology: Vol 1. Foundations* (2nd ed., pp. 3–87). Hoboken, NJ: Wiley.
- Toronchuk, J. A., & Ellis, G. F. (2013). Affective neuronal selection: The nature of the primordial emotion systems. *Frontiers in Psychology, 3*, 589.
- Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist, 14*, 249–264.
- Úbeda, F., & Gardner, A. (2011). A model for genomic imprinting in the social brain: Adults. *Evolution, 65*, 462–475.
- West, S. A., & Gardner, A. (2013). Adaptation and inclusive fitness. *Current Biology, 23*, r577–r584.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- Woody, E. Z., & Szechtman, H. (2011). Adaptation to potential threat: The evolution, neurobiology, and psychopathology of the security motivation system. *Neuroscience and Biobehavioral Reviews, 35*, 1019–1033.
- Zietsch, B. P. (2016). Individual differences as the output of evolved calibration mechanisms: Does the theory make sense in view of empirical observations? *Current Opinion in Psychology, 7*, 71–75.