evo-devo can enhance our understanding of phenomena such as morality. Perhaps the story will be different in other research areas. In our view, the approach is best equipped to add some new tools to evolutionary theoreticians' toolboxes, likely most relevant to those with a focus on the detailed intricacies of the developmental process (as opposed to the accompanying adaptive functions and behavior). Nevertheless, we will keep these new tools within reach, in case our challenge is met and they prove to be useful for the tasks we seek to accomplish.

Note

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The Role of Development on Evolutionary Psychology: Tinbergen Revisited

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Evolutionary theory has played a role in human psychological theory, at least since Darwin (1871, 1877). It was taken up by others—for example, Spencer (1878/1898), in his book *The Principles of Psychology.* In the early 20th century, Hall (1904), the first president of the American Psychological Association, also applied variants of this theory to humans' ontogenetic and phylogenetic development. Lorenz (1969), in his book *On Aggression*, and Tinbergen (1969), in his Nobel Prize lecture, specifically addressed applications of ethological ideas to human behavior. Soon after this, in the early 1970s, a group of ethologists concerned with human behavior emerged, primarily in Germany and the United Kingdom. This group used ethological approaches to examine human behavior and development, much of the work being done with children (Blurton Jones, 1972; Eibl-Eibesfeldt, 1989; McGrew, 1972; Smith, 1974). This body of work was never really mainstream in North American developmental psychology, perhaps because of its inductive orientation (Barlow, 1989), in contrast to the more deductive orientation of American psychology (Burghardt, 2005).

This changed over the next decades with the advent of behavioral ecology and sociobiology. A landmark was the publication of Wilson's (1975) "new synthesis," detailing the application of theoretical perspectives from Hamilton, Trivers, and others (and including Wilson's final chapter on humans). The past 30 years have witnessed a renaissance of evolutionary approaches to the study of human behavior and cognition, whether under the guise of sociobiology (e.g., Dawkins, 1976) or evolutionary psychology (e.g., Buss, 1989; Cosmides & Tooby, 1987). These generally gene-centered views of behavior and evolution, epitomized in the "selfish" gene idea (Dawkins, 1976), especially as applied to humans, have resulted in sociobiology being characterized by some as reductionistic and biological determinism (e.g., Laland & Brown, 2002). Relatedly, these approaches have paid little attention to the importance of ontogeny, as pointed out by recent exponents of evolutionary developmental psychology (Bjorklund & Pellegrini, 2002; Pellegrini & Smith, 1998) and by theorists emphasizing the importance of development in the evolutionary process via organic selection, epigenesis, or variants of these

processes (Bateson & Martin, 1999; Gottlieb, 2003; Harper, 2005).

Following on this tradition, Ploeger, van der Maas, and Raijmakers do an admirable job of specifying the importance of "development" as part an important complement to some key tenets of evolutionary psychology, as espoused by Buss (e.g., 1989) and Tooby, and Cosmides and Tooby (e.g., 1987). Ploeger et al.'s exposition is especially important in light of the recent explosion of interest in these applications of evolutionary theory to human behavior, in large part because of the popularity of "evolutionary psychology." This proliferation has resulted in a blurring of the assumptions and hypotheses associated with different models (see Burghardt, 2005; Laland & Brown, 2002; Stamps, 2003). There has been some tendency to label any theory of human behavior with an evolutionary orientation as "evolutionary psychology." This is problematic as different theories take different stances, often rather subtle, on important issues relevant to evolution, such as the interrelated roles of the environment and ontogenetic development.

Of course, concern with ontogeny in evolutionary theory was also voiced by persuasively by Tinbergen (1969) more than 50 years ago in his critique of Lorenz's views of instinct. Both Tinbergen and Lorenz studied instinctive behavior, or behavior reflecting a species' phylogenetic history rather than individual experience or reinforcement schedule (Burghardt, 1973). Instinct was considered as innate, and quite distinct from what was learned (Hinde, 1983; Laland & Brown, 2002). Instinctive behaviors were thought to be triggered by environmental stimuli. Learning might affect the range of environmental triggers but not the instinctive response. Lorenz's notion of filial imprinting is representative of this position: An organism is presented with a stimulus during a critical period in development and the instinctual behavior is activated, although the stimulus features were largely acquired.

Tinbergen (1969) disagreed with the position that the study of instinct should exclude most influences external to the organism. He stressed the role of ontogeny in the study of behavior and the details of behavioral development. Through the study of development, he argued, the relation between an organism's phylogenetic history and its current behavioral repertoire as well as function and proximal mechanisms could be properly understood. However, the working out of such a program required further advances in evolutionary theory and our understanding of genetic processes. Epigenetic theory (Gottlieb, 1998; Harper, 2005; Stamps, 2003) provided this impetus, also as suggested by Ploeger et al.

I have suggested (Pellegrini, in press; Pellegrini, Dupuis, & Smith, 20007) that "play" is an excellent choice to study the role of ontogeny. In many ways it is a paradigm example of the application of evolutionary theory to the study of human development. It has, for example, been studied by ethologists (e.g., Burghardt, 2005; Caro, 1995), sociobiologists (e.g., Fagen, 1981; Wilson, 1975), evolutionary psychologists (e.g., Symons, 1974), and evolutionary developmental psychologists (Bjorklund & Pellegrini, 2002). Indeed, Wilson suggested that the study of play was one of the most important areas for sociobiological study.

Play occurs in safe and familiar environments during the extended and protected juvenile period and in the presence of adequate resources (Burghardt, 2005). Play also follows exploration of that environment. When faced with a relatively unfamiliar but safe environment, play affords opportunity for behavioral and cognitive innovation and subsequent practice of newly developed behaviors and strategies (Bateson, 2005; Bruner, 1972; Špinka, Newbury, & Bekoff, 2001; Sutton-Smith, 1966). For example, when horses are observed in novel but safe environments, they exhibit locomotive play, possibly to learn and practice new behaviors appropriate for such an environment (Stamps, 1995). Experimental evidence with mice further suggests that locomotor motor play results in improved learning and plasticity (van Praag, Shubert, Zhao, & Gage, 2005); there is increased synaptic plasticity and neurotransmission in mice engaging in playlike voluntary exercise, relative to controls.

The role of play in ontogeny is especially relevant to Ploeger et al.'s discussion of the ways in which organisms' responses to challenges in the environment relate to the evolvability of a population. In terms of impacting evolution, play behaviors and subsequent accommodations to behavioral routines and strategies represent a low-cost way in which to develop alternative strategies in new and challenging environments. This is not to say that adults cannot also learn and develop alternative strategies, but it is probably less costly, and consequently more likely to spread through the population, if it is accomplished through play in childhood (Bateson, 2005). The ease with which play and play-related behavior spread through the population should relate to their being naturally selected. Specifically, when children are in a new but safe environment, they are able to experiment with a variety of behavior routines and subroutines. Like Sultan in Köhler's (1925) experiments, they construct through play varied responses to novel environments. Further, the costs associated with constructing and practicing new behavioral routines are low, relative to later in life, because they are in a safe environment and the behaviors are nonserious. Costs are also minimized by the extended parental care characteristic of the human juvenile period. That play is characteristic of the juvenile period suggests that it is used during this sensitive period to gauge and construct behaviors that will be useful throughout their development. From this view, play during the juvenile period is a low-cost strategy

for developing phenotypes that will be adaptive to individuals' current and subsequent environments.

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