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REVIEW

Animal cognition and animal behaviour

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Cognitive processes such as perception, learning, memory and decision making play an important role in mate choice, foraging and many other behaviours. In this review, I summarize a few key ideas about animal cognition developed in a recent book (Shettleworth 1998, *Cognition, Evolution and Behaviour*) and briefly review some areas in which interdisciplinary research on animal cognition is currently proving especially productive. Cognition, broadly defined, includes all ways in which animals take in information through the senses, process, retain and decide to act on it. Studying animal cognition does not entail any particular position on whether or to what degree animals are conscious. Neither does it entail rejecting behaviourism in that one of the greatest challenges in studing animal cognition is to formulate clear behavioural criteria for inferring specific mental processes. Tests of whether or not apparently goal-directed behaviour is controlled by a representation of its goal, episodic-like memory in birds, and deceptive behaviour in monkeys provide examples. Functional modelling has been integrated with analyses of cognitive mechanisms in a number of areas, including studies of communication, models of how predator learning and attention affect the evolution of conspicuous and cryptic prey, tests of the relationship betweeen ecological demands on spatial cognition and brain evolution, and in research on social learning. Rather than a 'new field' of cognitive ecology, such interdisciplinary research on animal cognition exemplifies a revival of interest in proximate mechanisms of behaviour.

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Throughout much of the 20th century, ethology and animal psychology developed independently (Richards 1987). Although there are many exceptions to this sweeping statement, there are also many reasons why, on the whole, there was little communication between the two fields. Ethology was developed primarily by zoologists in Europe, whereas animal psychology developed mostly in North America. Ethologists worked within the framework provided by evolutionary theory, whereas psychology in general was out of touch with evolutionary thinking, or even opposed to it (Plotkin 1997; Galef 1998). Ethologists tended to focus on innate behaviour of animals in the field, whereas psychologists studied learned behaviours of a few species in the laboratory. Thus, of Tinbergen's (1963) four questions about behaviour, function and evolution have been addressed primarily by biologists whereas important proximate mechanisms such as perception, learning and other aspects of cognition have traditionally been in the domain of psychology. Elegant mechanistic analyses of natural behaviours like echolocation or song learning have gone on somewhat independently of psychologists' attempts to develop general theories of cognitive mechanisms.

Recently, however, students of animal behaviour have witnessed the emergence of a number of subfields with names that promise an integration of psychological and biological approaches to mechanisms of animal information processing and decision making. Cognitive ethology (Griffin 1978; Ristau 1991), cognitive ecology (Real 1993; Dukas 1998a), evolutionary psychology (Daly & Wilson 1999) and comparative cognition (Wasserman 1993) are most prominent among them. At the same time, the currently very influential framework for research on animal behaviour, behavioural ecology, has evolved from an almost exclusive focus on the function of behaviour to embrace studies of proximate cause (e.g. Krebs & Davies 1997). Ideas and methods developed by psychologists inevitably play a role in such studies. For instance, the study of animal communication has seen discussions of 'receiver psychology' (Guilford & Dawkins 1991), the importance of UV sensitivity (Bennett et al. 1994), and how 'peak shift' generates supernormal stimuli (Girlanda & Enquist 1999). The richness and

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depth of an interdisciplinary approach to communication is abundantly evident in two recent books (Hauser 1996; Bradbury & Vehrencamp 1998). In other areas too, prominent research programmes have successfully integrated psychological and biological thinking about cognitive mechanisms. Some of them are outlined below.

In this article, I first discuss a few general issues in the study of animal cognition. Some of these are areas where misunderstandings or gaps in communication still seem to exist. Then I briefly review some areas where interdisciplinary research on cognition is proving especially illuminating. In a recent book (Shettleworth 1998), I argued at length that the most rewarding way toward understanding animal cognition is to integrate data and theory from biology and psychology. I tried to contribute to such an integration by juxtaposing different kinds of studies of animal information use that are not always considered together and to point out what they have in common and what unanswered questions and new theoretical perspectives such a juxtapostion generates. I particularly hoped to help students of animal cognitive processes coming from different backgrounds to appreciate the richness of what fields other than their own have to offer and to provide them with an entrée into what may be alien literatures. Over the years, others have made similar arguments (e.g. Rozin & Schull 1988; Stamps 1991; Yoerg 1991; Kamil 1988, 1998). Indeed, over 30 years ago Hinde's (1966) influential textbook of animal behaviour was subtitled *A Synthesis of Ethology and Comparative Psychology*.

WHAT IS COGNITION?

Cognition, broadly defined, includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it. Like most working definitions, this notion is soft around the edges, but it has the merit of encouraging a comprehensive study of animal information processing. Authors (e.g. Tomasello & Call 1997) sometimes write as if animal behaviour can be divided into the 'noncognitive' or reflexive and the 'cognitive', which usually means behaviour more complex or flexible than anything thought to be explicable by simple reflexes or associations. However, as discussed below, even simple associative learning can result in complex representational structures that allow a degree of flexibility sometimes attributed to 'higher' learning. It is usually impossible to know in advance of detailed experimental analysis what kind of process underlies behaviour. For instance, alarm calling and responding to alarms may be a reflex or, as outlined below, it may be mediated by a representation of the type of predator being signalled and modulated by contextual information like the proximity of kin (Holmes & Sherman 1983). A comprehensive study of comparative cognition that embraces all of these mechanisms invites one to analyse the function and evolutionary history of different levels of complexity within a single theoretical framework.

Except in the context of cognitive ethology (Griffin 1978, 1998; Ristau 1991), the study of animal cognition is not the study of animal consciousness. It is possible, indeed usual, to study the ways in which animals acquire information about the world through their senses, process, retain and respond to it without making any commitment about the nature of their subjective experience or awareness. This does not mean it is impossible to study patterns of behaviour in other animals analogous to behaviour accompanied by distinct states of awareness in humans, but such work eventually meets an impenetrable barrier: the animals cannot report verbally on their experiences.

A good example of this problem is provided by recent research on scrub-jays', *Aphelcoma coerulescens*, memory for specific episodes in which they stored food (Clayton & Dickinson 1999). In humans, episodic memory, memory for one's personal past, is generally distinguished from semantic memory, memory for facts and ideas. Episodic memory is an integrated representation of a unique event that includes what took place, where and when. Memory for objects, places and times have all been demonstrated in many species, but remembering specific events episodically is not the same thing. In Clayton & Dickinson's experiments, scrub-jays were allowed to store peanuts or waxmoth larvae in locations that changed on every trial. The birds were also taught that larvae were good to eat if retrieved 4 h after they were stored but decayed after 120 h. Peanuts never decayed. In the critical test trials, the birds stored peanuts and larvae in novel sites and searched for them 4 or 120 h later. So the jays could not smell the items, no food was provided in these tests. Scrub-jays prefer fresh larvae to peanuts. Therefore, if they knew not only what items they had stored where but also when that storing episode occurred, the birds should first probe the holes where they had hoarded larvae in the 4-h tests and those where they had hoarded peanuts in the 120-h tests. This is what they did, leading to the conclusion that scrub-jays have 'episodic-like' memory (Griffiths et al. 1999).

Why 'episodic like' and not simply episodic? Over the years since episodic memory was first discussed in cognitive psychology, ideas about its special attributes have evolved to include autonoetic consciousness, awareness that a particular episode was one's own experience. In effect, an episodic memory is a re-experience of part of one's personal past. In contrast, the what-where-when knowledge that Columbus was in America in 1492 is semantic memory. The jays showed that they knew what they had stored where and when, but even requiring them to make finer discriminations among remembered times, places and food types could never tell us whether or not they are aware that they had a particular experience in the past. Some may be willing to accept analogous behaviours in this and other cases as evidence for analogous subjective experiences (Griffin 1998; but see Macphail 1998), but it is not necessary to take a particular position on this controversial issue in order to investigate cognition.

COGNITION AND BEHAVIOURISM

Radical behaviourism is devoted to describing the control of behaviour by the environment. In contrast, cognitive

psychology is usually said to assume that subjects have mental representations that play a causal role in behaviour (Gallistel 1990; Hunt 1999). Within experimental psychology, the subfield of animal cognition developed in the 1970s and focused on documenting in nonhuman species processes such as memory and selective attention that were successfully being studied in people (see Hulse 1993). Even within this limited realm, however, the cognitive approach is still controversial (ALB-L 1999). Strict behaviourists question whether terms such as memory, attention, and the like (not to mention theory of mind, planning, or consciousness) are well enough defined to predict and explain behaviour unambiguously or whether they are theoretically vacuous terms that belong only in folk psychology. Whether humans or other animals are being studied, however, research on cognition is necessarily behaviourist in method even if not in philosophical outlook. A critical analysis of the relationship between environmental input and behavioural output is required to understand the processes that mediate between them. When humans are being studied, the behaviour measured is often verbal, but one of the biggest challenges for research on nonverbal species is determining how to formulate clear behavioural criteria for processes that are usually accessed verbally in adult humans. The research on episodic-like memory in scrub-jays is one example of an attempt to meet this challenge. A recent study of intentional deception illustrates other challenges that bedevil attempts to document more controversial aspects of animal cognition.

Nonhuman primates sometimes seem to conceal an act or a desirable object from another animal in a way that suggests they understand and are trying to manipulate the other animal's mental state (Whiten & Byrne 1988). Frequently, a plausible alternative to interpreting functionally deceptive behaviour as intentional deception is that the 'deceiver' has learned by trial and error to avoid performing certain behaviours in certain locations relative to the 'deceived'. For example, a subordinate animal may have learned that he will be punished if he eats a scarce food item or copulates with a desirable female while he can see a dominant animal's eyes. On this interpretation, functionally deceptive behaviour will occur only in situations that contain physical stimuli similar to those the deceiver has experienced in the past, through stimulus generalization. On the interpretation in terms of intentional deception, however, animals can practise deception even in physically novel situations.

A recent experiment with captive longtailed macaques, *Macaca fascicularis* (Kummer et al. 1996) provides a simple example of how responding to specific stimuli and responding on the basis of a concept of deception can be distinguished. The animals could drink from either one of two juice bottles while an observer had his backed turned, but occasionally the observer turned to face the monkey and made threatening noises and gestures when the animal drank. This treatment, simulating threat from a dominant macaque, taught the monkeys to drink mainly when the experimenter's back was turned. Did they understand the situation as one in which they could not drink when the dominant knew what they were doing? To answer this question, a screen was placed between the experimenter and one of the two bottles. A monkey that understands the situation as one in which drinking is permitted only when the dominant is ignorant should drink from the bottle behind the screen when the experimenter is facing the cage. Because the animals might eventually learn to use the screen, testing in such an experiment must either consist of a single trial or, if repeated trials are given, there must be no differential consequences for the alternative behaviours. This caveat applies to any experiment in which an account of behaviour in terms of some sort of concept or mental construct is to be distinguished from the possibility that subjects have associated specific behaviours with specific stimuli.

Kummer et al.'s (1996) monkeys did not prefer to drink behind the screen, thereby providing no evidence for intentional deception. As with any single set of observations, many reasons can be given for these results. Maybe the situation was too artificial or too little experience was given to reveal the macaques' natural abilities. Be that as it may, this experiment illustrates some important principles for any test of animals' social or physical cognition. The possibility that an animal has used a social or physical concept to solve a specific problem must be tested by seeing whether the apparent skill transfers to a conceptually similar but physically novel problem. Testing a mentalistic interpretation with more than one kind of observation, or from different metaphorical angles, is what Heyes (1993) has called 'triangulation'. Animals show many behaviours for which explanations in terms of human-like understanding readily come to mind: the animal has a cognitive map, a concept, a theory of mind, it can count, avoids risk, intends to warn its relatives, understands how tools work, and so on. A leap of imagination may be necessary to grasp that behaviours so readily explicable by such intuitively appealing mechanisms are accomplished in completely different ways by other species. However, progress is most likely to be made when alternative mechanisms are considered and experiments devised to pit them against each other.

REPRESENTATION AND GOAL-DIRECTED BEHAVIOUR

Although animals do sometimes respond to simple stimuli in simple ways when it appears otherwise, in other cases behaviour reflects a structured representation of some aspect of the world. Some issues involved in studying representational processes in animals and their relevance for ethology are illustrated by studies of the role of explicit representation of a goal in controlling goal-directed behaviour (McFarland & Bösser 1993). In some cases, no representation of an apparent goal need be assumed. Wood lice appear to seek dark places: they move around in the light and stop moving in the dark. However, any biological or man-made machines that reflexively move in the light and stop moving in the dark will tend to congregate in dark places. Thus although wood lice may behave as if they are seeking darkness, the proximate cause of their behaviour does not include a representation of dark places, nor need we assume wood

lice in the dark are aware in any sense of having reached their goal.

The same issue is familiar in behavioural ecology in discussions of 'rules of thumb'. Just because some pattern of behaviour tends to maximize energy intake per unit time, survival of close kin, or another fitness-related currency, this does not mean its proximal cause includes any representation of the currency that behaviour is maximizing. For instance, 'risk sensitive foraging' refers to choice of items or patches being influenced by the variance in food intake they offer. A simple case considers two patches offering prey at the same mean rate but with the intervals between prey captures more variable in one patch than in the other. If the predator could starve while waiting for prey at the common mean interprey interval, its best chance for survival is to forage in the more variable, or risky, patch: the one that has shorter, as well as longer, interprey intervals.

Foragers' choices are not often influenced by their overall energy budgets in the way risk-sensitive foraging theory predicts (Brito e Abreu & Kacelnik 1999), but they do respond to variances as well as mean intake rates (Kacelnik & Bateson 1996; Bateson & Kacelnik 1998). However, this does not mean animals are sensitive to risk as such. Psychological studies of choice between conventional schedules of reinforcement as well as experiments closely modelled on foraging situations show that food items are discounted in value the longer the time required to obtain them. This means that the short interitem intervals in a typical 'risky' patch are disproportionately overvalued. The outcome predicted by risk-sensitive foraging theory therefore 'falls out' from general principles of reinforcement (Kacelnik & Bateson 1996; Bateson & Kacelnik 1998; Kacelnik & Brito e Abreu 1998). Short-term maximizing rather than literal risk sensitivity also dominates behaviour when variance is held constant and only the predictability of food is varied. When starlings, *Sturnis vulgaris*, choose between two patches with equally variable interitem intervals but differing in predictability, they prefer the patch in which the next food item comes sooner (Bateson & Kacelnik 1997).

Similarly, behaviours that seletively benefit the actor's kin need not result from 'kin recognition' in any literal sense (Grafen 1990). Animals may, for instance, behave in a special way towards individuals that shared their natal nest, whether or not they are genetically related (Holmes 1986). Even when an actor is less likely to attack unfamiliar individuals if they share its own genetic makeup, this does not imply conscious recognition. Indeed it is now understood, although not always taken to heart, that many terms used descriptively in behavioural ecology too readily shade into mechanistic explanations, where the mechanism is assumed to be a representation, conscious or not, of the short-term function or goal of the behaviour (Kennedy 1992).

So when is analysis in terms of representation of a behaviour's goal better justified? Perhaps suprisingly, the best-studied example is food-rewarded bar pressing in rats (Dickinson 1994; Dickinson & Balleine 1994). What a rat learns when it comes to press a bar or run a maze for food is a long-standing controversy in psychology. Is a habit merely 'stamped in' by the food or is the rat's behaviour guided by a representation of the food? The first view leaves no role for knowledge about the food once the rat has acquired the habit of pressing the bar. The latter, more common-sense, view implies that the rat presses the bar because, in effect, it knows pressing leads to food and wants the food. The two possibilities may be distinguished by changing the value of the food to the rat after it has learned to bar-press and outside of the situation where it is pressing the bar. For instance, the rat may be taught an aversion to the food used as a reward by making it mildly ill after eating that food in its home cage. After recovering, it is again allowed to press the bar, but without any further rewards being given, so as to test stored knowledge about the food rather than new learning that bar pressing leads to disgusting food.

The results of experiments like that just outlined are said to show that instrumental responses may be controlled by representations of their reinforcers or that they are evidence of declarative rather than procedural knowledge (but see Spier & McFarland 1998). In the present example, this means that rats for which the food was poisoned press the bar less in the test than similarly treated rats for which the food was not devalued. In the most elegant of such demonstrations (Colwill 1994), each rat is trained to perform two responses, say pressing a bar and pulling a chain, each for a different food, say rat chow and sucrose. Devaluing one of these rewards influences only its response, showing, incidentally, that rats have fairly detailed knowledge of which responses lead to which rewards. These response–reward associations may also be conditionally controlled. Rats can learn, for example, that in the presence of a light, bar pressing leads to chow and chain pulling leads to sucrose while the reverse is true when the light is off and a tone is on. Here, if sucrose were devalued, the rat would reduce chain pulling during the light but reduce bar pressing during the tone. Such contextual modulation, by tones and lights or times and places, has been analysed only recently (Swartzentruber 1995), and its existence is not yet widely appreciated outside of animal learning psychology. However, it is important because it allows simple associative learning to be expressed in flexible and functionally appropriate ways. Conditional control also imparts flexibility to behaviours not explicitly trained in the laboratory. The audience effect in animal communication is one example, as when roosters alarm call more in the presence of a hen than when alone (Karakashian et al. 1988).

Studies of goal representation have analogues in recent studies of animal communication. Here the question is whether alarm calling and responding to alarm calls is reflexive or mediated by knowledge about what predator is being signalled. Exactly as in tests of goal representation (Seyfarth & Cheney 1997), the key to distinguishing these explanations is to manipulate the representation in one way and test behaviour in another. For example, female Diana monkeys, *Cercopithecus diana diana*, make a 'leopard' alarm call in response to either the growl of a leopard or a male Diana monkey's 'leopard' alarm. If a growl is played and then played again 5 min

later, females' calling habituates. Habituation is also observed if the growl is preceded by a male leopard alarm but not if it is preceded by a male 'eagle' alarm. Similarly, habituation transfers to a male eagle alarm from an eagle's cry but not from a leopard's growl (Zuberbühler et al. 1999). The fact that habituation transfers to very different sounds only if they signal the same predator indicates that responding to them must be mediated by some sort of representation of the predator. Diana monkeys' information about the predator significance of some calls is acquired through experience, perhaps associative learning (Zuberbühler 2000).

INTEGRATING THE BIOLOGY AND PSYCHOLOGY OF COGNITION

Methods and theories from cognitive psychology are increasingly being applied to the causal analysis of naturally occurring behaviours. At the same time functional modelling is shedding light on why cognitive processes work as they do. Neurobiology and modern comparative methods may also be part of the mix. The value of such integration is most obvious when it illuminates issues that remain puzzling when viewed from a single perspective. In this section I sketch some current areas of interdisciplinary research on animal cognition that illustrate the kinds of synergy that can result from combining diverse approaches.

Signalling and Responding to Signals

Ethologists have long realized that most other animals inhabit different sensory worlds from ours. von Uexküll's (1934/1957) imaginative depiction of a protozoan's 'umwelt' is a well-known example. In this context, the recent excitement (e.g. Cuthill et al. 1999; Sheldon et al. 1999) about discoveries that some birds signal in the ultraviolet, invisibly to us, seems surprising. Similarly, ethologists should not have to be reminded that other species do not necessarily see video images the way humans do (Fleishman et al. 1998). However, it is sometimes convenient to forget that the species-specific sensory organs and brains of receivers mediate between signals and their effects, and to leave the psychological details to be filled in after functional questions have been addressed. For example, fluctuating asymmetry in wild populations can be related to physical condition and/or fitness (Moller & Swaddle 1997), suggesting that symmetry might be a useful signal in mate choice. This raises the question whether differences in degree of asymmetry found in nature can actually be discriminated by animals (Swaddle 1999). Thinking about symmetry from the perceiver's point of view also suggests that animals that use symmetry of a particular structure as a signal should have evolved displays that make it easy for conspecifics to perceive that symmetry. For humans, bilaterally symmetrical structures are more readily seen as such if they are presented frontally rather than at an angle (Swaddle 1999; see also Shettleworth 1999). These insights immediately suggest a whole line of research on the relationship between symmetry perception and the functional design of displays involving symmetrical structures. The way in which animal signalling shapes and is shaped by animals' sensory systems (what has been called 'receiver psychology'; Guilford & Dawkins 1991) has already been beautifully documented in several model research programmes (e.g. Fleishman 1988; Endler 1992; Ryan 1998; see also Bradbury & Vehrencamp 1998).

Integrating information about perception with the study of communication also promises to shed new light on why animals sometimes have redundant signals with the same message (Johnstone 1997; Rowe 1999). One possible answer is that receivers react more quickly or reliably to two stimuli together than to either one alone. Most of the evidence for this statement so far comes from studies of people (Rowe 1999), but it could be tested in other species in ways relevant to signalling. During simple conditioning, discrete stimuli generally compete for control of behaviour (Rescorla & Wagner 1972; Miller et al. 1995). For instance, in the phenomenon of overshadowing, when a light and a tone together signal food, an animal learns less about the light than if it had been the only signal. Studies of communication suggest a variety of other modes of interaction that are ripe for further analysis (Partan & Marler 1999; Rowe 1999).

Learning and Evolution: Predators and Prey

Cognitive mechanisms have been especially well analysed in the area of foraging because the food-rewarded behaviour traditionally studied in animal learning laboratories is, in effect, foraging. Furthermore, because finding food is something many animals do repeatedly throughout their lives, learning would be expected to play an important role in it, even gradual learning of very fine discriminations over many experiences. By the same token, the perceptual and learning abilities of predators would be expected to shape the evolution of both camouflage in desirable prey and warning colours in undesirable ones (see Speed 2000). New insights in this area can arise from evolutionary models that incorporate realistic assumptions about discrimination learning. For instance, a long-standing puzzle is how the evolution of conspicuous warning colours could get started, since a single conspicuous individual should be especially likely to be attacked. However, avoidance learning by predators could still increase the fitness of conspicuous distasteful prey if those prey congregate near their relatives (Alatalo & Mappes 1996; but see Tullberg et al. 2000). Furthermore, if predators show peak shift (i.e. enhanced avoidance of prey more conspicuous than those they have already learned to avoid), conspicuous prey may evolve from a relatively inconspicuous ancestor even if it is solitary (Yachi & Higashi 1998). The way in which predators' memory works may also influence the evolution of warning signals (Speed 2000).

A complementary approach to modelling the impact of predator psychology on prey evolution is to establish a virtual ecosystem in the laboratory and observe how prey frequencies change when the learning and discrimination abilities of real predators have free play. This approach

has been used to test ideas about the evolution of cryptic as well as conspicuous (e.g. Tullberg et al. 2000) prey. Bond & Kamil (1998) trained blue jays, *Cyanocitta cristata*, to find images of several 'species' of moths in noisy computer displays that made the moths very difficult to detect. When the relative abundance of the different 'prey types' changed from day to day as a function of the jays' performance, characteristic frequencies of each type resulted. Training the predators in such a system may be very time consuming and not all species may be appropriate predators, but this approach has many advantages for investigating questions about the impact of cognition on evolution. With the blue jays and virtual moths, for example, precise control over the timing and sequence of prey encounters permits the mechanism of search image formation to be examined in the same context as the dynamic interactions between prey density and predator selectivity that search images are meant to explain (Bond & Kamil 1999).

Methods developed in operant psychology have been exploited most in addressing issues from optimal foraging theory (Shettleworth 1988). Early models of foraging often made unrealistic assumptions about animals' cognitive capacities, treating prey densities, travel times and other variables as if they were perceived and remembered with perfect accuracy. Often, however, predators' cognitive abilities constrain performance to be less than optimal. For instance, research on animal timing indicates that the times between items or patches, handling times and time horizons that feature in optimality models are remembered with an error proportional to their magnitude. This error is evident in laboratory simulations of foraging tasks (Brunner et al. 1992). And just as psychological studies of learning, timing and the like provide mechanistic accounts of foraging, optimality models raise new mechanistic questions. For example, laboratory studies of food-rewarded behaviour generally do not take into account the time horizon, or length of the session, but animals do learn the length of experimental sessions and may change their behaviour as time runs out just as optimality models predict (Plowright & Shettleworth 1991).

From Functional Modelling to Neuroscience

Studies of learning demonstrably important to animals in the wild have sometimes uncovered phenomena that initially seemed unlikely, even impossible, from the perspective of what was known about learning in the laboratory. Imprinting and song learning in birds are well-known examples (see Shettleworth 1994), analyses of which have also led to exciting discoveries in neuroscience (Bolhuis & Honey 1998; Hauser & Konishi 1999). The long-lasting memory of some birds for locations in which they stored food is another case, one which illustrates very well the interplay that can exist among diverse approaches to a single cognitive phenomenon.

Animals should invest in hoarding food only when they or their close kin derive more benefit from it than lazy conspecifics that spend no time hoarding but pilfer the hoards of others (Andersson & Krebs 1978). This functional argument was an important stimulus to studies of food-storing parids and corvids, which documented that these birds could remember the locations of many individual storage sites for days or even months (review in Shettleworth 1995). The apparent feats of spatial memory shown by food-storing birds in the field far exceeded anything known from other species in the laboratory. Consistent with this observation, when corvids' spatial memory was tested with methods developed for rats and pigeons like radial mazes and operant delayed matching to sample, species that stored more food tended to perform better than less dedicated storers, although the story was less clear for parids (chickadees and titmice). Comparisons of learning and memory in different species have a long history in psychology in attempts to trace the evolution of intelligence (Mackintosh 1988), but comparing closely related species thought to have divergent adaptive specializations of cognition is relatively new. Nevertheless, traditional theoretical and methodological tools are still needed to understand how to separate species differences in cognition from other influences on behaviour such as species differences in motivation and perception. More than a single set of tests should be used, factors such as the degree of difficulty of the test and the strength of the animals' motivation should be varied, and tests should be included in which the species are predicted not to differ as well as those in which they should differ on ecological grounds (Kamil 1988).

The fact that food-storing birds used spatial memory to retrieve stored food linked this research to work on the neuroscience of spatial memory and inspired the discovery that food-storing species of birds have a larger hippocampus relative to brain and body size than species that do not store food (Krebs et al. 1989; Sherry et al. 1989). Although the function of the hippocampus in mammals continues to be debated (Redish 1999), in birds it is required for successful retrieval of stored food and is involved specifically in spatial memory (Clayton & Krebs 1995; Hampton & Shettleworth 1996). More generally, any exceptional demand on spatial cognition may be reflected in a relatively enlarged hippocampus. Evidence consistent with this hypothesis has been found in rodents that differ in hoarding or territory size and in avian nest parasites (Sherry et al. 1992; Reboreda et al. 1996). Interestingly, a recent model of the evolution of brood parasitism predicts that parasites such as cuckoos should have good memories for the location and status of host nests (Pagel et al. 1999).

Cognitive Ecology?

The biology and psychology of cognition are being synthesized in a number of other areas. Flower constancy in bees has been elegantly related to detailed properties of memory (Chittka et al. 1999). The adaptive value of learning has been investigated by showing that growth or reproduction are greater in experimental environments where important resources like mates or oviposition sites can be associated with simple cues than in environments where the same resources are unpredictable (see Dukas &

Duan 2000). A model in which animals remember places where fights occurred and are capable of simple associative learning generates aspects of territoriality (Stamps & Krishnan 1999). Ethological thinking about the organization of behaviour provides new insights into how animals behave when they encounter learned cues to food or sex (Domjan 1994; Timberlake 1994). An interdisciplinary approach is well established in a few areas involving cognition such as animal communication (Hauser 1996; Bradbury & Vehrencamp 1998), but a recent increase in interaction across traditional psychology–biology boundaries has been very evident in other areas, of which spatial cognition and social learning are prime examples.

In the psychology laboratory, studying spatial learning traditionally meant putting rats in mazes and testing cognitive mapping versus simpler mechanisms like learning fixed routes or responses. Meanwhile, field work with bees, ants and birds was showing how animals navigate in their natural environments using landmarks, dead reckoning, a sun compass, and other means. Gallistel's (1990) integrative review of all this work heralded a broader and more synthetic study of spatial cognition, evidence of which can be seen in the conference reported in the *Journal of Experimental Biology*, January 1996, and in the book edited by Healy (1998). In the case of social learning, psychologists had been obsessed since the days of Thorndike by whether animals could learn by imitation, but virtually ignored other mechanisms of social transmission that could be important in nature. In the last 20 years or so, however, the interdisciplinary study of social learning has exploded, as witnessed by two major conferences and resulting books (Zentall & Galef 1988; Heyes & Galef 1996). A number of factors stimulated these developments. They included influential critical reviews of social learning (Galef 1976, 1988), field studies of social primates, analysis of some novel mechanisms of social transmission (e.g. Galef & Wigmore 1983), new theory and data about social foraging (e.g. Lefebvre & Palameta 1988; Giraldeau et al. 1994), and improved experimental designs for distinguishing imitation from other social influences on behaviour (Heyes & Dawson 1990; Whiten et al. 1996).

To some (Dawkins 1989; Kamil 1998), the kind of research being discussed here represents the study of animal behaviour returning to its roots in the 'four whys' of ethology (Tinbergen 1963), that is, to an integrated study of proximate mechanism and development along with function and evolution. Indeed, Kamil (1998) suggested that the term 'cognitive ethology' should be reclaimed from those interested primarily in animal consciousness (Griffin 1978; Ristau 1991) to refer to all research on animal cognition in its natural context. To others (e.g. Dukas 1998a; Chittka 1999; Giraldeau 1999; Weidenmuller et al. 1999; Healy & Braithwaite 2000), such research is the new field of cognitive ecology.

Real (1993) originally coined the term 'cognitive ecology' to describe research on the cognitive mechanisms underlying ecologically relevant behaviour. In addition to discussing ways in which better understanding of cognition might illuminate questions of interest to behavioural ecologists, Real (1993; see also Real 1991) outlined a functional framework for the study of cognition. One should begin, he suggested, with analysis of a cognitive task to be performed, then try to understand its mechanism, and finally consider the selective history and evolutionary implications of that mechanism. Thus cognitive ecology includes study of how cognitive mechanisms evolved along with studies of how they work and how they contribute to behaviour in situations of ecological relevance. These same issues arise in the study of human cognition (e.g. Anderson 1991), and the framework outlined by Real parallels a widely admired proposal for the study of perception (Marr 1982). Modelling the evolution of learning and memory is a persistent enterprise (e.g. Stephens 1991; Dukas 1998b), but with rare exceptions (e.g. Bateson & Kacelnik 1998; Dyer 1998; Dukas & Duan 2000), theorizing about the evolution of learning is not usually well integrated with detailed analysis of specific cognitive mechanisms in the way that 'cognitive ecology' seems to promise. In practice 'cognitive ecology' seems to refer at present primarily to studying how perception, learning, memory, decision making (i.e. cognition in the broadest sense), contribute to behaviour in ecologically relevant contexts. The danger in thinking of 'cognitive ecology' as naming a new field is that the research so labelled will be isolated from established work on animal and human cognition rather than becoming part of a cross disciplinary synthesis (Shettleworth 2000a).

An analogy might be drawn here with neuroethology, as both a thriving subfield of neuroscience with its own international society and meetings and an example of how ideas and techniques from a related scientific area are being brought to bear on mechanistic questions in ethology. 'Neuroethology' does describe a unique kind of research, but that research remains firmly at the intersection of the two established fields that it integrates. Neuroethologists must be both neuroscientists and ethologists. In a similar way, 'cognitive ecology' describes research at the intersection between cognitive psychology and behavioural ecology/ethology; it will probably be most productive if it remains connnected with both of them. 'Cognitive ecology' is also but one symptom of a more widespread movement to integrate evolutionary thinking with psychology (Daly & Wilson 1999). This article focusses on examples from nonhuman animals, but that is not meant to imply that the same approach does not apply to human cognition. Arguably, some controversial questions about the human mind, such as whether cognition consists of a collection of adaptatively specialized modules, can best be addressed with nonhuman species (Shettleworth 2000b).

CONCLUSIONS

The possible benefits of integrating mechanistic and functional, or psychological and biological, approaches to animal cognition have been discussed many times (e.g. Shettleworth 1984, 1998; Kamil 1988; Rozin & Schull 1988; Stamps 1991). Nevertheless, some of the barriers to interdisciplinary communication pointed out by Kamil &

Yoerg (1982) still seem to exist. Among them are differences in terminology and in attitudes to laboratory versus field research among workers from different backgrounds. Thinking in terms of proximal causes does not always come easily to people accustomed to thinking in terms of ultimate causes and vice versa, but such intellectual flexibility can surely be facilitated by more widespread interdisciplinary training. An earlier review of 'learning and behavioural ecology' (Shettleworth 1984) could point to only a few cases, mostly from foraging, in which any aspect of cognition was being studied in its ecological context. Developments in behavioural ecology, ethology and comparative cognition in the ensuing years have contributed to the much richer menu of cognitive mechanisms and functional problems sampled in this article. There is every indication that this richness is still increasing.

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