A Common, Conceptual Framework for Behavioral Ecology and Evolutionary Psychology

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Abstract: Since evolutionary psychology and behavioral ecology have much in common despite their using different objects for their study, one might expect these disciplines to share a common conceptual framework with associated definitions. Unfortunately, such agreement does not entirely exist. To address the problem, we propose a common, conceptual framework, the Adaptive Behavioral System (ABS), which organizes behavior within an evolutionary framework around an organism's life history tasks. An ABS includes strategies that use decision rules and employs tactics administered by a hypothesized construct, the Evolved Processing Unit (EPU). The ABS also includes observed or predicted behavior which can be tested experimentally – the ultimate test of construct validity. Use of the proposed framework should help the two disciplines focus on their common, core business of behavior and, ultimately, be to the benefit of both.

Keywords: Strategy, Tactics, Decision Rule, Adaptive Behavioral System, Fitness

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Introduction

Evolutionary psychology and behavioral ecology share many things – despite their choosing humans or non-humans respectively as the objects for their study (Hutchinson and Gigerenzer, 2005). Both accept the principles that organisms obtain information from their environment and, on the basis of that information and within the limits imposed by their genotypes and other constraints, produce a response (Giske et al., 2003). Both regard adaptations as traits honed by natural selection (Alcock, 2005; Buss, 2004). Both focus on the informational inputs, decision rules, and outputs which organize and influence an organism's behavioral interactions with its environment (Gross, 1966; Cosmides and

Tooby, 1987, 1995), and both hold that, ultimately, the study of an organism's behavior is the business of their discipline (Hutchinson and Gigerenzer, 2005).

Given such commonalties, one might expect the two disciplines to share a conceptual framework and definitions for its constructs. Testing theories developed in one discipline on the organisms of the other can only be to the benefit of both (Hutchinson and Gigerenzer, 2005). At the present time, however, much of the benefit that might be obtained from exchanging information between evolutionary psychology and behavioral ecology seems unnecessarily out of reach. Rather than sharing a common framework and definitions, the terminology and constructs used to refer to and describe behavioral systems and their constituent parts not only vary between the disciplines but also to a certain extent within the disciplines themselves.

The same information processing units are sometimes referred to as Darwinian algorithms, sometimes as psychological mechanisms, or mental organs, or sometimes simply as strategies (Buss, 2004; Cosmides and Tooby, 1987; Gaulin and McBurney, 2004). Evolutionary psychology frequently uses the label "psychological mechanism" to refer indiscriminately to tactics, decision rules, and to the organizing mechanism which utilizes these constructs. Psychological mechanisms now include everything from information processing systems to the affective states of hate and fear (Buss, 1995). In behavioral ecology, decision rules may be referred to as "rules of thumb"; in evolutionary psychology, as heuristics (Hutchinson and Gigerenzer, 2005). In both evolutionary psychology and behavioral ecology, decision rules and outputs are described variously and often interchangeably as strategies, tactics, or adaptations (Borgerhoff Mulder, 2007; Buss, 2004; Gross, 1996).

At an even deeper level, the tenets of behavioral ecology and evolutionary psychology are often seen at odds. Despite the acceptance by both disciplines that natural selection is the force that shapes adaptations and that adaptations are selected and evolve if they promote inclusive fitness (Alcock, 2005; Buss, 2004), the status assigned to fitness within the investigations of the two disciplines is often quite different. Behavioral ecologists assume that increased fitness benefits, direct or indirect, underlie the spread of any adaptation (Alcock, 2005). Kaplan and Gangestad (2005) concur that evolutionary psychology's examination of adaptations connects it intimately to life history theory and, thus, to an examination of an organism's fitness-maximizing strategies. However, Buss (1995) and Tooby and Cosmides (2005) regard humans as "adaptation executors" not "fitness strivers" or "fitness pursuers." Buss (1995) also argues that if humans were fitness strivers, we would attempt to maximize reproductive output to the exclusion of all else – a perspective not shared by behavioral ecologists. Tooby and Cosmides (2005) state that one reason evolutionary psychology is distinct from anything resembling human sociobiology "lies in its rejection of fitness maximization as an explanation for behavior."

Despite this difference in theoretical position much research in the two disciplines is structured similarly. Behavioral ecologists almost always ignore the number of offspring produced and study, instead, how a particular adaptation contributes to some fitness proxy, for example, net energy intake rate (e.g., Giraldeau and Caraco, 2000; Figure 6.1). Evolutionary psychologists may study mate choice (Buss and Schmitt, 1993) or resource distribution (Smith, Kish and Crawford, 1987). Reeve and Sherman (2007) argue that any test of a hypothesis concerning the adaptive significance of human behavior must include a fitness value or payoff, but this need not be number of offspring. It could as easily be

men's copulatory frequency or nutritional outcomes for mothers (Borgerhoff Mulder, 2007), and one need not resort to counting babies (Crawford, 1993).

Borgerhoff Mulder (2007) argues that only the more extreme positions (always or never counting offspring) are problematic and are largely responsible for creating the division between the disciplines. What the researcher measures depends entirely on whether or not they define an adaptation in terms of its current function or in terms of its evolutionary development. Reconciling the differences and increasing communication between the disciplines, therefore, may be mainly a matter of moderating these extreme positions.

Communication between the disciplines and calls for its improvement are nothing new (Daly and Wilson, 1999; Hutchinson and Gigerenzer, 2005). But to easily evaluate and apply the theories and findings of one discipline to the experimental subjects of the other requires a common conceptual framework with agreed-upon definitions. The purpose of the present paper is to propose exactly that. First, we describe a conceptual framework that gives an evolutionary (i.e., adaptive) context for organizing and examining informational inputs, decision rules, and outputs. Next, we define the framework's component parts. We then give examples (based on instances found in the literature) of how both simple and complex behaviors of both humans and non-human species can be analyzed within our framework. Lastly, we provide a discussion and some conclusions about the framework's utility for behavioral ecology and psychology.

The Adaptive Behavioral System (ABS)

Description

An adaptive behavioral system (ABS) is a conceptual framework which analyzes and organizes behavior within an evolutionary context with reference to an organism's life history tasks. It regards mechanisms with behavioral outputs as adaptations, at least in terms of the environment in which the mechanisms evolved. Thus, like Hutchinson and Gigerenzer's (2005) argument of "ecological rationality", the ABS avoids the necessity of demonstrating that today's environment is the same as the "environment of evolutionary adaptedness" (Tooby and Cosmides, 1992). The primary assumption of an ABS is that the mechanism has been shaped by natural selection and has evolved because of its contribution to an organism's inclusive fitness.

An ABS looks first at behavior in terms of the general and specific life history (adaptive) problems it might address. It then considers three stages or processes of decision-making and response production: (1) Inputs - information (in one form or another) from the internal and external environments of the organism; (2) Information processing and selection of outputs using particular decision rules; and, (3) Outputs – the behavioral, somatic, affective, and cognitive tactics which are finally applied and may be typically observed.

The "Mechanism" Problem: Process or Structure?

Considerable imprecision currently exists, at least in the literature of evolutionary psychology, in distinguishing between the structure which accomplishes the information processing-decision making and the processes which it runs. As already noted in the Introduction, evolutionary psychology frequently uses the label "psychological

mechanism" to refer to tactics, decision rules, *and* to the physical structure which administers them. Part of the confusion may be due to the fact that we usually do not know the exact neurological components which accomplish information processing-decision making tasks. Part may come from the inexactitude of the terminology. When authors refer to a "mechanism", it is not always clear whether they are referring to a structure or a process. As a means of avoiding this confusion, the ABS includes a hypothetical structure for the second stage, the Evolved Processing Unit (EPU).

The Evolved Processing Unit (EPU)

Although much of the current terminology used in behavioral analysis comes from game theory (e.g., strategies, tactics, etc.), a more useful analogy for the information processing, decision-making structure might exist in the field of computing. A computing system can be regarded as being organized not unlike an ABS: its complex structure is typically broken into input (and input devices), processing or computing, and output (with output devices). The physical structure which carries out the computing or information processing is the Central Processing Unit or CPU. If the term "evolved" is substituted for "central", CPU become EPU, the acronym for "evolved processing unit." The Evolved Processing Unit (EPU) is the information processing-decision making structure of the ABS.

The function of an EPU is to run the inherited, genetic programs (the decision rules by which an organism's response to environmental input is determined), to select the particular tactics employed by the strategy (Gross, 1996), and to trigger a particular response. Thus, an EPU receives environmental input, processes that input in terms of possible costs and benefits (the particular "if-then" program which the EPU runs), and selects an appropriate output. This does not preclude the possibility that learned "programs" may also mediate behavior and should sometimes be included in an ABS. As an evolved processing unit, however, the EPU is constrained by natural selection acting on genetically transmissible information. The ability or tendency to learn "programs" might more appropriately be regarded as a tactic which the EPU invokes (See Definition of Terms).

The Boundaries of an ABS

While all adaptations function ultimately within the context of inclusive fitness the scope of a particular ABS, i.e., its boundaries, is largely determined by the specific problem it addresses. Defining the scope of that problem is largely at the discretion of the researcher. This discretion is similar to that required of a modeler in setting the strategy set and rules of thumb for a proposed behavioral model (Hutchinson and Gigerenzer, 2005). An ABS is not "a basic building block" or indivisible unit of behavior. Smaller ABSs may be nested in one or more larger, more encompassing ABSs, and may be shared by others which are non-related. For example, an ABS for ingesting available food when hungry can be organized within an ABS for foraging; an ABS for foraging may also include an ABS for searching for the food to be ingested and an ABS for fighting. The ABS for fighting could also be included in other ABSs which have nothing to do with food (e.g., mate competition). Thus, an ABS may be constructed by someone wishing to analyze a particular response to a particular stimulus or by someone wishing to take a broader view. The boundaries of the ABS are largely determined by the boundaries of the task to which it is applied.

A desired goal of any conceptual system should be not only to explain observed behavior but also to produce predictions which can be subsequently tested by experiment (Hutchinson and Gigerenzer, 2005). Such predictions are the foundation of any scientific investigation and their confirmation will also provide the support required to substantiate the validity of any hypothesized ABS. Thus, an ABS should not only describe and explain the behavior observed in a particular species, but it should describe and explain it in a way that generates testable predictions. This is accomplished in the final component of an ABS description, the Observed/Predicted Behavioral Output.

Definition of Terms

The inputs, decision rules and outputs included in an ABS are broken into and analyzed according to the following categories: General Adaptive Problem; Specific Adaptive Problem; Strategy; EPU; Decision Rule(s); Tactic(s); and, Observed/Predicted Behavioral Output.

Adaptive Behavioral System (ABS): a conceptual framework which organizes the informational inputs, decision rules, and behavioral outputs by which an organism attempts to interact adaptively with its environment.

General Adaptive Problem: Ultimately, a problem of survival or reproduction, (the determinants of fitness), but may refer to a specific set or sub-set of problems in a hierarchy, e.g., mate selection.

Specific Adaptive Problem: The specific problem which the strategy, EPU, decision rule(s), and tactics address.

Strategy: A summary description of one or more decision rules used to achieve a goal (i.e., solve a specific problem of survival/reproduction) through the use of its selected tactics and which is in evolutionary competition with other strategies.

EPU: a physiological and/or morphological structure by which a strategy is instantiated.

Decision Rule: An operational definition of the strategy encoded in the EPU.

Tactics: cognitive, affective, somatic, and, ultimately, behavioral outputs of a decision rule by which accomplishment of the strategy is attempted.

Observed/Predicted Behavioral Output: Behavior typically observed or predicted as a result of the decision rule.

Selected Examples of Adaptive Behavioral Systems

The following examples were selected to represent both simple and complex behavior of both humans and non-human species, and many use observed behavior cited in the literature of behavioral ecology and/or psychology. The intention is to demonstrate the range of behaviors which can be captured by the ABS framework. Because one of the major benefits derived from including an EPU within an ABS is the clear separation created between the physiological or morphological mechanism and the program which it runs, one or more EPUs consisting of sets of neurons are hypothesized for each of the examples provided. These EPUs are included purely for illustrative purposes, and we do not wish to imply that these exact neural mechanisms actually exist and perform the described duties (although they may). These hypothetical structures merely describe how neural networks might be involved in solving the particular ecological problem and

acknowledge that larger problems often consist of several smaller problems. Other neurophysiological structures could also be proposed.

Choosing Where to Live
Species: Planarian.
General Adaptive Problem: Survival.
Specific Adaptive Problem: Choosing a safe habitat.
Strategy: Select the habitat with the lowest risk of being detected by a visual predator.
EPU: Two paired, fronto-lateral photoreceptors which fire at a rate based on the intensity of stimulation (faster for brighter light), and a set of a few neurons which compares the firing rates of the photoreceptors and stimulates muscles contra-lateral to the side with the lowest firing rate or intensity.
Decision Rule(s): Always choose the darkest available location.
Tactic(s): Muscle contractions leading to l/r turn.
Observed/Predicted Behavioral Output: Planarians move towards and gather in dark areas.

Obtaining Energy to Live (1)
Species: All.
General Adaptive Problem: Survival.
Specific Adaptive Problem: Obtaining/replacing energy used in metabolic activities.
Strategy: Intake energy whenever needed.
EPU: Sets of neurons which fire when cellular activity decreases, or when energy reserves (e.g. fat) are low, or are being depleted, and which initiate foraging behavior for the appropriate food.
Decision Rule(s): Hunt for food when reserves are low.
Tactic(s): Search, capture, eat.
Observed/Predicted Behavioral Output: Foraging, feeding.

Obtaining Energy to Live (2)
Species: Chickadee.
General Adaptive Problem: Maximizing net energy intake rate (NEIR).
Specific Adaptive Problem: Choosing between habitat patches with variable amounts of food.
Strategy: Remain in a patch if NEIR is above the habitat average.
EPU(s): One set of neurons fires at a "many captures" rolling average rate (habitat average). A second set of neurons suppresses firing of the first set by an amount corresponding to a memory trace of migration travel time/cost between patches. A third set of neurons clocks time since last prey capture and if the time exceeds the inverse of the adjusted "many captures" rolling average rate, the chickadee leaves the current patch to forage elsewhere.
Decision Rule(s): Change patches when time between captures exceeds giving up time (GUT).
Tactic(s): Remain/depart, foraging, feeding.
Observed/Predicted Behavioral output: Chickadee leaves/stays in patch when food availability is low/high (Smith and Sweatman, 1974).

Avoiding Toxic Food
Species: Human.
General Adaptive Problem: Avoiding toxic substances.
Specific Adaptive Problem: Preventing the assimilation of allylisothiocynate when ingested as it prevents normal uptake of iodine into thyroid tissue.
Strategy: Expel any food ingested containing allylisothiocynate (especially when most susceptible).
EPU: A group of neurons sensitive to the presence of allylisothiocynate which trigger gagging, spitting, and/or vomiting when they fire, but whose firing threshold increases with development.
Decision Rule(s): gag, spit, vomit if allylisothiocynate detected.
Tactic(s): Gagging, spitting, vomiting.
Observed/Predicted Behavioral output: Gagging, spitting, vomiting (especially during childhood) whenever broccoli and/or Brussels sprouts are ingested (Nesse and Williams, 1994).

Finding a Mate (1)
Species: Moth - Male.
General Adaptive Problem: Reproduction.
Specific Adaptive Problem: Locating a female partner.
Strategy: Locate a female partner by backtracking a pheromone plume.
EPU: One group of neurons which detects wind direction, one group which fires when female pheromone detected and triggers up-wind flight; a second group of neurons which detects cessation of firing in first set and triggers back and forth cross-wind flight.
Decision Rule(s): Head upwind when pheromone detected; cast back and forth if plume suddenly disappears.
Tactic(s): Fly, turn l/r.
Observed/Predicted Behavioral Output: Males approach a female dispensing pheromone (Kennedy, 1983).

Finding a Mate (2)
Species: Scorpionfly - Male.
General Adaptive Problem: Reproduction.
Specific Adaptive Problem: Securing mating opportunities.
Strategy: Choose the mating tactic with the greatest expected fitness given current constraints.
EPU: Assuming a sexual interest has been triggered, a set of neurons fires at a rate commensurate with the scorpionfly's condition – at a high rate if the scorpionfly is capable of capturing food, at a low rate if it is in relatively good condition but not good enough to capture a food item. If the neuron set fires at a high rate, a food item is caught and used to attract females; if the neuron set fires at a low rate, a salivary mass is secreted and used to attract females; if the neuron set fails to fire, the male searches for and attempts forced copulation with a female.
Decision Rule(s): If food availability and physical condition permit, capture prey and offer it to female (preferred tactic); if no prey can be captured but physical capability exists, offer

salivary mass to female (second choice); if no prey can be captured but not physically capable of secreting salivary mass, attempt forced copulation (third choice).
Tactic(s): Prey capture, prey offering, saliva secreting/offering, forced copulation.
Observed/Predicted Behavioral Output: Depending on the physical capability of a male scorpionfly and the availability of food items, capable males choose first to fertilize a female by offering a potential mate captured prey, second a gift of salivary mass. If all else fails, a male attempts forced copulation (Thornhill, 1981).

Increasing Number of Offspring
Species: Meadow vole - Male.
General Adaptive Problem: Maximizing number of direct descendents.
Specific Adaptive Problem: Overcoming limited reproductive potential of a single female.
Strategy: Maximize the number of females inseminated.
EPU: Neurons which fire and increase hormonal levels when a female is encountered; another set of neurons which "records" a memory (sight/smell) of a female after intromission-ejaculation and fires, inhibiting the firing of the first set when a "familiar" female is later encountered; a third group of neurons which fires when it detects increased hormonal levels and triggers sexual approach to the female.
Decision Rule(s): Only approach novel females.
Tactic(s): Sexual interest/disinterest, approach, avoidance.
Observed/Predicted Behavioral output: male preference for novel females, mate switching, polygyny (Dewsbury, 1981).

Improving Viability of Offspring (1)
Species: Bushcrickets.
General Adaptive Problem: Maximizing quality of offspring.
Specific Adaptive Problem: Choosing the highest quality male.
Strategy: Always select the loudest calling male.
EPU: "A simple negative feedback loop in the ear of bushcrickets which adjusts the sensitivity of the ear according to the loudness of the signal. The consequence is that the female's brain is totally unaware of all but the loudest male cricket in the vicinity." (Römer and Krusch, 2000). A set of a few neurons which compares the firing rates of the two ears (audio receptors) and stimulates muscles on the side with the lowest firing rate or intensity.
Decision Rule(s): Approach the loudest calling male.
Tactic(s): turn l/r, approach.
Observed/Predicted Behavioral Output: "The consequence behaviorally is a rule of thumb for mate choice of simply heading toward the male that appears loudest" (Römer and Krusch, 2000).

Improving Viability of Offspring (2)
Species: Human – Female.
General Adaptive Problem: Survival of offspring.
Specific Adaptive Problem: Ensuring adequate paternal support for mother and offspring.
Strategy: Accompany ovulation with sexual interest only when in a committed relationship.

EPU: One group of neurons which fires at an increasing rate when it detects an internal state of "romantic commitment" to a male partner (output from another ABS); another neuronal group which fires when it detects the hormone precursor of ovulation; and a third which fires (triggering sexual interest and associated behaviors) when it detects the firing of both of the other neuron sets.
Decision Rule(s): Generate state of sexual interest when ovulating, but only if committed to a partner.
Tactic(s): Sexual interest (becomes input to appropriate sexual behavior ABS).
Observed/Predicted Behavioral Output: Only women committed to a relationship demonstrate a change in sexual desire over the menstrual cycle, with the peak occurring around the time of ovulation (Pillsworth, Haselton and Buss, 2004).

Avoiding Predators and Disease
Species: Human.
General Ecological Problem: Survival.
Specific Ecological Problem: Maintaining good health by avoiding disease.
Strategy: Avoid likely contagious carriers/sources of disease.
EPU: A set of neurons which records memory (physical appearance, smell, etc.) of average ingroup members, a second set of neurons which compares present conspecifics with memories of ingroup members and fires when non-normative comparisons are detected, and a third set of neurons which trigger an internal state of disgust and other behavioral and cognitive responses that compel avoidance.
Decision Rule(s): Avoid any conspecific with physical/behavioral features that are judged to be normatively unusual.
Tactic(s): Encoding, retrieval, and comparison of memories; avoidance, disgust.
Observed/Predicted Behavioral Output: avoidance of and prejudice towards those who are asymmetrical, disabled, or members of unfamiliar ethnic outgroups (Schaller, Park and Faulkner, 2003).

Discussion

As soon as one begins to analyze an organism's observed behavior within an ABS, several issues become apparent. First, as obvious as it seems, both evolutionary psychology and behavioral ecology should distinguish between processes in which *behavior* is involved and processes where it is not (Cosmides and Tooby, 1987). Both disciplines focus on behavior for their studies (Hutchinson and Gigerenzer, 2005), and, ultimately, an ABS should do the same. The problem of an organism's obtaining energy to sustain cellular activity might be framed in terms of chemical transport across a cell membrane, feeding behavior, or patch choice, but both behavioral ecology and evolutionary psychology are concerned primarily with the latter two. Second, as noted previously, behavioral analysis can occur on many levels, and no level of analysis is more "correct" than any other. Both foraging and patch choice also include feeding. Patch choice includes foraging as well. The scale of the ABS described is determined by the level of analysis desired by the researcher. Furthermore, the researcher can conceptualize several ABSs as being

structured hierarchically – the output of one ABS becoming the input of another – reminiscent of Tinbergen's model of behavior (Tinbergen, 1951).

Each major task or problem can be broken into tasks and sub-tasks. The output of any set of decision rules may accomplish a task directly (through a tactic), or may lead to another set of decision rules (another strategy). Some problems are solved by solving two or more concurrent problems (Hutchinson and Gigerenzer, 2005) or by solving two or more consecutive sub-problems, i.e., solution of the first sub-problem provides the informational input needed to solve the second sub-problem, and so on. Some problems may require solving a number of concurrent sub-problems which may not be linked directly, but the solutions of which are all needed to solve the "meta" problem. In the example of sexual interest in the human female, detection of both a committed relationship *and* ovulation were required to produce the increased interest. A variation of concurrent sub-problems is described by Hutchinson and Gigerenzer (2005) where a non-sequential combination of cues (information from any subset of several cues within a larger set) is required to reach a threshold triggering the behavior.

Another issue mentioned earlier but deserving further elaboration concerns the Evolved Processing Unit (EPU). Ironically, one of the greatest benefits to evolutionary psychology and behavioral ecology in defining the EPU might be that once defined, the EPU can be set aside and attention shifted elsewhere. Behavioral ecologists and evolutionary psychologists are concerned primarily with how organisms *respond* to their environments (their decision rules and behavior), rather than with the morphological or physiological mechanism which administers those processes (Cosmides and Tooby, 1987). Concern with the mechanism itself is more properly the interest of disciplines such as neuroethology (Camhi, 1984), and great strides are being made in elucidating the neural basis of decision making (Schultz, 2004). This does not mean, however, that it is not beneficial to include the EPU when considering an ABS. Defining its hypothetical structure does much to eliminate the confusion between structure and process which currently exists. Furthermore, as can be seen in the examples provided above, describing even a hypothetical structure may be valuable in helping to analyze the process(es) undertaken by the organism in its problem solving or cost-benefit evaluation and that analysis can produce other testable hypotheses.

Another benefit obtained from defining an EPU within the framework of the ABS, is the clarification it gives to the "behavior-as-adaptation" confusion often encountered in the literature. Despite how both behavioral ecology and evolutionary psychology sometimes refer to it (Alcock, 2005; Buss, 2004), behavior is not an adaptation; it is the tactical output of an adaptation. By defining behavior as a tactic employed by an EPU, the ABS eliminates this problem and this source of possible confusion.

Each ABS and, thus, each set of decision rules it includes, is bounded by the perceived environmental information relevant to the particular adaptive problem being considered. Similarly, all tactics available to the organism are limited by the constraints of the possible phenotype set available to the animal and the morphological and physiological constraints on what the animal can/cannot do including its "evolutionary baggage" (Gould, 1989).

The organizational structure of the ABS also provides for current theories of state dependence (Clarke and Mangel, 2000). If secretion of a hormone is a tactic, and the presence of the hormone brings about a particular internal state, then that state must also be

a tactic. Giske et al. (2003) has produced a model of simulated genotypes that develops "feelings" or affects which influence the genotypes' survival and reproduction. Similarly, generalized internal states such as rage or fear are more appropriately defined as tactics (outputs), and if denoted as the output of one ABS they may also function as inputs for another ABS. Thus, within this framework, internal states are not regarded as psychological mechanisms, as they are by some researchers in the field (e.g. Buss, 2004).

Use of the term "tactics" within the ABS necessitates a few words to help distinguish them from "strategies" – two terms often used interchangeably in the literature (Gross, 1996). In practice (at least as included within an ABS), strategies can be easily differentiated from tactics. Strategies involve decisions; tactics do not. Strategies produce outputs based on informational inputs and the inherited decision rules. Tactics are those outputs. Tactics are selected by the decision rule, but involve no decision-making themselves. Finally, only strategies are in evolutionary competition with one another.

Lastly, it might be noted that the approach of the ABS to organizing behavior is very similar to how computer scientists have analyzed behavior when producing artificial life (Terzopoulos, 1999). Giske et al.'s (2003) model of artificial reproducing agents with its framework of inputs, decisions, and outputs is similar to the ABS. DiPaola, Akai, and Kraus (2007) developed a "virtual beluga" for display in aquaria by programming a computer with a similar framework of inputs, "action selection mechanisms", and outputs. Approaching behavior from the "bottom up" of computer programming seems to yield a remarkably similar analysis to the "top down" analysis of the ABS.

Conclusions

The ability of the adaptive behavioral system (ABS) to narrow the gap existing between the conceptual thinking of behavioral ecology and evolutionary psychology can be seen in the two examples included under the heading Improving the Viability of Offspring. Both behavioral ecology and evolutionary psychology have dealt with the problems of mate selection, sometimes from very different angles. Putting such studies into the framework of the ABS, however, draws attention to the commonalties. Both bush crickets and humans can contribute to their own fitness by improving the viability of their offspring by choosing mates which possess either "good" genes and/or the necessary resources. When the female bush cricket perceives "only the loudest male cricket in the vicinity" (Römer and Krusch, 2000), it is attracted to choose the most suitable, available mate. When the human female experiences sexual interest when ovulating only when committed to a partner (Pillsworth et al., 2004), she engages in a fundamentally similar process. Commitment to a relationship, like attraction to the loudest call, is presumably a filter for choosing appropriate co-parents.

The conceptual framework of the ABS appears capable of organizing most if not all examples of behavior of both humans and non-human species. Because of its widespread applicability, the ABS can become an important conceptual tool of evolutionary psychologists and behavioral ecologists alike. Not only can it produce consistency in behavioral analysis in an evolutionary framework within each discipline, it effectively builds a bridge between behavioral ecology and evolutionary psychology. Through the use of such a framework, the findings and methodology of each discipline may be applied or compared to those of the other. Testing the theories of each with the subjects of the other can lead to a more robust understanding (Hutchinson and Gigerenzer, 2005), and the end

result can only be mutually beneficial.

Fitness will always be a factor, whether acknowledged or not, in any analysis of adaptations. Those organisms with the most efficient adaptations and/or the most efficient ABS will tend to leave more offspring and have higher fitness than those with a less efficient ABS. But this is not to say that any organism, human or otherwise, intentionally tries to maximize fitness, and neither is it to say that the proximate purpose of any given adaptation is to increase fitness. This confusion may be an unfortunate result of the "shorthand" often employed by practitioners within the disciplines. Regardless of their ultimate function, the vast majority of adaptations do not *directly* increase an organism's reproduction. Instead, they may serve only to increase foraging efficiency or to decrease possible negative effects of incest. Few organisms, if any, have the wherewithal, never mind the desire, to know how fitness might be maximized.

Declaring the difficulty of measuring fitness, or appreciating that adaptations often contribute to fitness only indirectly, however, does not mean that fitness is not still part of the overall equation. Although few studies in either discipline will actually engage in counting offspring, any declaration by evolutionary psychologists that fitness is, therefore, irrelevant immediately begs the question: In what sense is evolutionary psychology truly evolutionary? Fitness is the basis of natural selection. Remove fitness, and you must come up with a replacement driver of the evolutionary process.

The conceptual framework proposed here is based on evolutionary logic and is consistent with both behavioral ecology and evolutionary psychology. The ABS rests on the assumption that genetically predisposed behavior is influenced by and influences an organism's life history. The organism approaches its life's tasks through the making of a series of strategic choices (using inherited decision rules) and deploys various tactics which should serve, on average, to increase its fitness. How the need to carry out these life history tasks affects the organism's behavior, and the strategies, decision rules, and tactics the organism employs is the core business of both disciplines. The conceptual framework of the ABS can help each discipline focus more consistently on that business, ultimately, we hope, to the benefit of both.

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