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## 7. Applications of Artificial Intelligence to Animal Behavior

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### INTRODUCTION

The conceptual tools used to investigate animal behavior not only limit our abilities to explain reality, they also reflect the ways in which human thought processes are structured by biological organs and cultural legacy. Two styles of thinking, "linear" and "synthetic" (Table 1) represent diverse approaches to the study of animal behavior. Conceptual tools developed in the field of artificial intelligence (AI) provide ways of integrating these two styles. AI tools match the way biologists think about behavioral processes. In essence, AI programming is a reflective "backside of the mirror", shared in common by scientists from different disciplines.

Miscommunication regarding interpretation and explanation of animal behavior has occurred when researchers differed in their definition of and style of addressing a problem (e.g. Beach 1950; Lehrman 1953; Lorenz 1965). In other realms of human interaction, two individuals functioning under different styles of thinking are likely to interpret a phenomenon differently and disagree over an explanation of the phenomenon, even though each may be accurate from their own limited perception of the world (Harrison & Bramson 1982; Tanenbaum 1989).

The integration of linear and synthetic styles of thinking in AI programming resulted from a stimulating and lengthy debate over how (and whether) computers can be programmed to mimic the human mind (Dreyfus 1979; Waltz 1982; Searle 1984; Denning 1986). Our purpose in this chapter is to explain that even though AI may not have yet achieved the goal of making computers act as if they think, AI does provide powerful tools for integrating linear and synthetic approaches to interpreting, explaining and predicting animal behavior.

Table 1. Characteristics of two styles of thinking, which often result in miscommunication regarding interpretation and explanation of animal behavior.

Source	Linear style	Synthetic style
Lorenz 1977	<u>"objective"</u> experimental approach test hypotheses analysis deduction; logic	<u>"subjective"</u> comparative approach develop hypotheses understanding induction; intuition
Harrison & Bramson 1982; pp 98-99	<u>"analyst"</u> general rules describes things systematically offers substantiating data structured, rational examination reason, logic	<u>"synthesist"</u> concepts; opposing viewpoints speculative arguments ignores data qualifying phrases humor, sardonic
Searle 1984; pp 71-75	<u>"scientific explanation"</u> physics and chemistry prediction deduce what will happen regularity within a population straight forward laws of statistical mechanics same result from same path	<u>"common sense explanation"</u> natural science explanation deduce what has happened individual variation complex interrelated networks different paths lead to same result
Tanenbaum 1989 pp 58, 85, 95, 109 158-159	<u>"male"</u> sequential ideas slow process focused on one idea and problem impose limitations, follow rules to maintain order start with component parts Interruptions resisted continuity important define concepts	<u>"female"</u> random information and ideas rapid insight several simultaneous problems ignore preset rules and regulations to address problem start with overview interruptions not a problem change/ improvement welcome explore and play with ideas
Application to models of animal behavior in present paper	linear programming stepwise flowchart create one model cause and effect population-level rules prespecified parameters rules of behavior do not change confounding variables controlled spatially homogeneous, constant environment large populations forward chaining	parallel process programming modular structure create alternative models cyclical individual level rules dynamic linkages changing rules of behavior variables not controlled suitable for heterogeneous, fluctuating environment small populations backward chaining

As long as explanation is an acceptable goal for the study of animal behavior, no synthesis is needed. However, if scientists seek to apply knowledge of animal behavior to managing populations affected by human activities, the integration of linear and synthetic approaches is imperative. This integrative task is a challenge, because when we talk about a synthetic structure of behavior, we tend to lose those readers who operate from primarily a linear style. Likewise, synthetic thinkers have difficulty following a logical development of AI applications to modeling behavior. However, despite evidence that differences in the predominant style of thinking may be as deeply rooted as biological differences between individuals (Tanenbaum 1989), we retain faith that each reader can comprehend both styles when the difference is made explicit (Harrison & Bramson 1982).

Thus, this chapter is intended as an overview to provide entry to the animal behavior literature for those who are well versed in AI and an introduction to "soft" AI programming tools for those who study animal behavior. Since the jargon in both fields has become dense, references to semi-popular as well as technical works are included. Wherever possible, we refer readers elsewhere for definition of concepts. Our purpose is to give an overview, in typical synthetic style, exploring relations among ideas by discussing concrete examples.

In this chapter, we seek (a) to define a basic integrative structure used by ethologists in analyzing behavior, (b) to identify some of the limitations of linear approaches to modeling behavior in heterogeneous environments, and (c) to illustrate some ways that AI concepts can be used to overcome such limitations. This is quite a different approach from the usual discussion of how artificial intelligence relates to the cognitive capacities demonstrated by human and nonhuman animals. Thus, we first provide some background so readers have a better perspective on the experiences that have shaped our view of the question "how have conceptual tools influenced the interpretation and explanation of behavior."

## BACKGROUND

When Konrad Lorenz sat next to the moor pond and lectured his student assistants on the basic concepts of ethology, he used common mechanical analogies that even the untutored mind could understand, such as the description of motivation subsequently criticized as the "flush-toilet model" (Nisbett 1976; Lorenz

1981; Toates 1986). Working on his philosophical treatise titled *Behind the Mirror* at the time (Lorenz 1977), Lorenz was intensely interested in how our own perceptual capabilities shape our views of reality and the way we approach science. He was interested in explanation, not prediction. He argued that the linear and synthetic approaches were both necessary for good science, citing the productive collaboration when Niko Tinbergen was able to test the hypotheses that arose from Lorenz's intuitive knowledge base.

Our research group has been stimulated to readdress this issue from quite a different perspective as we tried to communicate across disciplines in which people formulate the basic question of "knowledge representation" in quite different ways (Table 2). For the modern ethologist, computer models have become an extension of perceptual capabilities, generating predictions against which reality can be tested. However, it is difficult to communicate with nonspecialists about the structure and content of such models. Mechanical analogies such as flush toilets and thermostats were common knowledge of an earlier era, unlike the sophisticated gaming, optimization, homeostatic, time-sharing, and contingency models of today.

Our research group has been interested in modeling population dynamics and animal movements in patchy environments that are not stable over time (Coulson et al. 1987; Makela et al. 1988; Saarenmaa et al. 1988; Folse et al. 1989; Roese 1989). This set of problems required a synthetic as well as a linear perspective, because it violated the assumption of a homogeneous, constant, environment containing animals that behave like gas particles or unintelligent robots. We needed to test alternative models to be able to deduce rules of behavior based on how the animal rather than the investigator perceives the environment.

Using a synthetic style, we sought to develop and share a basic "shell program", or common structure, containing modules that could be expanded to model the content of both invertebrate and vertebrate behavior. We encountered the practical problem that the computer programmers on our team had little experience with animal behavior or behavioral concepts. Their first inclination was to generate their own structures for behavioral processes.

For effective interdisciplinary communication, we needed to address the differences in knowledge base as well as different styles of thinking. These two components of "knowledge base" and

**Table 2.** Questions raised by separate disciplines involved with creating models of knowledge representation.

Discipline	Question	References
Computer engineer	How can machines be designed to operate beyond human capabilities?	Albus 1981; Raibert & Sutherland 1983; Poggio 1984 Denning 1985
Knowledge engineer Van Horn	How can computers be programmed to solve similar to human experts?	Kurzweil 1985; Bobrow & Stefik problems 1986; Davis 1986; 1986
Philosopher	How does human knowledge match the real world?	Dennett 1984; Tennant 1984; Denning 1986
	Can computers think?	Searle 1984
Experimental psychologist	What is the most parsimonious way of representing human interactions with the real world?	Rolls & Rolls 1982; Staddon 1983; Toates 1986
Comparative psychologist	To what extent do other species solve problems the way humans do?	Dewsbury 1978; Pearce 1988; Colgan 1989
Ethologist	How does an animal's knowledge match the real world?	Tinbergen 1951; Lorenz 1981; Boden 1984; Alcock 1989
Behavioral ecologist	How are animals designed to solve ecological problems?	Krebs & McCleery 1984; Stephens & Krebs 1986; Alcock 1989
Simulation modeler	How can computers be programmed to behave like animals, populations and ecosystems?	Hassell & May 1984; Starfield & Bleloch 1986; Reiter 1986; Saarenmaa et al. 1988; Folse et al. 1989
Resource manager	How can a computer help people solve problems involving management of biological resources?	Rykiel et al. 1984; Marcot 1984; Starfield & Bleloch 1986; Coulson et al. 1987

"procedures" are basic to the manner in which AI programming mimics human thought processes involved in knowledge representation (Davis 1986).

As a result of a linear style of analysis, the knowledge base in behavioral studies has been separated into components of motivation, learning, perception and coordination of action patterns. A synthetic overview of these components is provided in the following section. The examples used below to illustrate the concepts represent a common knowledge base for anyone who has had a basic course in animal behavior. They were chosen so readers unfamiliar with the behavioral literature could understand the knowledge base from which the overview was derived.

## THE BASIC STRUCTURE OF BEHAVIORAL PROCESSES

Dennett (1984) warned computer programmers against rediscovering "cognitive wheels" already designed in other disciplines. The cognitive structure used in the study of animal behavior is outlined in Figure 1. The input and output of the system is defined as stimulus and response messages, respectively. The four components of this basic structure include: perception, action, motivation, and learning systems.

This basic structure of behavioral processes has been similar throughout the works of the classical ethologists to the present day. Admittedly, the ways in which this structure is described have varied among disciplines over the years. We choose to describe this structure using terms common to AI, to better suggest the appropriate application of techniques described in the last section of this chapter.

We think of this structure as a basic "shell" for knowledge, which could be made operational in a work environment such as that provided by an artificial intelligence style program shell (e.g. Glymour et al. 1987; Richmond et al. 1987). These four components of the basic shell are described in more detail in the following subsections.

### Stimulus and response messages

The basic structure of behavior typically is represented as a series of stimuli and associated responses, as if there are sets of external objects and internal objects, which "pass" messages to one another (Figure 1). In this subsection, we discuss the



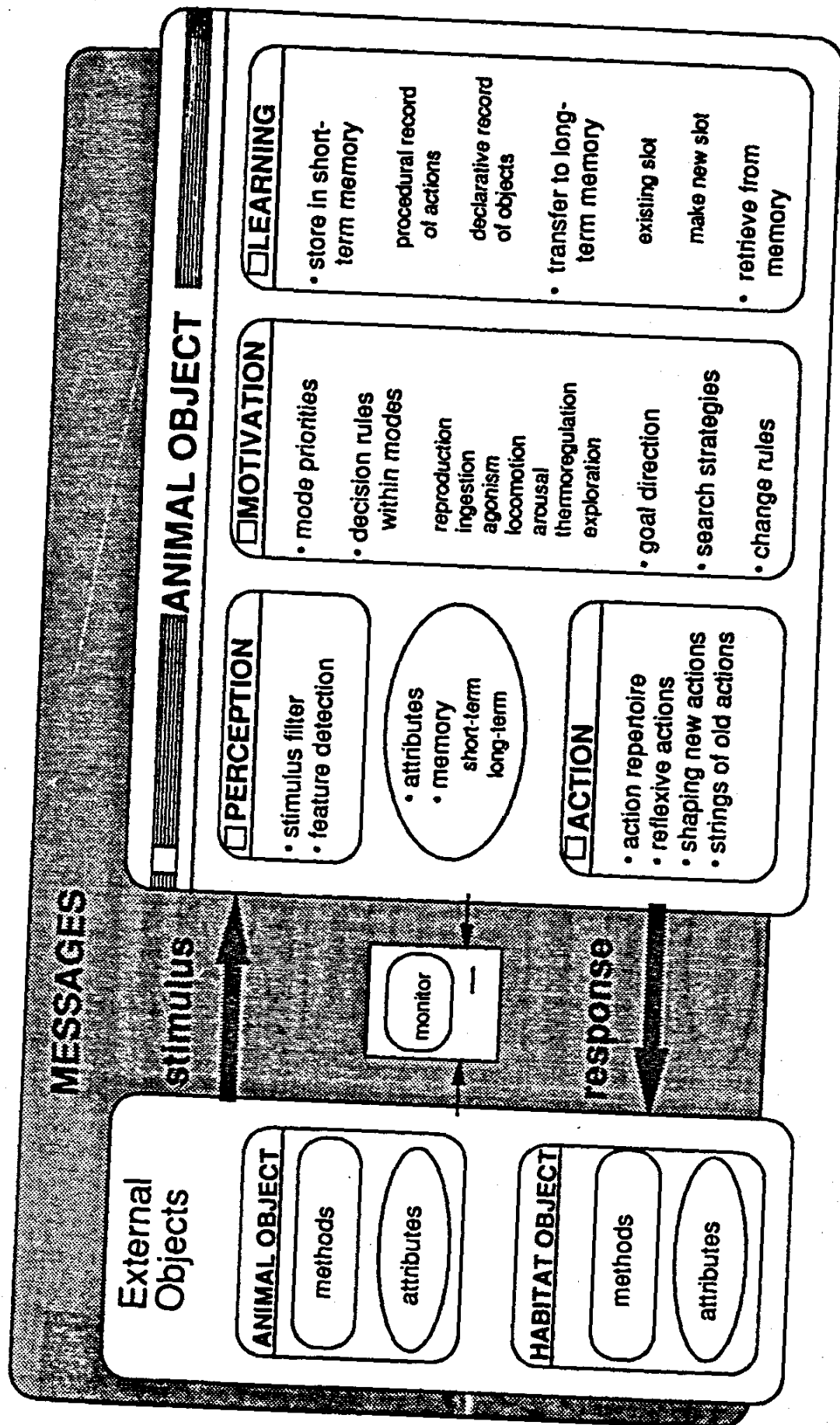


Figure 1. Basic shell structure of animal behavior.

concepts of a dichotomy between internal/external information and the message versus the meaning of a stimulus.

The pairing of stimulus and response is central to all analyses of behavior and must be clarified prior to looking at the separate components. When the stimulus message always elicits the same response message, the process is considered to be relatively hard wired, or innately determined by developmental processes resistant to environmental perturbation (Heuer & Sanders 1987). When the correspondence between stimulus and response is not one to one, intervening variables influencing the meaning of the message are important. The intervening variables (processes) are the components we identified above as motivational systems and learning (Staddon 1983; Toates 1986).

The internal/external dichotomy. Our human perceptual apparatus makes an artificial distinction between processes within the body, relatively hidden from view, and visible processes outside the body. An obvious analogy is the input and output of a computer program, the contents of which remain a "black box" for the outside observer who can only monitor what goes in and what comes out.

This dichotomy sometimes is confusing to the introspective synthesist who accepts mental states as part of reality (see Dupré Volume I). Are you not aware of the internal messages sent by a gnawing, empty stomach? The major issue is that an external observer is unaware of your internal messages, unless that observer has some way of monitoring what happens inside. A linear style of thinking requires special tools to collect data on what goes on inside other organisms. Thus, linear thinkers reserve the concept of "stimulus" to refer to information originating outside the organism and reject the notion of mental states. To the synthetic thinker, the information exchanged between two objects is a "message", whether it is from outside or inside the organism. To avoid confusion in the general structure of animal behavior, we reserve the term "stimulus message" to refer to information of external origin.

In the modeling of internal systems, a synthesist would treat a system as a series of components, or interactive objects. For example, the internal processes of the stomach appear relatively hidden from the conscious processes of the brain until a certain threshold is reached. A threshold can be modeled as a decision point at which a message is passed between internal objects. This

is the approach used by object-oriented programming as we will describe later.

From a synthetic approach, the basic structure of behavior is a way of representing knowledge and does not imply a direct correspondence to physiological systems. In contrast, computer representations of information processing in neuronal networks have been developed (Poggio 1984; Ullman 1986; Tank & Hopfield 1987) and criticized as inadequate to ever represent the functions of a mind (Searle 1984). Whether computer models of neuronal networks represent a mind, or predict behavior, may be irrelevant to the neurophysiologist seeking better ways to represent interactions among neurons that are known to be branched rather than linear processes. Our brains are inadequate to understand much more than the input and output of such complex neuronal network computer models.

Message vs. meaning. How simple the study of animal behavior would be if the same stimulus message always resulted in the same response message. However, the meaning of a male songbird's song differs for another territorial male, a nonterritorial floater male, or a nesting female. In response to the same song, the neighboring territorial male approaches and displays, the floater male leaves quietly, and the nesting female remains nearby the singing male. A linear approach to determining general rules of behavior for animals is quite different than that required for billiard balls because the internal state of the animal changes.

The difference between the message and the meaning lies in the way the stimulus information is processed (see Smith 1977 and in Volume I). Not only is the information processed differently by intervening factors described as motivational systems, the roles of learning and developmental history of individuals are also important. For this reason, motivational systems and learning processes are two of the components containing rules within the structure of the basic animal behavior shell (Figure 1). Although individuals may initially share a common set of information-processing rules characteristic of the species, those rules change with age (e.g. young male songbirds do not sing) and with experience (e.g. floaters start singing when they acquire a territory). The specific information stored in memory also influences how an individual processes information from a stimulus (e.g. how vigorously it was chased).

If our basic shell structure of behavior is to accommodate diverse species, we need to be able to represent sensory

capabilities and response repertoires (Figure 1), which differ characteristically among species. Developmental processes and learning influence the variation in response to stimuli expressed among individuals of the same species. However, with regard to differences between species, variations in perceptual systems and activation systems also need to be considered (e.g. the messages received by a wasp are different than those received by a songbird).

### Perceptual systems

Two major concepts in the study of perceptual systems suggest it is appropriate to model incoming information as discrete messages. First, the sensory system of a given species is tuned into certain channels of information better than other channels (stimulus filters). Second, specific features of incoming information are often recognized in the central nervous system, which detects information that has been biologically important in the evolutionary history of the species (feature detection). These two concepts are illustrated below by the classic example of the Griffin and Roeder study of bats and moths (Roeder 1965; Alcock 1989).

Stimulus filters. The hearing system of noctuid moths is tuned with maximum sensitivity to the frequency range of their predators, bats. Unimportant information is thus filtered out by the sensory system. Moths receive messages within a narrow acoustic channel as if tuned into the emergency channel of a CB radio. In contrast, larvae of the moth are tuned to the frequency range of the sounds made by their main predators, wasps. The hearing of bats is maximally sensitive to ultra-high frequencies corresponding to their sonar system, but also includes a broad range of pitches as low as squeaks audible to the human ear.

Feature detection. Up to a certain threshold of sound intensity, moths turn and fly away from a source of sound that mimics sonar pulses from a distant bat. In response to very loud sonar pulses, moths fall in a fluttering dive that confuses a bat closing in for a kill. This feature detection is encoded in two sensory cells within the hearing system of the moth. The A1 cell fires in response to low intensity sound. The A2 cell fires in response to high intensity sound, sending a neural message that temporarily blocks coordination of the wing movements and makes the moth fall.

Thus, it is very appropriate to model incoming stimuli as discrete messages that are mapped to characteristic (and usually adaptive) responses.

### Action systems

The responses of animals are coordinated in certain recognizable action patterns that reoccur (Lorenz 1958; Tinbergen 1960). Such action patterns can be modeled as discrete response messages. The set of response messages typical of a species is called its "action repertoire". Those actions that are paired reliably and rapidly with specific stimulus messages are called "reflexive". New response messages may be acquired by "reshaping" old actions, or combining "sequences" of old actions. The concepts of action repertoire, reflexive action, shaping actions and action sequences are illustrated below with examples that are common knowledge of practicing ethologists (Ridley 1987; Alcock 1989).

Action repertoire. A species' repertoire of action patterns is like a list of preprogrammed messages ready to be sent. For example, all herring gulls perform certain recognizable action patterns such as the "long call", "choking", or "forward display" (Tinbergen 1960). The action repertoires of duck species differ quite a bit from those of gulls, and comparisons among duck species provide insight as to their evolutionary history (Lorenz 1958; Ridley 1986; see also Burghardt & Gittleman this volume). The number of actions in a species' repertoire is, for practical purposes, a finite set (Fagen 1978).

Certain subsets of action patterns are likely to be highly correlated in time (Bekoff 1977; De Gheff 1978; Packard & Ribic 1982), giving rise to the notion that a motivational system (e.g. hunger, reproduction, migration) controls their expression. However, a particular action pattern may occur in the context of several motivational systems (Lorenz 1981: 198; Colgan 1989: 41); for example, a digger wasp may sting an enemy (defensive mode) or a caterpillar (reproductive mode).

Reflexive actions. Reflexive actions solve predictable problems that have been encountered by many individuals in the past history of a species. For example, herring gull chicks run to cover and crouch to the ground in response to the raucous warning call of adults. When a covey of quail is flushed, each individual scatters

in an unpredictable direction. Those individuals that did not possess such hard wiring must have been eaten in previous generations of the species. Reflexive actions occur when split-second timing of an appropriate response(s) has been adaptive.

Although reflexive actions are typical of simple organisms, they also occur in complex vertebrates responding to reliable cues in the environment. For example, many single-cell organisms, insects and fish follow simple rules of orienting toward a light, thermal or chemical gradient. Kittens orient toward warmth and a familiar odor. Dogs salivate in response to the taste of food. Thus, reflexes are analogous to rules that map stimulus messages directly to response messages without intervening variables.

Shaping new actions. For those preoccupied with an anthropocentric view of behavior, the list of potential actions appears to be a *tabula rasa* (clean tablet ready to be written upon). However, even in humans, new actions arise as a modification of actions existing previously in the repertoire. The process of acquiring a new action is called "shaping"; for example, pigeons can be taught to turn in circles by delivering a reward each time the pigeon makes a move that closely resembles turning (Gardner & Gardner 1988). After an individual has learned a new action, it is as if a new message has been added to the action repertoire.

Sequences of old actions. Sequences of old actions also can become new messages. Anyone who has learned to play golf remembers a time when each separate component of the golf swing required conscious effort. However, after the sequence of actions was repeated many times, it became an "unconscious" discrete motion, interrupted only if the player thought too much about it. Even the complex show routines of marine mammals are built on previously existing sets of behaviors.

### Motivational systems

Ethologists think of the rules governing behavior as occurring in clusters with a hierarchical organization (Dawkins 1976; De Gheff 1978). The components of this model include rules for implementing (1) priority of modes, (2) decision rules within modes, (3) goal direction, and (4) search strategies (Figure 1). To the computer programmer or neurophysiologist, this may appear as an unnecessary or even incorrect structure,

probably because it reflects the organization of human minds (analogous to software) more than the body (analogous to hardware). Nevertheless, the components have provided a useful approach for analysis of the dynamics of behavior within a species and for comparisons within a motivational system across species (Colgan 1989).

Motivational systems are like modules of a computer program, which contain "action rules" and "stop-action rules" relative to some "goal" state (Dawkins 1976). Examples of motivational systems (Figure 1) include: reproduction (social interaction, mate choice and parental care), ingestion (hunger, thirst and foraging), agonism (fight and flight), locomotion (movement and migration), arousal (activity and rest), thermoregulation, and exploration (search and play). Although behaviorists may quibble over a basic set of motivational systems common to all organisms (Toates 1986), this list has worked fairly well for us. Some of these modules may be unimportant for certain taxonomic groups or research questions. However, this basic structure is consistent with most models of animal behavior.

Mode priorities. The relations among motivational systems may be complex, involving inhibition, facilitation, neutrality or time sharing (McCleery 1983). From an analytical perspective, animals "decide" which motivational system has highest priority at a specific moment. From a synthetic perspective, each system decides its own priority and the highest priority system takes control of the animal.

Each motivational system is not totally independent from other systems. For example, a deer that finishes ruminating at daybreak may arise and forage. However, as air temperature rises, it may seek a cooler location to feed. If a coyote approaches, it may flee; or the deer may chase the coyote if its fawn is hidden nearby.

Interactions between motivational systems have been quite elegantly determined for the simple nervous system of the sea slug (*Pleurobranchia*). Escape takes precedence over all other systems, egg laying inhibits feeding and supersedes mating and reorientation, but feeding is more likely than mating, reorientation and withdrawal from touch (Kovac & Davis 1980; Alcock 1989; Colgan 1989).

Decision rules within modes. Within a particular mode (motivational module), an animal acts as if it chooses from a set of

action patterns in the repertoire (messages). The probability of one action occurring given that another has occurred previously has been analyzed for diverse invertebrates and vertebrates (Dawkins 1976; Sustare 1978).

This probabilistic approach to understanding internal behavioral processes has been extended to include response contingencies relative to external messages. For example, the probability that a digger wasp digs a new burrow or enters an existing burrow has been analyzed relative to the action probability of others in the population (Dawkins 1982: 118-132).

**Goal direction.** Acting as independent modules, some motivational systems appear to monitor the state of the individual relative to a set point (template or tolerance range) and assume high priority when the difference (between the actual state and the set point) passes a threshold (Staddon 1983; Toates 1986). Internal processes (e.g. changes in hormones, gut fill, or blood glucose) may change the actual state relative to the goal state, as well as external information (e.g. photoperiod, temperature, or ingestion of food). Although goal directed behavior may appear to the synthesist to imply intentionality (Dennett 1988), the linear analyst would argue there is no need to construct intervening variables that cannot be measured (Toates 1986).

In the simplest model of goal directed action (adapted from Staddon 1983), four functions are involved (Figure 2). The "set point function" evaluates the goal state relative to the actual state and sets the probability of action. The "action transfer function" decides on the appropriate action to reduce the discrepancy. The "incentive function" may override (inhibit or facilitate) the action probability, depending on input from memory and other modes. The resulting response message is the input to an external "contingency function". This function of external objects produces the stimulus message that is the input to internal objects at the "set point function". Thus, contingency functions are part of the external objects that send messages to organisms in our basic shell structure of behavior (Figure 1).

**Search strategies.** The complexity of search patterns modeled for animals ranges from random movement to insight (Schöne 1984; Pearce 1988). We use the term "insight" to refer to apparent internal manipulation of information yielding an appropriate response not previously executed. Between these extremes are



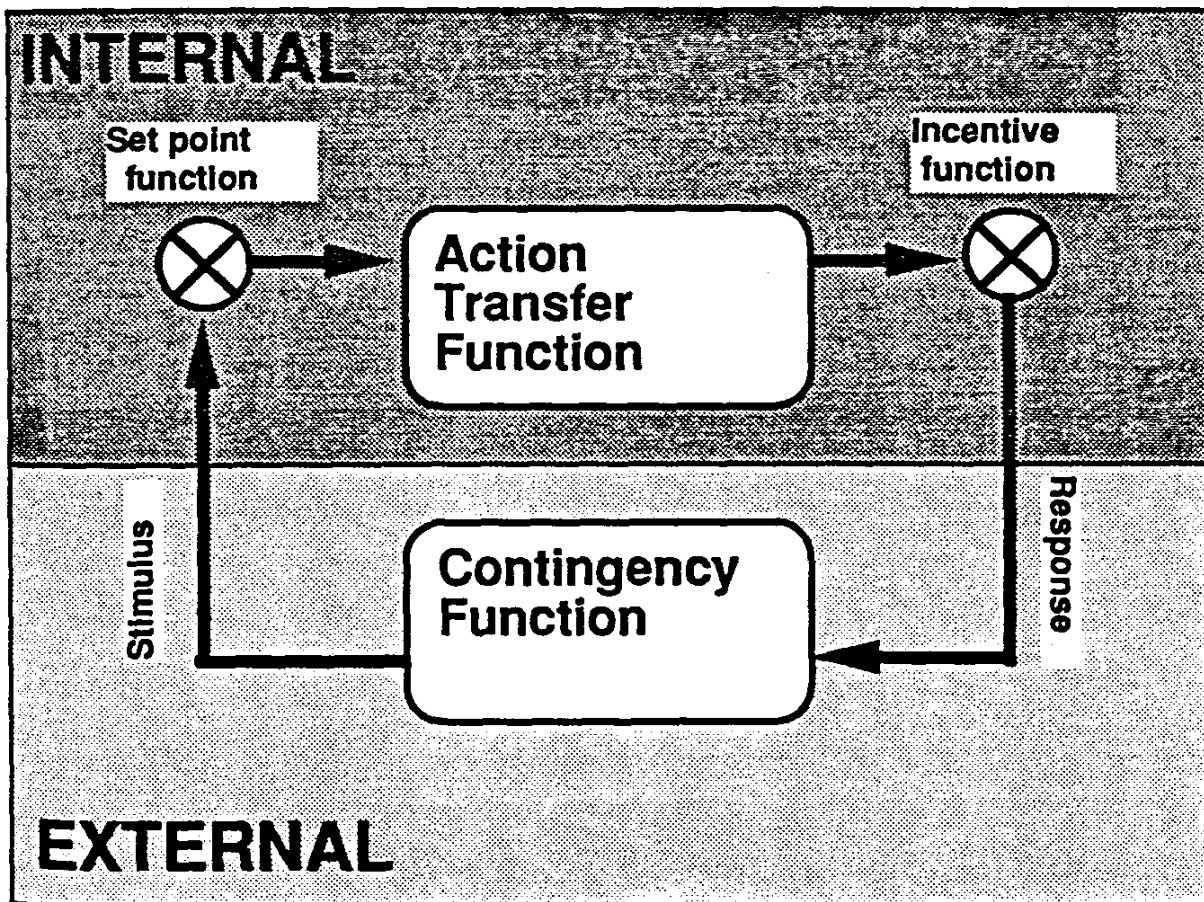


Figure 2. Basic homeostatic representation of a motivational system.

intermediate types of search strategies, including: specific rules that increase probability of encounter (Shettleworth 1983; Schöne 1984); repeating previous sequences that were successful (Gardner & Gardner 1988); and evaluating changes in the rate of return within patches (DeVries et al. 1989). Although we do not yet know of examples of invertebrates showing insightful behavior, the other types of search strategies occur in both vertebrates and invertebrates.

These strategies may be categorized as sets of discrete decision rules (algorithms), continuous functions, backward chaining based on a memory of previous solutions to a problem, and forward chaining based on projection of probable causal relationships. Each of these strategies has a direct counterpart in AI programming (Waltz 1982; Charniak & McDermott 1985), as described in the last section of this chapter. We do not imply that the behavioral strategies were independently derived from the AI strategies, rather both reflect processes of the human mind.

### Learning systems

The debate over learning theory (Fox 1983) illustrates the difference between a linear style of analyzing brain structures and the synthetic style of studying cognitive capacities. The components of learning processes (Figure 1) include storage and retrieval of information from the knowledge-base called memory (Kendrick et al. 1985; Squire 1986; Thompson 1986). Conscious and unconscious decisions influence whether information enters short-term memory and then whether (and in what form) it is stored in long-term memory (Atkinson & Shiffrin 1971). Retrieval is a separate process.

Memory. Short- and long-term memory are involved in building an internal representation of external processes (Narayanan 1986; Squire 1986). The capacity to store information from messages received and delivered would be quickly overwhelmed if there was not some way of erasing irrelevant information.

Memory appears to involve explicit declarative as distinct from implicit procedural knowledge (Alper 1986; Squire 1986). Procedural knowledge is acquired during processes involving motor responses (e.g. rehearsal of skills, priming, classical conditioning) and is thought to occur in a primitive portion of the brain, the cerebellum (Alper 1986). Storage of procedural knowledge need not be conscious and is basic even to invertebrates

that do not have the specific brain structure (hippocampus) responsible for declarative knowledge (Squire 1986; Mishkin & Appenzeller 1987).

Declarative knowledge involves facts, episodes, lists and routes of everyday life, including events specific to a time and place (episodes) and reference to associated facts from the context of an experience (semantics) (Squire 1986). Declarative knowledge allows an animal to record and access the particular encounters that lead to behavioral change. It stores the attributes of objects and relationships among objects and is only found in organisms (e.g. mammals) with a well developed hippocampus, which supports conscious decisions in humans.

As an initial model, we suggest procedural memory involves storing information about response messages and internal messages regarding the state of the organism (attributes), whereas declarative memory involves storing information about patterns of stimulus messages, memory networks, and attributes of external objects. The former appears adequate for backward chaining based on previous experience; however, the latter appears necessary for planning or projecting future results of alternative actions.

Storage and retrieval of information. Learning can be viewed as the process by which an organism or machine decides which information to store as an internal representation of the the external world (Forsyth 1986). Learning theorists have found it useful to distinguish between nonassociative (habituation, sensitization) and associative learning (classical conditioning) categories (Dewsbury 1978; Thompson 1986).

The "quick" learning that occurs in biologically adaptive circumstances appears distinct from the "slow" learning that occurs in the novel laboratory environment (Gardner & Gardner 1988). For example, Shettleworth (1983) observed that a marsh tit cocks its head after hoarding a seed. Later, the bird uses visual information to return to holes where it hid seeds. The bird behaves as if there is an "open slot" for information associated with each seed. In contrast, repeated pairing of stimulus and reward is required for a rat to learn to press a bar.

For synthetic thinkers, the process of storing information appears to involve pattern matching to a preexisting "slot" (Tennant 1984; Gardner & Gardner 1988). The concept of cognitive structures explains that if the incoming information can be mapped into an existing slot, it will be stored and retrieved

rapidly. If the incoming information does not match existing slots, the process of constructing a new slot takes time or repetition. Organisms differ in the ability to "make new slots" as a result of their evolutionary histories. However, from the perspective of a linear style, it is very difficult to collect data on the intangible intervening variable of a memory slot or template (Johnston 1988) even though the concept is used in AI models of memory (Narayanan 1986).

Certain sensory channels involve more rapid learning than others (Alcock 1989: 45). For example, a rat will not learn to avoid the taste of water associated with a shock to the tail, even though it learns after one experience to avoid the taste of water it drank prior to vomiting. Such species-specific constraints have defied the linear approach that seeks to derive general laws of learning applicable to all organisms.

Evolutionary biologists have recognized a continuum ranging from "restricted developmental programs" that are closed to irrelevant information, to "open developmental programs" that store information about external processes (Mayr 1974; Alcock 1989). The concept of an open versus restricted developmental program is better suited to a linear style of analysis than the previous distinction of genetic versus learned control of behavior (e.g. Johnston 1988).

Invertebrates tend to fit the restricted model and vertebrates to fit the open model; however, the variation is actually related to life history traits (Horn 1978). Restricted developmental programs are fast and reliable in solving predictable problems when many expendable copies of the organism are produced. Although an "expensive" open program that picks up specific information about a problem is more flexible and durable in dealing with unpredictable problems, it suffers the limitations of slower operation and potential disruption due to an inappropriate developmental history. An optimal degree of flexibility may involve sensitive periods in which an "innate school marm" (Lorenz 1965) tells the system what kind of information to store from incoming messages (Bateson 1979).

## LIMITATIONS OF PREVIOUSLY APPLIED TOOLS

The synthesis of components of behavior into a common structure probably has not been explicitly outlined previously due to the prevalence of the linear style of thought that focuses on universal laws rather than providing an overview of how

components interrelate. Historically, mechanical models for describing the complexity of motivational processes were criticized when systems analysis, optimization models and game theory approaches were borrowed from disciplines other than ethology (Krebs & McCleery 1984; Maynard Smith 1984; Toates 1986; Mangel & Clark 1988; Colgan 1989). However well-matched to the questions they address, such analytical tools are based on the assumption of a stable, homogeneous environment (or at least one in which stochastic fluctuations are bounded and represented by mean values; Mangel & Clark 1988).

Tools based on a linear style of thinking have limited our ability to represent the following: (1) an environment that is spatially heterogeneous; (2) changing contingency rules due to environmental processes; (3) changing response rules due to internal processes; (4) incomplete rather than global knowledge; (5) goal-directed search patterns; (6) interaction between motivational systems; (7) individual differences resulting from historical differences during development; and (8) "transparency" of the content of computer programs. Each of these limitations are briefly outlined below and illustrated by criticisms of optimal foraging behavior as reviewed by Pyke (1984), Stephens & Krebs (1986) and Pierce & Ollason (1987). Applications of object-oriented programming as a synthetic approach to overcoming such limitations are discussed afterwards.

### Spatial heterogeneity

The legacy of MacArthur & Pianka (1966) led many modelers to represent resources as homogeneously distributed "prey" or disjunct "patches" within which resources were homogeneously distributed (reviewed by Schoener 1971). An elegant application of the marginal value theorem (Charnov 1976) allowed modelers to use optimization algorithms to predict behavior (Pyke 1984; Stephens & Krebs 1986). Optimization is a linear style because it involves a search for general laws, a deduction of what will happen in the future, and a model to be tested analytically.

Although homogeneous or clumped distributions of resources may be an appropriate representation for nectar feeding insects and birds (Pyke 1984), resource distributions for most other species are more complex (Lessels & Stephens 1983). To simplify such complexity, the probability of encountering prey

has been modeled as if a forager is stationary and the habitat "flows" past its senses in one dimension (Owen-Smith & Novellie 1982; Arditi & Dacorogna 1988). However, the practical difficulties of translating from the real environment to the model environment are complex and some have argued that patchy distributions can only be determined *a posteriori* in terms of the forager's behavior (Hassell & May 1984).

For many larger vertebrates, researchers collect information about the location of individuals in relation to vegetation patches. However, we still understand very little about how animals perceive discontinuities in their environments compared to patches perceived by researchers.

Providing more of a synthetic perspective, Senft et al. (1987) have stressed the importance of a hierarchical approach to understanding ungulate foraging patterns. They found it inappropriate to model the landscape as discrete patches. For example, elk feeding in mountain meadows encounter a series of decisions. For ungulates, hierarchical decisions may involve seasonal movements among pastures, then decisions made within pastures (e.g. the number of bites per step and the choice of plant parts at a feeding station). At decision nodes higher in the hierarchy (earlier in the sequence), input from other motivational systems may be more important than at nodes lower in the hierarchy.

### Changing contingency rules

Optimization and game theory approaches assume that the environment is stable over time. If this assumption is violated, the usual approach is to take an average of the expected fluctuations or to limit tests of the model to a time frame that can be considered invariant. To accommodate such limitations, "dynamic optimization" procedures have been developed, involving a sequence of decisions (Mangel & Clark 1988).

Few models have allocated to patches the "rules" for changing over time, although seasonal changes in vegetation and prey distribution are well documented. Animals that deal with seasonal variation may not be optimally designed for all seasons. One approach has been to argue that animals merely "satisfy" their resource requirements, performing at what appear to be less than optimal levels during resource-poor periods (Bekoff et al. 1989), but nevertheless minimizing the risk of dying (Krebs & McCleery 1984).

## Changing response rules

A major difficulty in testing optimality models has been in detecting when a behavior that appears not to be optimal is in the process of change, tracking changes in the environment (Pierce & Ollason 1988). Game theory (Maynard Smith 1984) provides a stimulating intellectual approach when the optimal behavior for one individual depends on the actions of others in the environment. One solution has been to model conditional strategies as sets of tactics (subroutines) that are activated by specified conditions in the environment. For example, the optimal time for a territorial bird to switch to flocking in winter has been analyzed by comparing the cost/benefit ratio of the three strategies: territoriality, flocking, and switching (Davies & Houston 1984).

In contrast to models based on discrete strategies, traits subject to natural selection are likely to result in incremental responses to some environmental cue. A modeling approach that provides for variation in response rules observed in a real population is needed. Furthermore, rules of response change during development (Chalmers 1987). If we are truly to examine parent-offspring conflict, such rules for changing rules need to be included in models.

## Incomplete knowledge

Many optimality models of foraging (and other behaviors) assume that the organism has perfect knowledge of the environment and can calculate when the rate of return within a patch falls below alternative patches (DeVries et al. 1989). However, in the real world, individuals only have access to (not perfect knowledge of) information available within their habitual range of movement. The information that is actually used may depend not only on their perceptual capabilities, but also on their ability to store information in memory (reviewed by Roese 1989).

## Goal directed search

Most models of optimal foraging assume patterns of movements with encounter rates that are random or drawn from an *a priori* probability distribution even though many foragers search systematically (Pyke 1984). Simulations of movement patterns based on a random or *a posteriori* analysis of turn angles

and distances traveled have been used in analysis of radio-tracking data (Siniff & Jensen 1969; Bekoff & Mech 1984; Brody 1988). However, such approaches ignore what is known about motivational systems and goal-directed search.

### Interaction between motivational systems

One of the assumptions of an optimality approach to modeling foraging behavior is that natural selection influencing evolution of foraging traits has been independent of selective factors influencing other behavioral traits. Likewise, systems approaches to modeling motivational systems typically account for so many details within one system that interactions with other motivational systems have been excluded (Rolls & Rolls 1982; LeMagnen 1986; Toates 1986). Successful analysis of the interactions among systems (McCleery 1983) has been limited to the laboratory environment.

During field work, researchers typically follow individuals for long periods during which the animals switch among several modes of behavior. For such data, transitions between activities organized by different motivational systems can be difficult to analyze.

### Individual history

The search for general principles is easily obscured by the history of living organisms and their ecosystems (Hull 1984; May & Seger 1986). Field studies of long-lived animals in a fluctuating environment have demonstrated that the behavior and reproductive success of an individual may be dependent on demographic and environmental characteristics at the time of its birth (Clutton-Brock 1988). May & Seger (1986) called for modeling populations as aggregates of individuals. Łomnicki (1988) reviewed some analytical approaches to representing variation in a population due to categories of individuals.

Few models have incorporated constraints on an individual's behavior, which arise because it happened to be born into a particular territory that differed from other territories in the population, or to a particular mother whose behavior influenced the manner in which it learned to forage. However, such complexities of the real world influence the variance in success of individuals and the complications of testing the validity of models (e.g. Chepko-Sade & Halpin 1987; Clutton-Brock 1988).



## Transparent computer programs

At the end of his review of motivational systems, Toates (1986) rather plaintively commented that soon scientists would need to exchange programs rather than reprints. If the complexity of biological models reaches such a level, the contents of programs need to be accessible to people other than those who built them. Unfortunately, the structure and content of programs often are so complex that only the behavior is reported. The result has been a proliferation of models that are untested, providing the function of illustrating a conceptual framework but not fitting into the scientific method of testing alternative hypotheses and rejecting those that yield invalid predictions (Thompson 1981).

## ALTERNATIVE AI APPROACHES APPLYING OBJECT-ORIENTED PROGRAMMING

The limitations described above are common frustrations expressed by scientists who take a synthetic rather than reductionist approach and who seek to apply conceptual models to real world problems. Linear thinkers who accept a universal model "as reality" are likely to perceive the problems we identified above, not as limitations, but rather as the assumptions that give elegance and clarity to a model. In contrast, resource managers tend to take a very different view of the world, perceiving reality to be the "problem-in-the-field" and modeling to be one step in finding solutions to complex problems.

Resource management questions led us to take another look at the tools available in AI programming (Coulson et al. 1987). For example, these questions spanned micro- to macro- geographical, temporal, and biological scales, such as the following. (1) How can outbreaks of pine bark beetles be predicted and controlled (Rykiel et al. 1984)? (2) How does the size and mosaic of cotton fields influence biological control of pests by a parasitoid wasp (Makela et al. 1988)? (3) How can damage by moose foraging on pine seedlings be reduced (Saarenmaa et al. 1988) and habitat quality be assessed (Roese 1989)? (4) How can brush treatments in cattle pastures be designed to minimize impact on deer habitat (Folse et al. 1989)? (5) How do adaptations to a fluctuating environment influence individual reproductive success (Coulson et al. 1987) and population dynamics (Wilber 1987) in an aseasonal ungulate? (6) How can large herbivore populations

be managed (Starfield & Bleloch 1985)? (7) How does social structure influence population dynamics (Graham 1986)? (8) How can wildlife habitat be classified (Marcot 1984)? (9) How can interaction between large carnivores and visitors be reduced in parks (Ruth & Packard unpublished data)?

In the following subsections, we provide examples of how AI programming concepts have been used to address the limitations identified in the previous section. The particular style of programming is described as "object-oriented" (Bobrow & Stefik 1986; Stefik & Bobrow 1986) in contrast to the procedural style typical of other approaches. The application of object-oriented programming to animal behavior is still in the initial exploratory stage; however, the following examples provide insights for future elaboration.

### Spatial heterogeneity

Habitat patches (spatial heterogeneity) can be represented as objects in the environment, each object having a set of descriptive attributes and arranged within a hierarchical class (Saarenmaa et al. 1987). For example, Makela et al. (1988) represented a wasp world as one type (class) of habitat object (cotton field) with three member units (field 1, field 2, field 3). Each field contained a different set of interconnected parcels. The attributes of a cotton field were defined once and all units of the class inherited those attributes. Likewise, the attributes of parcels were defined once and each instance inherited the "information slots" for attributes. Examples of attributes of parcels included: list of neighbors, number of egg-laying sites, number of immature females, number of mature females.

Several features of this object-oriented structure are intuitively appealing to biologists. First, a continuous environment is represented by units that correspond to our conceptual framework of foraging relative to patches. This appeals to a basic "Gestalt" recognition of discontinuities in the environment (Lorenz 1981: 44; Allman 1986). Second, we tend to lump certain units as more similar than others, organizing information in hierarchical classes (Dawkins 1976). Third, we attach similar attributes to all members of a class (e.g. all vertebrates have forearms), while recognizing that each member may have a slightly different form of a particular attribute (e.g. the forearm of a bat differs from an elephant; Lorenz 1981: 94).

Different types of habitat patches can be represented via object-oriented programming. For example, Saarenmaa et al. (1988) mentioned three classes: forest compartment, farmland, and water. Folse et al. (1989) created one class of habitat object that included three types of vegetation patches in a cattle pasture (e.g. untreated-shrub, root-plowed-shrub, sprayed-shrub) defined by the values of attributes. The vegetation attributes were determined by field data from a sample in each shrub type. The model environment was complex, representing 265 instances of vegetation patches in the pasture.

The linkages between habitat objects can be represented in a dynamic manner (Folse et al. 1989). Travel routes for deer moving between patches were represented as a network; however, not every patch was linked to all its neighbors. For example, deer do not readily move across root-plowed shrub patches, so habitat patches of this vegetation type were not in the network and functionally blocked movement between neighboring patches. The linkages among habitat patches were changed between subsequent runs of the model to examine the effect of vegetation pattern on simulated deer movements under three conditions: no shrub treatment, many small, or several large root-plowed patches of equivalent total area.

The spatial representation of the habitat objects can be stored in a series of map layers in a computer database commonly referred to as a Geographic Information System (GIS) (Coulson et al. 1987). This approach was used to represent the habitat of cougars in Big Bend National Park (Ruth & Packard, unpublished data.). Habitat patches were digitized using a GIS; based on characteristics of slope, aspect and soil type. The resulting list of patches and corresponding attributes were used as input to the object-oriented model and served as a network for simulated movement of the cougars (Folse et al. in press). To validate the model, simulated movements can then be compared with data acquired via radio-telemetry.

This direct interface between landscape-based spatial data and object-oriented models may not seem terribly exciting to the analytical modeler. However, the breakthrough will be clear to anyone who has struggled with analyzing radio-telemetry data on a grid-point basis, which is divorced from the biological and topographical realities of the landscape. Previous tools for analyzing home range were based on assumptions that animal use of space fits a distribution similar to an ellipse (Ford & Krumme

1979). Such assumptions are difficult to accept when a cougar's home range includes a massive cliff, lake, or campground.

Furthermore, the tools provided by GIS and object-oriented modelling provide the flexibility to switch between grid-based analysis at the micro-level, as is suitable for studying foraging paths (Roese 1989) and the coarse-grained analyses over larger patches, as is suitable for studying seasonal changes in animal distribution (Folse et al. 1989). Within the GIS data base, the environment can be represented as both points and patches. This flexibility provides options for redefining patches as meaningful to the animal in contrast to the researcher. For example, a researcher may perceive the difference between untreated-shrub and root-plowed shrub patches to be important, whereas the deer may respond in terms of edges and interiors.

### Changing response rules

The animal object that interacts with its environment can receive stimulus messages and send response messages to external objects (Saarenmaa et al. 1988). External objects may be habitat objects or they may be other animal objects (Coulson et al. 1987; Folse et al. 1989). The exciting aspect of this structure is that it provides for dynamic modification of the program rules and memory content during simulations.

Use of object-oriented programming to simulate changes in response rules due to nutritional state were illustrated by Saarenmaa et al. (1988). In this prototype model, the moose-object had a specified daily intake requirement, monitored by a state variable "nutritional-balance". It met this goal state by searching for a patch containing young trees, entering the patch and consuming pine (protein and energy) and hardwoods (minerals). When the nutritional balance was positive, the moose did not consume vegetation. An internal function simulated metabolism of food for each day, reducing the nutritional balance as a function of time.

In contrast, external events in the moose model (Saarenmaa et al. 1988) drove the motivational system corresponding to "activity". A clock sent a message when it was daylight, resetting the "shelter balance" of the moose-object to a threshold level where the moose-object sought the nearest mature forest stand for resting.

One value of the object-oriented programming environment is the ease in which rules for changing responses can be attached

to objects. Each object has a set of attributes and a set of procedures (Bobrow & Stefik 1986; Saarenmaa et al. 1988). The attributes and rules of one object are relatively hidden from another object. The language in which the program is written is at a higher level, such that it "automatically" takes care of bookkeeping details (e.g. how objects exchange messages). The user is thus freed to focus more on the content of the model. Furthermore, the model can be "event-driven" rather than "time-driven", more closely approximating the real world (Folse et al. 1989).

An object-oriented program can exchange messages with other chunks of programs (Denning 1985), making it possible to link complex models of motivational systems to the object-oriented model. For example, Folse (unpublished data) has expanded the deer model to include a complex chunk of programming simulating rumination processes.

In an AI program (LISP language), the types of dynamic modifications are limited only by the programmer's imagination, so flexibility need not constrain a modeler in making the best formal representation suitable for a certain question. The program can modify motivational rules dependent on age, setting bounded rules for changing rules. For example, the rules controlling movements of a cougar kitten will differ in certain motivational systems from those of its mother (Figure 3). The transition from one developmental stage to another may be modelled by transferring the attributes of an individual (an "instance" in AI jargon; Saarenmaa et al. 1988) of an immature class to a new instance of a mature class of object and erasing the immature instance in species with discrete life stages (Makela et al. 1988). For slowly maturing vertebrates whose behavior changes as a result of individual history of development, rules for changing rules could be triggered by certain threshold values, such as weight.

### Changing contingency rules

The values of attributes in each instance of habitat-objects can be updated periodically, unknown to the animal-objects. Thus, contingency rules may change due to processes within the habitat-object or by an external model of ecological processes. Changes induced by procedures within a habitat-object were illustrated by Saarenmaa et al. (1988). Feeding by a moose object was simulated by a message sent from the moose-object to

SETS OF METHODS	OBJECT CLASSES	
	Adult female	Juvenile male
MODE PRIORITIES	<ol style="list-style-type: none"> <li>1. agonism</li> <li>2. ingestion</li> <li>3. thermoregulation</li> <li>4. arousal</li> <li>5. reproduction/social</li> </ol>	<ol style="list-style-type: none"> <li>1. agonism</li> <li>2. ingestion</li> <li>3. thermoregulation</li> <li>4. arousal</li> <li>5. reproduction/social</li> </ol>
MOTIVATION		
Agonism	<ul style="list-style-type: none"> <li>• hide from intruders</li> <li>• flee if there is an escape</li> <li>• attack if cornered</li> </ul>	<ul style="list-style-type: none"> <li>• hide from intruders</li> <li>• flee if there is an escape</li> <li>• freeze if cornered</li> </ul>
Ingestion	<ul style="list-style-type: none"> <li>• hunger rises to an asymptote at five days as an inverse function of time since last meal</li> <li>• when hungry search for prey</li> <li>• assess vulnerability when prey is encountered</li> <li>• attack vulnerable prey</li> <li>• eat from kill</li> </ul>	<ul style="list-style-type: none"> <li>• hunger rises to an asymptote at 24 hours as an inverse function of time since last meal</li> <li>• when hungry search for mother</li> <li>• suckle from mother when she responds by nursing</li> <li>• follow mother when no nursing</li> <li>• feed from mother's kill</li> </ul>
Thermoregulation	<ul style="list-style-type: none"> <li>• monitor body temperature</li> <li>• move to shade when hot</li> <li>• move to breeze if no shade</li> <li>• move to sun when cold</li> <li>• move to shelter from wind when cold in sun</li> </ul>	<ul style="list-style-type: none"> <li>• monitor body temperature</li> <li>• move to crevice when cold</li> <li>• approach warm body when cold</li> <li>• move to shade when hot</li> </ul>
Arousal	<ul style="list-style-type: none"> <li>• movement potential declines to nil in 12 hr after last sleep</li> <li>• duration of sleeping bout is direct function of duration of previous activity bout</li> </ul>	<ul style="list-style-type: none"> <li>• movement potential declines to nil in 6 hr after last sleep</li> <li>• duration of sleeping bout is a direct function of duration of previous activity bout</li> </ul>
Reproduction/ Social	<ul style="list-style-type: none"> <li>• approach offspring at least once a day</li> <li>• nurse offspring if it requests</li> <li>• leave offspring when it finishes nursing</li> </ul>	<ul style="list-style-type: none"> <li>• approach mother when near</li> <li>• approach siblings when mother is not near</li> </ul>
Exploration	<ul style="list-style-type: none"> <li>• visit nearby patches that have not been encountered recently</li> </ul>	<ul style="list-style-type: none"> <li>• approach new objects within 5 m of den</li> <li>• practice action repertoire with sibs</li> </ul>
LEARNING	<ul style="list-style-type: none"> <li>• store new patches in memory</li> <li>• update attributes of memory-net</li> <li>• actions leading to prey encounter</li> <li>• actions leading to social encounter</li> </ul>	<ul style="list-style-type: none"> <li>• store new patches in memory</li> <li>• update attributes of memory-net</li> <li>• actions leading to prey encounter</li> <li>• actions leading to social encounter</li> </ul>

Figure 3. Preliminary set of rules for an adult and juvenile cougar, illustrating how several motivational systems may be represented in a rule of thumb model.

the patch-object (patch-objects were one class of habitat-objects). The patch-object contained procedures to reduce its attribute values for pine and hardwood by an amount corresponding to what the moose-object ate.

When more than one animal-object is in the population, the attributes of a patch-object may thus change from the time an individual first visits a patch to the time it returns. Such options were useful for modeling movements of nectar feeding birds (Triono et al. unpublished data), based on observations that one bird may drain a flower of nectar, reducing the value of a patch for individuals that follow (Pyke 1984). Internal rules may also change the attribute values of habitat objects, e.g. by simulating nectar production within a flower. Folse (unpublished data) has expanded the deer model to monitor the effects of several deer feeding in habitat patches.

In concept, seasonal changes in attributes of patches could be simulated by linking with an external model. For example, expert systems have been developed to choose an appropriate model of bark-beetle population dynamics, transfer input from the user to the model and transfer the model's output to the user (Rykiel et al. 1984). This approach was developed at a time when several complex models of bark beetle and forest dynamics had been developed, each with slightly different yet complementary characteristics. The concept was a pioneering step in integrating programming techniques developed in the field of artificial intelligence (e.g. expert systems) with traditional systems modeling techniques. There is no reason why the concept cannot be extended to include geographical data bases and input from external models that change the attributes of patches within the geographical data base (Coulson et al. 1987).

### Incomplete knowledge

The discrepancy between what an animal "knows" about its environment and the actual environment may be modeled by an "internal representation" of the environment. Folse et al. (1989) illustrated how a deer-object can be programmed to build a memory network of the habitat objects that it passes through during an initial phase when it explores its model environment. The model environment can be represented as a network of habitat patches. When the deer-object enters a patch, it searches its memory and adds a new memory-patch if the habitat-patch is not in memory. Thus, the linkages among memory-patches are

dynamic and represent a subset of habitat-patches known to an individual deer. Another individual might have a slightly different representation of the environment in its memory-net.

Incomplete knowledge of the environment does influence behavior of a model that simulates movement among habitat patches. Folse et al. (1989) modeled a simple goal directed search, representing a deer looking for water. They found that the distance traveled by a deer-object with a memory net was always shorter (by a factor of 100) than a deer-object with no memory (which moved randomly among patches). Furthermore, when the attribute values of the patches were changed, the path to the goal was shortened (by a factor of 3) after the deer-object "learned" of the modifications and updated its memory-net.

Within a patch, limited information is available to a browsing ungulate as it moves from shrub to shrub. Using a "rule-of-thumb" modeling approach, Roese (1989) illustrated how the distance of detection can influence the path of a moose-object moving during a foraging bout. As a moose moves from one feeding station to another, only a subset of plants are detected (perceptive field), of which a smaller subset are within reach (consumptive field). Roese (1989) found that a larger perceptive field significantly reduced foraging efficiency, as the moose-object spent more time deciding what to eat rather than eating.

### Goal directed search

Search processes are well-defined techniques in AI programming (Charniak & McDermott 1985). For example, a robotic arm given the task of stacking blocks may use a "backward-chaining" or "forward-chaining" strategy (Waltz 1982). In the backward-chaining strategy, a solution to the problem is found by following the decision path of previous solutions that were successful. In the forward-chaining strategy, the solution is found by an internal representation of subsequent moves, discarding projected decision paths that were not successful in the internal analysis. There are many options for searches within these two basic approaches. For example, in a "depth-first" search strategy, one path is explored at a time, whereas in a "breadth-first" search strategy, several paths are explored in parallel (Saarenmaa et al. 1988). Certain search strategies (e.g. A\* used by Folse et al. 1989) utilize heuristic (i.e. rule-based) information to improve search efficiency. All of



these methods are well-tested modules that can be inserted into models developed by different laboratories.

Saarenmaa et al. (1988) compared the behavior of a moose-object using three different search strategies. They found that a random search (the strategy most often used in foraging models) resulted in a greater nutritional deficit and more evenly distributed frequency of visiting patches, compared to a local search or global search strategy. The local search strategy differed from the global search in that the moose object decided to which adjacent patch it would move rather than evaluating all patches within the model environment. Both the local and global search resulted in frequent visitation to "good" patches and infrequent visitation to "poor" patches and similar performance in terms of mean nutritional deficit. However, the local search strategy resulted in a greater variance in the index of nutritional deficit. Where risk-sensitive foraging is important, variance in intake may be a critical factor (Stephens & Krebs 1986).

Therefore, the type of search strategy can influence the behavior of an animal-object. To devise more predictive models, it will be necessary to identify ways of testing which search patterns most closely represent the actual behavior of animals in the system to be modeled. AI tools provide specific definitions of alternative search strategies, potentially taking the mystery out of vague notions of animal intelligence (Pearce 1988), which have defied operational definitions in the past. For example, a researcher might test actual behavior against the outcome predicted by alternative models based on random search, forward chaining, or backward chaining.

From our synthetic perspective, it does not matter whether animals actually use the search processes in the model, only whether one of several alternatives better matches the behavior of animals observed in the field. Of course from the perspective of a linear style, the task of developing an algorithm that provides a one-to-one match with biological mechanisms and accurately predicts individual behavior appears insurmountable. At issue is the recognition that any model, no matter how complete, will not be able to predict where you will eat dinner tonight. However, based on statistical data, a model may be able to identify which options are more likely than others.

## Interaction between motivational systems

The object-oriented programming approach encourages modeling at a level where interactions between motivational systems can be considered. By using a modular style, it is easier to modify the "rules-of-thumb" for one motivational system without disturbing the rest of the program. Thus, sensitivity testing is made easier in exploring unusual behavior of the model when rules from different systems interact in unanticipated ways. We have set up the structure for simulating interactions among motivational systems and have a research tool to begin exploring the pattern of emergent properties resulting from interactions of behavioral decision rules internally consistent within each system.

The degree of elaboration within a motivational system and in interactions between systems depends, in part, on the scale of the research question. For example, in modeling foraging paths of moose, Roese (1989) considered only one motivational system, essentially considering a moose to be an "eating machine". Empirical data on foraging paths of moose can be obtained by following individual animals or trails in the snow. However, information on animal movements obtained from radio-telemetry accumulates over a much longer time span, broader geographic scale and less frequent sampling schedule. The questions of moose movements addressed by Saarenmaa et al. (1988) were at this broader level, involving movements between forest stands. Thus, it was important to consider whether moose could be discouraged from foraging in a patch of optimal nutritional value if no daytime shelter was nearby.

In their prototype model, Saarenmaa et al. (1988) took the parsimonious approach of assuming a moose to be an "eating/resting machine". The moose-object chose between two basic behavioral modes, foraging and resting. The nutritional balance directed the moose to seek a patch suitable for feeding. Daylight raised the priority of the resting mode, directing the moose-object to seek shelter. When the nutritional deficit was extremely severe, the moose-object fed during the day in the most sheltered patch available.

The deer-object modelled by Folse et al. (1989) was an "exploring/drinking machine". Although it only contained rules for the motivational systems of exploring and finding water, the program was expanded subsequently to include three additional motivational systems (feeding, thermoregulation, resting) with

little effort due to the modular nature of the program (Folse unpublished data).

In developing the most parsimonious set of rules they thought were needed to explain cougar movements, researchers included four motivational states (Figure 3). However, simulated movements based on these rules did not approach a realistic pattern of movement based on telemetry data (H. Mueller personal communication). The exercise forced the field researchers to reexamine their database and assumptions.

### Individual history

Object-oriented simulation procedures can accommodate variation among individuals due to learning, developmental history, geographic variation or fluctuations in environmental factors. The memory of hardware used in AI modelling is large enough to store at least several thousand instances of objects, representing individuals in a population (Folse, unpublished data). This magnitude is adequate for complete representation of all known individuals in many existing populations of large vertebrates. For example, the cougar population of Big Bend National Park is estimated at less than 100 individuals and the threatened southern sea otter population consists of less than 2,000 individuals (Brody 1988).

Conceptually, it should be possible to allow properties of populations to emerge from the combined decisions of individuals within the population (Reiter 1986; Huston et al. 1988). Often it is easier to test individual decision rules than population processes, particularly with long-lived vertebrates.

A major programming break-through was needed to solve the problem of synchronizing individual instances of objects with processes that are event-driven rather than time-driven. In the model of Makela et al. (1988), the decisions of each individual were made sequentially at each time step. In contrast, the event-driven model of Folse et al. (1989) has been expanded to include ten deer with memory-maps based on their individual experience during exploratory trips. As long as the deer-objects do not send messages to each other, their decisions are made in parallel and it does not matter if one individual finds water after 25 decision events and another finds it after 100 events. However, to model the interaction between a cougar and her cub, the parallel processes of decisions will have to be synchronized periodically. AI solutions to such problems are currently being explored for

managing computer communication networks (Denning 1985) and complex systems (Gelernter 1989). One solution has been developed involving sliding windows of time in which individuals are resynchronized (Folse & Schnase unpublished data).

### Transparent computer programs

One of the basic principles in AI programming is to make the content of programs "transparent" to the user (Bobrow & Stefik 1986). Transparency refers to the use of natural language interfaces or subroutines that allow the user to examine the rule-base contained in the program. For example, an expert system for diagnosis of an illness can be programmed such that the user can ask why the system made a certain diagnosis. In traditional programming approaches, this principle is implemented via program documentation. Like program documentation, transparency is often overlooked even in AI programming.

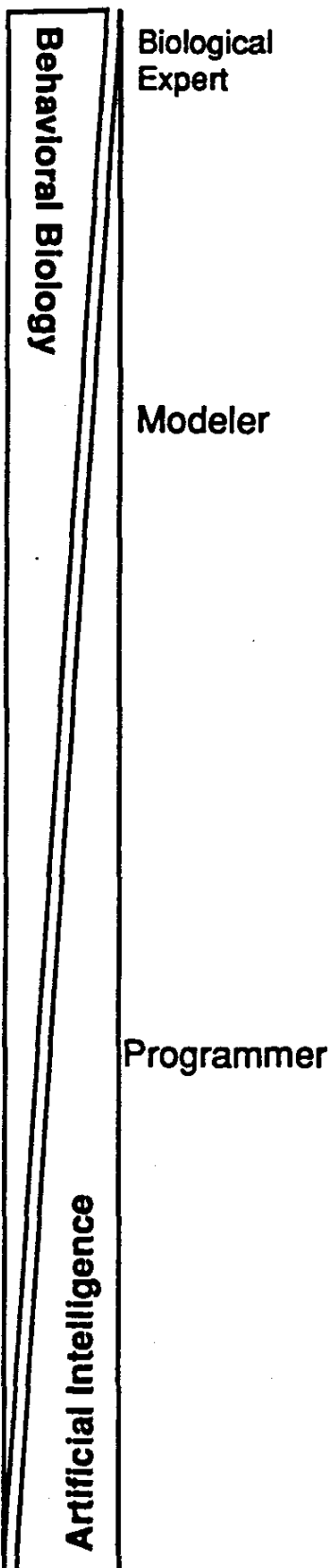
The basic method involved in AI programming is one that increases the communication between the scientist who knows a lot about the real world and the computer programmer who knows how to implement the model representation of that world. To construct an expert system, people in three roles are involved: the expert, the computer programmer and the knowledge engineer (Van Horn 1986). The role of the knowledge engineer is to package the knowledge of the expert in a form compatible with the information that can be put into the computer by the programmer.

In modeling animal behavior, the modeler assumes the role of knowledge engineer. We have found that the basic model of behavior illustrated in Figure 1 aided immensely in defining the role of the knowledge engineer in three steps required in developing an object-oriented model of behavior (Figure 4).

In the first step, the modeler interacts with the biological expert to arrive at a clear definition of the biological problem. This involves listing the relevant types of animals and habitat characteristics, the state variables important to monitor, and behavioral rules. Each box in Figure 1 and linkage between boxes is fully examined at this stage. Decisions are made regarding which boxes are to be left empty. The biological expert specifies the user input and the output of the model.

In the second step, the modeler restructures the information in an AI compatible form. This involves defining animal- and habitat-objects in the model world. The number of instances (individuals) in each object class is specified, as are the

## Conceptual Framework



## Steps in Developing an AI Model

### 1. Definition of Biological Problem

- lists of types of animals and habitat characteristics
- lists of state variables
- lists of behavioral rules
- specify user input and model output

↕ few programming constraints

### 2. Restructure in AI Compatible Form

- list object classes in model environment
  - animal object classes
  - habitat object classes
  - instances of classes
- list state variables for each object class
- sets of behavioral rules for each compartment
  - perception
  - motivation
  - learning
  - action
- monitoring objectives
  - display windows and graphics
  - interactive user interface

↕ consider programming constraints

### 3. Develop AI Program Outline

- define object classes
- list instance variables for each attribute
- list sets of instance methods for each system
  - interface with other systems within object
  - interface with other object classes
  - change value of instance variables
  - monitor changes in instance variables
- list interface methods
  - code for displays
  - natural language interface

↓ raw program code:program documentation

Figure 4. Steps involved in developing an object oriented model using the basic shell structure of behavior.

attributes (state variables) of each object class. For each object class, sets of behavioral rules are developed within the following subsystems: message sending (input/output corresponding to perception and activation), motivation, and learning. Finally, objectives for monitoring the behavior of the model are implemented by defining the options for windows, gauges, dynamic graphic displays and user interfaces.

In the third step, the modeler interacts with the programmer in developing an AI program outline that documents the program in modules corresponding to the way the information was organized in steps 1 and 2. The programmer's job is to define object classes (including attribute variables and their methods), set up main simulation drivers, and create the user interfaces. For each object class, the programmer creates code for the methods specifying interfaces with other internal classes and external objects, the changes in attribute values due to internal processes, and the displays that monitor changes in attribute values and make the program transparent to the biological expert.

Ideally, an untutored user should be able to interact with an AI program to learn of its structure and content. The program should be modularized such that packages of information can be substituted with little disturbance to operations in the rest of the program (Denning 1985). Only when technology reaches such achievable functions will behavioral biologists from different laboratories truly be able to place confidence in the internal validity of models and proceed with the empirical testing required to reject alternative models.

## CONCLUSIONS

The tools we use to communicate about complex behavioral processes influence the way we think about, interpret and explain those processes. Early ethologists used analogies based on mechanical, hierarchical or feedback mechanisms to describe behavior. Such linear processes have been adequate for analysis of linear causality resulting in a reductionist approach to science. However, the synthetic approach required in resource management is based on what has previously been criticized as subjective, intuitive thought, in which the emergent properties of the whole are more than the sum of the parts.

The programming tools developed in the field of artificial intelligence allow users to capture knowledge in a form that represents synthetic thought. For example, animals and patches

in the environment can be represented as objects. Each object has slots for information about state variables (attributes) and behavioral rules (methods). Since the bookkeeping details of structure and communication between objects are handled by the higher level programming language, the user is freed to elaborate more regarding the content of the knowledge base and rules. We illustrated some ways in which this approach has been used to address questions involving spatial and temporal heterogeneity, interacting motivational systems, individual history, incomplete knowledge and goal-directed search.

In the past decade, analytical approaches to modeling behavior involved optimality theory and game theory. Empirical approaches to simulating behavioral processes involved elaborate homeostatic, contingency or compartment models. Although researchers who built their own computer programs were satisfied with the tools available to them, such models are opaque to researchers in other laboratories who seek to duplicate results.

We envision that the next decade will benefit from a proliferation of transparent programs based on artificial intelligence programming techniques, in which the structure and content of behavioral models will be accessible to even untutored users. Such accessibility will depend on appropriate structure as well as technology developed in expert systems to allow users to interact using command language phrases, menus, or function keys. Communication among laboratories will be greatly facilitated if the structure of such programs is similar, providing for modules to be easily replaced to simulate the results of alternative variants of a behavioral trait.

We presented a basic structure representing four components of behavior: perceptual systems, action systems, motivational systems, and learning systems, and discussed the major conceptual framework of each component. This basic framework not only aids in intellectual communication across disciplines, it also could provide the basis for a program shell that would provide a work environment with tools to integrate knowledge regarding individual decision rules, population dynamics and population genetics.

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#### LITERATURE CITED

- Albus, J. 1981. *Brains, Behavior and Robotics*. New York: McGraw Hill.
- Alper, J. 1986. Our dual memory. *Science* 7, 44-49.
- Alcock, J. 1989. *Animal Behavior: An Evolutionary Approach*. 4th Edition. Sunderland, Massachusetts: Sinauer Associates.
- Allman, W.F. 1986. Mindworks. *Science* 7, 22-31.
- Arditi, R. & Dacorogna, B. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist* 131, 837-846.
- Atkinson, R.C. & Shiffrin, R.M. 1971. The control of short-term memory. *Scientific American* 225, 82-90.
- Bateson, P.P.G. 1979. How do sensitive periods arise and what are they for? *Animal Behaviour* 27, 470-486.
- Beach, F.A. 1950. The snark was a boojum. *American Psychologist* 5, 115-124.
- Bekoff, M. 1977. Quantitative studies of three areas of classical ethology: Social dominance, behavioral taxonomy, and behavioral variability. In: *Quantitative Methods in the Study of Behavior* (ed. by B. A. Hazlett), pp 1-46. New York: Academic Press.
- Bekoff, M. & Mech, L.D. 1984. Simulation analyses of space use: Home range estimates, variability and sample size. *Behavior Research Methods Instrumentation and Computers* 16, 32-37.



- Bekoff, M., Scott, A.C., & Conner, D.A. 1989. Ecological analyses of nesting success in evening grosbeaks. *Oecologia* 81, 67-74.
- Bobrow, D. & Stefik, M.J. 1986. Perspectives on artificial intelligence programming. *Science* 231, 951-957.
- Brody, A. 1988. A simulation model for assessing the risks of oil spills to the California sea otter population and an analysis of the historical growth of the population. In: *Population Status of California Sea Otters* (ed. by D. B. Siniff & K. Ralls), pp. 191-274. Washington, D.C.: Minerals Management Service Report No. 88-0021.
- Chalmers, N.R. 1987. Developmental pathways in behaviour. *Animal Behaviour* 35, 659-674.
- Charniak, E. & McDermott, D. 1985. *An Introduction to Artificial Intelligence*. Reading, Pennsylvania: Addison Wesley.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9, 129-136.
- Chepko Sade, B.D. & Halpin, Z.T. (eds.). 1987. *Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics*. Chicago, Illinois: University of Chicago Press.
- Clutton-Brock, T.H. (ed.) 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago, Illinois: University of Chicago Press.
- Colgan, P. 1989. *Animal Motivation*. New York: Chapman & Hall.
- Coulson, R.N., Folse, L.J. & Loh, D.K. 1987. Artificial intelligence and natural resource management. *Science* 237, 262-267.
- Davies, N.B. & Houston, A.I. 1984. Territory economics. In: *Behavioral Ecology: An Evolutionary Approach* 2nd Edition. (ed. by J. R. Krebs & N. B. Davies), pp. 148-169. Sunderland, Massachusetts: Sinauer Associates.
- Davis, R. 1986. Knowledge-based systems. *Science* 231, 957-963.
- Dawkins, R. 1976. Hierarchical organisation: A candidate principle for ethology. In: *Growing Points in Ethology*. (ed. by P. P. G. Bateson & R. A. Hinde), pp. 7-54. Cambridge: Cambridge University Press.
- \_\_\_\_\_. 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford: Oxford University Press.
- De Gheff, V.J. 1978. Hierarchical cluster analysis. In: *Quantitative Ethology* (ed. by P. W. Colgan), pp. 115-144. New York: John Wiley & Sons.

- DeVries, D.R., Stein, R.A., & Chesson, P.L. 1989. Sunfish foraging among patches: The patch departure decision. *Animal Behaviour* 37, 455-464.
- Dennett, D. 1984. Cognitive wheels: The frame problem of AI. In: *Minds, Machines and Evolution* (ed. by C. Hookway), pp. 129-151. Cambridge: Cambridge University Press.
- \_\_\_\_\_. 1988. Précis of *The Intentional Stance*. *Behavioural and Brain Sciences* 11, 495-546.
- Denning, P. J. 1985. The evolution of parallel processing. *American Scientist* 73, 414-416.
- \_\_\_\_\_. 1986. Will machines ever think? *American Scientist* 74, 344-346.
- Dewsbury, D. A. 1978. *Comparative Animal Behavior*. New York: McGraw Hill.
- Dreyfus, H. 1979. *What Computers Can't Do*. New York: Harper & Row.
- Fagen, R.M. 1978. Repertoire analysis. In: *Quantitative Ethology* (ed. by P. W. Colgan), pp. 25-42. New York: John Wiley & Sons.
- Folse, L.J., Packard, J.M., & Grant, W.E. 1989. AI modelling of animal movements in a heterogeneous habitat. *Ecological Modelling, Special Issue, Artificial Intelligence and Expert Systems in Ecology and Natural Resource Management* 46, 57-72.
- Folse, L.J., Mueller, H.E., & Whittaker, A.D. In press. Object-oriented simulation and geographic information systems. *AI Applications in Natural Resource Management* 4.
- Ford, R.G. & Krumme, D.W. 1979. The analysis of space use patterns. *Journal of Theoretical Biology* 76, 125-155.
- Forsyth, R. 1986. Machine learning. In: *Artificial Intelligence: Principles and Applications* (ed. by M. Yazdani), pp. 205-225. London: Chapman and Hall.
- Fox, J.L. 1983. Debate on learning theory is shifting. *Science* 222, 1219-1222.
- Gardner, R.A., & Gardner, B.T. 1988. Feedforward versus feedbackward: An ethological alternative to the law of effect. *Behavioral and Brain Sciences* 11, 429-493.
- Gelernter, D. 1989. The metamorphosis of information management. *Scientific American* 261, 66-73.
- Glymour, C, Scheines, R., Spirtes, P., & Kelly, K. 1987. *Discovering Causal Structure: Artificial Intelligence, Philosophy of Science, and Statistical Modeling*. New York: Academic Press.

- Graham, L. A. 1986. *HAREMS: A Generalized Data Base Manager and Simulator for Barrier Island Feral Horse Populations*. Atlanta, Georgia: Cooperative Park Studies Unit Technical Report 32.
- Harrison, A.F. & Bramson, R.M. 1982. *Styles of Thinking: Strategies for Asking Questions, Making Decisions, and Solving Problems*. Garden City, New York: Anchor Press/Doubleday.
- Hassell, M.P. & May, R.M. 1984. From individual behaviour to population dynamics. In: *Behavioural Ecology* (ed. by R. M. Sibly & R. H. Smith), pp. 3-32. Oxford: Blackwell Scientific Publications.
- Heuer, H. & Sanders, A.F. (eds.) 1987. *Perspectives on Perception and Action*. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Horn, H.S. 1978. Optimal tactics of reproduction and life history. In: *Behavioral Ecology: An Evolutionary Approach* 1st Edition. (ed. by J.R. Krebs & N.B. Davies), pp. 411-429. Sunderland, Massachusetts: Sinauer Associates.
- Hull, D. 1984. Historical entities and historical narratives. In: *Minds, Machines and Evolution* (ed. by C. Hookway), pp. 17-41. Cambridge: Cambridge University Press.
- Huston, M., De Angelis, D., & Post, W. 1988. New computer models unify ecological theory. *BioScience* 38, 682-691.
- Johnston, T.D. 1988. Developmental explanation and the ontogeny of birdsong: Nature/nurture redux. *Behavioral and Brain Sciences* 11, 617-663.
- Kendrick, D.F., Rilling, M.E., & Denning, M.F. (eds.) 1985. *Theories of Animal Memory*. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Kovac, M.P. & Davis, W.J. 1980. Neural mechanisms underlying behavioral choice in *Pleurobranchia*. *Journal of Neurophysiology* 43, 469-487.
- Krebs, J.R. & McCleery, R.H. 1984. Optimization in behavioral ecology. In: *Behavioral Ecology: An evolutionary approach* 2nd Edition. (ed. by J.R. Krebs & N.B. Davies), pp 91-121. Sunderland, Massachusetts: Sinauer Associates.
- Lehrman, D.S. 1953. A critique of Konrad Lorenz's theory of instinctive behavior, *The Quarterly Review of Biology* 28, 337-363.
- Lomnicki, A. 1988. *Population Ecology of Individuals*. Princeton, New Jersey: Princeton University Press.

- Lorenz, K.Z. 1958. The evolution of behavior. *Scientific American* 199, 67-78.
- \_\_\_\_\_. 1965. *Evolution and Modification of Behavior*. Chicago, Illinois: University of Chicago Press.
- \_\_\_\_\_. 1977. *Behind the Mirror: A Search for a Natural History of Human Knowledge*. New York: Harcourt, Brace & Jovanovitch.
- \_\_\_\_\_. 1981. *The Foundations of Ethology*. New York: Springer Verlag.
- MacArthur, R.H. & Pianka, E.R. 1966. On optimal use of a patchy environment, *American Naturalist* 100, 603-609.
- Makela, M.E., Stone, N.D., & Vinson, B. 1988. Host parasitoid population dynamics in a heterogeneous environment. In: *Artificial Intelligence and Simulation: The Diversity of Applications* (ed. by T. Henson), pp. 228-223. San Diego, California: Simulation Council Incorporated.
- Mangel, M. & Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, New Jersey: Princeton University Press.
- Marcot, B.G. 1984. Use of expert systems in wildlife habitat modeling. In: *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates* (ed. by J. Verner, M.L. Morrison & C. J. Ralph), pp. 145-150. Madison, Wisconsin: University of Wisconsin Press.
- May, R.M. & Seger, J. 1986. Ideas in ecology, *American Scientist* 74, 256-267.
- Maynard Smith, J. 1984. The evolution of animal intelligence. In: *Minds, Machines and Evolution* (ed. by C. Hookway), pp. 63-71. Cambridge: Cambridge University Press.
- Mayr, E. 1974. Behavior programs and evolutionary strategies, *American Scientist* 62, 650-659.
- McCleery, R.H. 1983. Interactions between activities. In: *Animal Behaviour 1. Causes and Effects* (ed. by T. R. Halliday & P. J. B. Slater), pp. 134-167. Oxford: Blackwell Scientific.
- Mishkin, M. & Appenzeller, T. 1987. The anatomy of memory. *Scientific America* 256, 80-89.
- Narayanan, A. 1986. Memory models of man and machine. In: *Artificial Intelligence: Principles and Applications*. (Ed. by M. Yazdani) pp. 226-259, New York: Chapman and Hall.
- Nisbett, A. 1976. *Konrad Lorenz*. London: J.M. Dent & Sons, Ltd.
- Owen-Smith, N. & Novellie, P. 1982. What should a clever ungulate eat? *American Naturalist* 119, 151-178.

- Packard, J.M. & Ribic, C.A. 1982. Classification of behavior of sea otters (*Enhydra lutris*). *Canadian Journal of Zoology* 60 1362-1373.
- Pearce, J.A. 1988. *An Introduction to Animal Cognition*. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Pierce, G.J. & Ollason, J.G. 1987. Eight reasons why optimal foraging theory is a waste of time. *Oikos* 49, 111-118.
- Poggio, T. 1984. Vision by man and machine. *Scientific American* 250, 106-116.
- Pyke, G.H. 1984. Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics* 15, 523-575.
- Reiter, C. 1986. Toy universes. *Science* 7, 54-59.
- Richmond, B., Peterson, S., & Vescuso, P. 1987. *An Academic Users Guide to Stella*. Lyme, New Hampshire: High Performance Systems
- Ridley, M. 1986. *Animal Behaviour: A Concise Introduction*. Oxford: Blackwell Scientific Publications.
- Roeder, K.D. 1965. Moths and ultrasound. *Scientific American* 212, 94-102.
- Roose, J.R. 1989. *A Simulation Model of Ruminant Foraging Strategies*. Ph.D. Dissertation, Texas A & M University.
- Rolls, B.J. & Rolls, E.T. 1982. *Thirst*. Cambridge: Cambridge University Press.
- Rykiel, E.F. Saunders, M.C., Wagner, T.L., Loh, D.K., Turnbow, R.H., Hu, L.C., Pulley, P.E., & Coulson, R.N. 1984. Computer-aided decision making and information accessing in pest management systems with emphasis on the southern pine beetle, *Dendroctonus frontalis*, (Coleoptera: Scolytidae). *Journal of Economic Entomology* 77, 1073-1082.
- Saarenmaa, H., Stone, N.D., Folse, L.J., Packard, J.M., Grant, W.E., Makela, M.E., & Coulson, R.N. 1988. An artificial intelligence modelling approach to simulating animal/habitat interactions, *Ecological Modelling* 44, 125-141.
- Schöne, H. 1984. *Spatial Orientation and the Control of Behavior in Animals and Man*. Princeton, New Jersey: Princeton University Press.
- Schoener, T. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2, 369-404.
- Searle, J. 1984. *Minds, Brains and Science*. Cambridge, Massachusetts: Harvard University Press.
- Senft, R.L. Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sola, O.E. & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37, 789-799.

- Shettleworth, S.J. 1983. Memory in food-hoarding birds. *Scientific American* 248, 102-110.
- Siniff, D. & Jessen, C. 1969. A simulation model of animal movement patterns. In: *Advances in Ecological Research* (ed. by J.B. Cragg), pp. 185-219. New York: Academic Press.
- Smith, W.J. 1977. *The Behavior of Communicating*. Cambridge, Massachusetts: Harvard University Press.
- Squire, L.R. 1986. Mechanisms of memory. *Science* 232, 1612-1619.
- Staddon, J.E.R. 1983. *Adaptive Behavior and Learning*. Cambridge: Cambridge University Press.
- Starfield, A.M., & Bleloch, A.L. 1986. *Building Models for Conservation and Wildlife Management*. New York: Macmillan.
- Stefik, M. & Bobrow, D.G. 1986. Object-oriented programming: themes and variations, *AI Magazine* 4, 40-62.
- Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Sustare, B.D. 1978. Systems diagrams. In: *Quantitative Ethology* (ed. by P. W. Colgan), pp. 275-311. New York: J. Wiley & Sons.
- Tanenbaum, J. 1989. *Male & Female Realities: Understanding the Opposite Sex*. Sugar Land, Texas: Candle Publishing Company.
- Tank, D.W. & Hopfield, J.J. 1987. Collective computation in neuronlike circuits. *Scientific American* 257, 104-114.
- Tennant, N. 1984. Intentionality, syntactic structure and the evolution of language. In: *Minds, Machines and Evolution* (ed. by C. Hookway), pp. 73-103. Cambridge: Cambridge University Press.
- Thompson, N.S. 1981. Towards a falsifiable theory of evolution. In: *Perspectives in Ethology, Volume 4 Advantages of Diversity*. (ed. by P.P.G. Bateson, & P.H. Klopfer), pp. 51-74. New York: Plenum Press.
- Thompson, R.F. 1986. The neurobiology of learning and memory. *Science* 233, 941-947.
- Tinbergen, N. 1951. *The Study of Instinct*. Oxford: Oxford University Press.
- \_\_\_\_\_. 1960. The evolution of behavior in gulls. *Scientific American* 203, 118-130.
- Toates, F.M. 1986. *Motivational Behavior*. Cambridge: Cambridge University Press.

- Ullman, S. 1986. Artificial intelligence and the brain: computational studies of the visual system. *Annual Review of Neuroscience* 9, 1-26.
- Van Horn, M. 1986. *Understanding Expert Systems*. New York: Bantam Books
- Waltz, D.L. 1982. Artificial intelligence. *Scientific American* 247, 118-133.
- Wilber, J.P. 1987. *Effects of Seasonally Varying Dietary Crude Protein Levels on Collared Peccary Population Dynamics - A Simulation Study*. M. Science Thesis. Texas A&M University.

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# Interpretation and Explanation in the Study of Animal Behavior

Volume II: Explanation, Evolution,  
and Adaptation

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EDITED BY

Marc Bekoff and Dale Jamieson

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