The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

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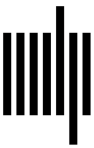

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9 Comparative Developmental Evolutionary Psychology and Cognitive Ethology: Contrasting but Compatible Research Programs

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Comparative developmental evolutionary psychology (CDEP) is the name I have given to the kinds of studies my colleagues and I have done (Parker 1990; Parker and Gibson 1990; Parker et al. 1994; Byrne 1995; Russon et al. 1996; Parker et al. 1999). My work in this area has focused on the following questions: What are the patterns of similarities and differences in cognitive abilities among humans, apes, and monkeys? How, when, and in which species have these patterns evolved (Parker and Gibson 1977, 1979)?

In addition, I have focused on the similarities and differences in the developmental extent and timing of these abilities among primate species (Parker 1977). In accord with their developmental focus, my comparative studies and those of my colleagues have used a variety of frameworks from developmental psychology, including Piagetian and neo-Piagetian stages, to compare abilities across cognitive domains.

Also, in accord with their evolutionary focus, studies of this kind have used evolutionary methodologies. I have used cladistic methods to identify cognitive adaptations and to pinpoint their origins; I have used heterochronic concepts to reconstruct evolutionary changes in the extent and timing of cognitive development. These studies have revealed a pattern of terminal addition of new stages of cognitive development in ape and human ancestors as well as a pattern of accelerated rates of cognitive development in humans compared with great apes (Parker 1996; Parker and McKinney 1999).

Beginning in the 1970s and 1980s, comparative developmental evolutionary psychology has grown up coincidentally with, but largely isolated from, the development of a parallel field known as cognitive ethology (CE). This essay compares and contrasts cognitive ethology and comparative developmental evolutionary psychology. It suggests ways each of the two research programs could benefit by adopting elements of the other and how both programs could benefit from strengthening their ties with evolutionary biology. It also briefly contrasts these programs with that of evolutionary psychology (EP).

Both cognitive ethology and comparative developmental evolutionary psychology are based in evolutionary biology, particularly animal behavior. As such, both focus to varying degrees on Tinbergen's (1963) four kinds of problems in the study of animal behavior: proximate causation, ultimate causation or adaptive significance, phylogenetic history, and ontogeny. These in turn map onto various subfields of evolutionary biology, including genetics, physiology, ecology, systematics, and phylogenetics. Table 9.1 summarizes these relationships.

Both CE and CDEP reject behaviorism and embrace folk psychology to address animal mentalities (Jamieson and Bekoff 1996). Researchers in both programs therefore have had to respond to charges of anthropomorphism (Mitchell et al. 1997). They differ primarily in the psychological frameworks and methods they have adopted. Whereas cognitive ethologists use frameworks from cognitive psychology, CDEP researchers use frameworks from developmental psychology.

The origins of cognitive ethology have been traced to Donald Griffin's (1978) papers on animal awareness, which explicitly turned the attention of ethologists and animal behaviorists to questions of animal minds and animal consciousness (Ristau 1991). It is fair to say that Griffin's work was grounded in the concepts of species-specific animal learning (Hinde and Stevenson-Hinde 1973; Roitblat et al. 1984) that emerged out of the ethology-comparative psychology wars in the 1950s and 1960s.

Cognitive ethologists differ from both comparative psychologists and animal behaviorists and from classical ethologists in focusing on animal consciousness, awareness, and intention-

Table 9.1
Treatment of Tinbergen's (1963) four complementary lines of inquiry by cognitive ethology, evolutionary psychology, and comparative developmental evolutionary psychology

Subdisciplinary bases of the four lines of inquiry	Cognitive Ethology	Comparative Developmental Evolutionary Psychology	Evolutionary Psychology
Proximate causation: molecular biology, physiology and anatomy, animal behavior	Yes	Yes	Yes, but weakly so
Ultimate causation or adaptive significance: genetics, behavioral ecology	Yes, strongly so	Yes, but weakly so	Yes
Evolutionary history: comparative paleontology, animal behavior, phylogenetics	Yes, but rarely	Yes, but often poorly	No
Ontogeny: developmental biology, evolutionary developmental biology	Yes, but rarely	Yes	No

ality. Burghardt (1997) has gone so far as to suggest that understanding private experience should be a fifth aim of ethology. Critiques of CE have focused on the difficulties of defining consciousness operationally (Dawkins 1995; Bekoff and Allen 1997).

Cognitive ethology has also been influenced by concepts of information processing from the newly emerging field of cognitive psychology (Newell 1990). Consistent with learning theory and information processing theory, it focuses primarily on species-typical modes and mechanisms of information processing, rather than on development (Hoage and Goldman 1986; Ristau 1991).

Consistent with the discipline's origins in ethology, the most salient feature of cognitive ethological studies is their focus on the behavior of animals in their natural habitats. This explains their strong focus on the ultimate causality or adaptive significance of cognition. The resulting realization that each species is uniquely adapted to its peculiar niche may have discouraged systematic comparative studies of cognition using an integrated framework (Bailey 1986).

In contrast, the origins of CDEP can be traced (Parker 1990) first to the use of models of children's language acquisition by ape language researchers (Gardner and Gardner 1969; Patterson 1980; Miles 1983; Gardner et al. 1989; Savage-Rumbaugh et al. 1989) in the late 1960s and the 1970s and 1980s. Second, it can be traced to subsequent use of stage models of cognitive development in human infants and children (Jolly 1972; Chevalier-Skolnikoff and Poirier 1977; Redshaw 1978; Antinucci 1989; Parker 1977, 1990). CDEP is based in comparative psychology and animal behavior, more specifically that arising from primatology and biological anthropology.

It differs from cognitive ethology, however, in its lesser emphasis on behavior in natural settings. Most CDEP studies done to date have been on captive animals, some in colonies, some cross-fostered, and others in laboratory settings. There are some important exceptions, however, including work on cognition in wild chimpanzees (Boesch and Boesch 1984; Boesch 1991a,b, 1993; Boesch and Boesch-Achermann 2000; Matsuzawa 1994).

CDEP also differs from cognitive ethology in comparing primate cognition in terms of achievements of developmental stages within and across traditional domains of cognition (physical, logical-mathematical, and social) in humans. Physical cognition includes knowledge of objects, space, and causality; logical knowledge includes classification, seriation, and number; social knowledge includes imitation, pretend play, self-awareness, and theory of mind.

Most CDEP studies have focused on the highest levels of species-typical abilities achieved by monkeys or apes relative to those of human children (Chevalier-Skolnikoff and Poirier 1977; Mitchell and Thompson 1986; Whiten and Byrne 1988; Antinucci 1989; Parker and Gibson 1990; Whiten 1991; Boysen and Capaldi 1993; Parker et al. 1994; Russon et al. 1996; Whiten and Byrne 1997; Parker et al. 1999). These comparative studies of the terminal levels of development achieved by related species add a new dimension to comparative psychology, first because they allow systematic comparisons among related human and nonhuman primate species, second because they can be used to reconstruct the evolutionary origins of specific cognitive abilities (Chevalier-Skolnikoff 1976; Parker and Gibson 1977; Parker 1991; Povinelli 1994; Byrne 1995).

Comparative studies that describe the pace and sequence of cognitive development across diverse domains and subdomains further increase the heuristic power of CDEP studies because they allow systematic comparisons of the sequence in which knowledge in various domains develops among related primates and the pace or speed at which it develops. These comparative developmental data also provide material for the reconstruction of patterns of heterochrony in the evolution of cognitive development (Parker 1996).

Heterochrony refers to changes in the pace and/or timing of development in descendant and ancestral species (Gould 1977; McKinney and McNamara 1991, 1997). Its component processes can produce significant changes among related species in a short time, with relatively few mutations. The nature of these changes can be inferred from comparative data on the timing and pace of development in related species. The identification of abilities that are shared among an in-group of closely related sister species such as the great apes, but not by the next most closely related out-group such as lesser apes or Old World monkeys (shared derived character states), provides the basis for this analysis (Brooks and McLennan 1991).

Specifically, comparative developmental data imply that human cognitive development entailed the addition of several new subperiods of cognitive development following divergence from our common ancestor with chimpanzees. These are Piaget's late preoperations, early and late concrete operations, and early formal operations subperiods of cognitive development (Piaget and Inhelder 1969). Second, human development entailed the elaboration and acceleration of late sensorimotor and early preoperations subperiods compared with those of the great apes (Parker 1996; Parker and McKinney 1999). Third, it entailed the realignment of developmental patterns, resulting in more synchronous development across domains (Langer 2000a,b).

In contrast to CDEP researchers, cognitive ethologists, like classical ethologists, have studied a broad range of vertebrate species, With some notable exceptions (e.g., Herzog et al. 1992; Bekoff 1995), however, as with their disciplinary cousins the comparative psychologists, cognitive ethologists have studied distantly related model species such as the white rat, the pigeon, and the rhesus monkey (Beach 1965). These species were selected for convenience of study rather than for clades of closely related sister species, such as the great apes, that share adaptations because of a recent common ancestry (see Parker and McKinney 1999 for references). The breadth and selection of their subjects has generally precluded phylogenetic reconstruction of the evolution of characteristics in related clades (Martins 1996).

Ironically, given its more limited scope, the CDEP focus on a clade of closely related primate species has facilitated efforts to reconstruct cognitive evolution. Likewise, its focus on comparative development has facilitated efforts to reconstruct the evolution of cognitive development in apes and humans through heterochrony (Parker 1996; Parker and McKinney 1999).

Although they are beginning to engage in phylogenetic reconstruction, comparative developmental psychologists often lack training in framing and testing adaptive hypotheses and in reconstructing the evolution of character states. The extension of CDEP training to include life history theory, cladistics, and phylogenetics would greatly aid these efforts (Parker and McKinney 1999).

The boundaries between CE and CDEP—and also between these approaches and those of comparative (CP) and evolutionary psychology—are somewhat fluid. Many of the same topics are investigated by researchers in these four groups, including language and communication, imitation and other forms of social learning, culture, theory of mind, spatial cognition, number, deception, and object concepts. Some researchers, primarily by virtue of their taxonomic focus on primates, cross boundaries of the subfields (e.g., Cheney and Seyfarth 1990; Vauclair 1996; Tomasello and Call 1997). Evolutionary psychologists tend to focus primarily on the ultimate causes or adaptive significance of behaviors, but they also study such proximate factors as facial symmetry and hourglass figures involved in intersexual choice, and they postulate mental modules that mediate these and other behaviors (e.g., Geary 1998). The similarities and differences between CE and CEDP are summarized in table 9.2.

Finally, CE and CEDP researchers have shared experiences of attacks from comparative psychologists. Most notable in the case of CEDP were the ape language wars (Terrace et al. 1979; Sebeok and Rosenthal 1981). This attack effectively limited funding for research in acquisition of language by apes. Similarly, comparative psychologists have harshly criticized CE researchers for their focus on consciousness (Bekoff and Allen 1997). Likewise, tensions between neo-Piagetians and neoinnatists in developmental psychology (Fischer and Bidell 1991) promise to extend to studies of cognition in nonhuman animals as neoinnatist methodologies are adopted by students of primate cognition.

Neoinnatists are cognitive developmental psychologists who reject constructivist models of human development in favor of models of innate organization of cognition. Most of their work is based studies of young infants using a habituation paradigm that infers cognitive abilities from preferential looking patterns (Baillargeon 1987a, b; Spelke et al. 1992). Their work suggests that human infants are born with essentially mature cognitive systems. Consequently, they reject stage or sequence models that would facilitate comparisons of species-typical developmental patterns.

Neoinnatists, like evolutionary psychologists, frequently argue that human cognitive abilities are modular, that is, are more or less discrete and independently evolved (Tooby and Cosmides 1992). This conclusion is contested by biological anthropologists and biologists who use life history models emphasizing that humans are a long-lived, slow-maturing species with a low reproductive rate and a large, slow-developing brain (Martin 1983; Gibson 1990, 1995; Deacon 1997).

Recently some cognitive ethologists and evolutionary psychologists (Hauser 1998) have begun to use perceptual and habituation tests developed for human infants by neoinnatists (Carey and Gelman 1991). These tests allow them to compare human and nonhuman primates, but they are not developmental in the strict sense because they are not part of a stage or sequence model.

Future Prospects

Clearly both CE and CDEP researchers could benefit from adopting certain elements from each

Table 9.2
Contrasts between cognitive ethology and comparative developmental evolutionary psychology

	Cognitive Ethology	Comparative Developmental Evolutionary Psychology
Disciplinary origins	Comparative psychology, ethology/animal behavior, cognitive psychology	Comparative psychology, animal behavior, biological anthropology, developmental psychology
Key concepts	Species-specific learning, consciousness, adaptation	Species-specific developmental stages, adaptation
Topics	Communication, intentionality, consciousness, self-awareness, cognitive maps, number, Social learning	Developmental stages in physical knowledge, logical knowledge, social knowledge, symbolic knowledge, self-awareness
Some key researchers	Griffin, Ristau, Burghardt, Bekoff	The Gardners, Redshaw, Jolly, Miles, Patterson
Methodologies	Observation in wild, model testing, Experimental playback	Observation, Clinical-critical testing, Cross-fostering experiments
Taxa	Distantly related model species of birds and mammals: pigeons, plovers, snakes, bats, rats	Closely related sister species: great apes (in-group) in contrast to monkeys (out-group)
Goals	Identifying species-specific learning abilities; discovering adaptive significance of abilities	Identifying similarities and differences among primates; reconstructing the evolution of cognitive development

other. Cognitive ethologists could benefit from investigating and/or devising comparative developmental models. Although Piagetian models are the only comprehensive models of human cognitive development, investigators of other taxa might base their comparative studies on a detailed longitudinal study of cognitive development in another species, e.g., cetacean or carnivore species.

The Piagetian framework has several advantages for comparative studies of primate cognition. These include its apparently epigenetic nature, which results in an ordinal developmental scale in some domains (Uzgiris and Hunt 1975), and its comprehensiveness across physical, logical, and social domains. Perhaps its greatest advantage lies in its focus on the organization of spontaneous behavior, that is, the sequence, timing, goals, reinforcers, and modalities of behavior (Parker 1977). Finally, its focus on the most complex abilities alerts investigators to the absence of such abilities in related species. For these reasons, it seems desirable to base a comparative framework on the development of the most cognitively complex species in a clade rather than on that of a less cognitively complex species.

Cognitive ethnologists could benefit from returning to the classical ethological practice of comparing closely related species and reconstructing the evolution of behavior. By focusing on cognitive development in clades of closely related species, they could generate comparative data that would allow reconstruction of the origins of shared derived character states, and in the case of developmental data, reconstruction of the evolution of developmental patterns.

Comparative developmental evolutionary psychologists, on the other hand, could benefit from extending their scope to include cognitive development in clades of nonprimate mammals and birds. This would greatly expand their knowledge of animal adaptations and provide material for adaptive models based on convergent evolution.

CEDP researchers could benefit from the investigation of systematics and phylogenetics and evolutionary developmental biology. These subfields provide critical tools for reconstructing the evolution of character states and developmental patterns, and for framing and testing adaptational hypotheses.

Both programs, but especially CDEP, would be enhanced by increasing their focus on cognition in wild populations of monkeys and apes (McGrew 1992; McGrew et al. 1996; Boesch and Boesch-Acherman 2000). CDEP researchers need to keep abreast of field studies of nonhuman primates to understand the kinds of ecological contexts in which various species live. This is particularly important for the generation of adaptive hypotheses.

Both CE and CDEP programs could benefit from investigations of paleontological data and paleoenvironments in which the putative ancestors of their study clade existed. In the case of hominids, this should include archeological data on past technologies (Wynn 1989; Gibson and Ingold 1993; Mithen 1996). Likewise, both research programs could benefit from comparative studies of brain development in closely related species—a growing trend in biological anthropology (Gibson and Peterson 1991; Deacon 1997; Parker et al. 2000).

This advice applies even more urgently to evolutionary psychologists, who, despite their interest in understanding the adaptive significance of human behaviors, typically neglect to use the comparative method in reconstructing the evolution of human behavior. The need to close this anomalous gap in their investigations was addressed recently by Marc Hauser in his plenary address to the Human Behavior and Evolution Society (Hauser 2000). There are encouraging signs that this group is beginning to recognize that the failure to use comparative data robs them of the chief tools of evolutionary reconstruction.

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