Cognitive ethology, the field initiated by Donald R Griffin, was defined by him as the study of the mental experiences of animals as they behave in their natural environment in the course of their normal lives. It encompasses both the problems defined by Chalmers as the ‘hard’ problem of consciousness, phenomenal experience, and the ‘easy’ problems, the phenomena that appear to be explicable (someday) in terms of computational or neural mechanisms. Sources for evidence of consciousness and other mental experiences that Griffin suggested and are updated here include (1) possible neural correlates of consciousness, (2) versatility in meeting novel challenges, and (3) animal communication which he saw as a potential ‘window’ into their mental experiences. Also included is a very brief discussion of pertinent philosophical and conceptual issues; cross-species neural substrates underlying selected cognitive abilities; memory capacities especially as related to remembering the past and planning for the future; problem solving, tool use and strategic behavioral sequences such as those needed in anti-predator behaviors. The capacity for mirror self-recognition is examined as a means to investigate higher levels of consciousness. The evolutionary basis for morality is discussed. Throughout are noted the admonitions of von Uexküll to the scientist to attempt to understand the Umwelt of each animal. The evolutionary and ecological impacts and constraints on animal capacity and behavior are examined as possible.

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INTRODUCTION

What is it like to be a bat?’… the title of a philosophical essay by Nagel. He argued that we could never know what such an experience was like, for as human beings/scientists, we have no way of determining or understanding the nature of any bat mind state. In correspondence with Nagel and in his writings, Donald R. Griffin, the founder of ‘Cognitive Ethology’ argued otherwise… that it was indeed possible to make at least a start into such investigations, and even, assuming evolutionary continuity of mental experience, to imagine some of the experiences of other organisms. Cognitive Ethology was to be a beginning scientific exploration of the mental experiences of animals, particularly as they behave in their natural environments in the course of their normal lives. The mental experiences included, among others, awareness, purposes, consciousness, and general and specific cognitive capacities.

His endeavor provoked considerable controversy. But as Griffin had earlier remarked in 1958, concerning biologists’ great reluctance to consider the possibility of animals’ use of sonar for echolocation (now well established), ‘Excessive caution can sometimes lead one as far astray as rash enthusiasm.’

He proposed exploring several lines of evidence for this new field: (1) possible neural correlates of consciousness; (2) versatility of organisms in adapting to new challenges for which they have not been either genetically prepared or had pertinent learning experiences; (3) communication by animals, that can be interpreted as reporting subjective experiences.

Findings have potential impacts on human behavior. We are more likely to be concerned about animal’s well being and conservation of their habitat if we understand them to be conscious, intelligent beings.
A BRIEF FORAY INTO PHILOSOPHICAL ISSUES CONCERNING COGNITIVE ETHOLOGY

Awareness and Consciousness
The problems Griffin raises about consciousness are what the philosopher Chalmers, in a seminal paper, has termed the (phenomenal) ‘hard’ problems and the ‘easy’ problems. The latter, in Chalmers’ view, are those in which, using methods of cognitive science, the phenomena appear to be explicable (someday) in terms of computational or neural mechanisms. The ‘easy’ problems entail cognitive abilities including discriminating, integrating information, deliberately controlling behavior, and accessing and reporting mental states among others. (It should be noted that many scientists would consider that such ‘easy’ problems require more than a neural/computational approach, a very reductionistic type of explanation.) The ‘hard’ problems are the phenomenological ones, the very experience of a mental state, a perception, a pain, ‘what it is like to be xxx.’ In the past, most scientists have avoided the ‘hard’ problems. Many philosophers, however, including Aristotle, Descartes, and contemporary philosophers of mind have been concerned with issues of animal consciousness and reason. The philosopher Searle is probably most closely aligned with the stances of Griffin, and considers that a main issue is not whether nonhuman animals are conscious, but which animals are conscious and to what level of consciousness.

Even Darwin entitled a book ‘The Expression of the Emotions in Man and Animals.’ As Griffin notes, Darwin’s inclusion of mental continuity in evolution is far more reasonable a scientific approach than beginning with the denial of such capacity. Griffin further suggests that a yet more conservative, neutral approach would be to assume \( p = 0.5 \) with respect to the probability of consciousness in animals and then to increase or decrease that probability as data are accumulated.

Nevertheless, despite confusion over definitions, more (not all) contemporary animal behavior scientists appear to grant, to at least some species, phenomenological ‘awareness’ or ‘primary consciousness,’ if not the higher levels of consciousness. Those higher levels are often termed ‘sentience,’ described as the depth of awareness of self and others. Sentience includes self-awareness (both self as a body entailing self-recognition and self including a mental entity existing in a continual fashion in the past, present, and future), metacognition (the ability to think about the contents of one’s own mental states/feelings), and Theory of Mind (various abilities including perspective taking, empathy, and generally the ability to model another’s mental and physical perspective).

Approaches to the Study of Animal Capacities
A significant contribution to the study of animals is the concept von Uexküll proposed in 1909, that of the ‘Umwelt,’ meaning the environment as an organism perceives it and interacts with it. Several organisms can appear to live in the ‘same’ environment, but in effect those environments are vastly different, with each organism sensing and emphasizing different aspects, interacting differently, using the environment differently.

Another approach to species comparisons is a ‘functional’ one. Thus ethologists describe and compare foraging strategies, food preparation/storage, territory selection/defense, selection/creation of a home, mate selection, parenting behavior and the concomitant cognitive skills required in each. We have learned that cognitive abilities in one sphere need not generalize to another. Such modularity raises the issue of ‘what’ has evolved? What circuitry? Are there ‘core knowledge systems’ common to humans and some other species or can abilities in one sphere generalize to another(s) . . . over the eons or possibly in an organism over a lifetime? We do find many examples of one available biological ‘solution’ being used over evolution for other purposes.

Truly appropriate comparisons of abilities across species likewise entails understanding the developmental and learning processes involved: does the capacity occur full-blown in all species members? What experiences/learning trials were required; how many; over how long a time?

Work with captive species has revealed abilities possibly latent in the natural environment. In a few instances, captive great apes have been observed to actively teach as distinguished from exhibiting a behavior which may be copied. For example, the signing chimpanzee (Pan troglodytes) Washoe actively molded the hands of young chimpanzee Loulis into the sign for food, a training technique often used by humans with Washoe. Some captive apes, in particular, young apes, achieve abilities not observed in the field, e.g. spontaneous pointing, and do so more readily if they have more (positive) interactions with humans. Even monkeys can be specifically taught to point and then they generalize to use the skill in a communicative manner in varied circumstances.

We need to recognize that some observed behaviors may be ‘default,’ those exhibited in urgent
circumstances or in the presence of very potent stimuli, and can be detrimental in that particular situation. In less constrained circumstances, the organism may have reacted differently. For example, the beavers' cognitive abilities utilized in dam construction and repair have been denigrated, because some experimental work indicated that a beaver plastered mud over a loudspeaker that produced white noise, a sound similar to water rushing through a leak. That behavior can likewise be interpreted as a useful failsafe, while dam repair is achieved more flexibly in many circumstances.

In short there is a need for cautious conclusions and openness to various approaches.

NEUROLOGICAL AND NEUROANATOMICAL ISSUES

Neural Correlates of Consciousness

Despite intensive efforts to date (2012), research to find Neural Correlates of Consciousness (NCC) has not revealed structures or processes unique to humans that are necessary for consciousness. It must also be noted that neither have any necessary and sufficient neural correlates of consciousness been determined. We have learned that consciousness involves many levels of brain functioning from brainstem to the cortex.

A proper discussion of NCC is beyond the scope of this ms. Refer to Griffin and Speck or resources concerning neural studies and theories as they relate to the possibility of demonstrating consciousness in nonhuman animals. Evidence includes pharmacological interventions that can affect human conscious behavior, use of human consciousness studies, such as binocular rivalry and blindsight and relating all these to similar investigations and behaviors in nonhumans. Further supportive evidence for widespread consciousness is offered by Panksepp’s research emphasizing deep, old subcortical systems that generate affective consciousness and emotional expression. Quite similar systems occur in all mammals and some birds. When stimulated in humans, they produce intense emotional feelings and associated behaviors. In nonhumans, stimulation produces similar behavioral and physiological responses and, it is interpreted, similar conscious feelings. Not all agree.

Referring to this and other research, a group of eminent cognitive scientists recently signed the ‘Cambridge Declaration on Consciousness,’ basically stating that humans are not unique in possessing the neurological substrates that generate consciousness.

Brain Structures Underlying Cognitive Capacities

Despite current disagreements about directly linking specific neural activity or areas with consciousness, certain brain structures have been shown to play significant roles in both humans and other species, underlying similar kinds of cognitive competencies. In particular, the hippocampus (in vertebrates) is intrinsic to learning and storing spatial information, such as landmarks, distances and directions, all of which can figure importantly in locating food, territory and dwelling sites, scatter hoarding, migration, and mating. Some avian species, particularly corvids, typically investigated in the laboratory, exhibit astonishing abilities to cache food for times of scarcity, some species retrieving in a matter of hours, others in months. Hippocampal size varies with spatial demands placed on animals by their ecology, with increasing neurogenesis rates for winter storage and declines during spring. For example, in black-capped chickadees (Poecile gambeli) large differences in memory and hippocampal size occur over both large continental scale differences in winter severity as well as over small spatial scales that occur with the increasingly harsh conditions as one ascends a mountain; significant differences occur over as little as 600 m of elevation. Hippocampal size also varies with mating systems; polygamous species needing to roam over larger territories to find mates have a larger hippocampus than do monogamous species.

Homologous brain structures have been sought for the language learning of human children and nonhuman animals’ vocal communicative development. Many parallels have been found in avian song learning such as babbling and sound crystallization. Yet, among primates, it is chimpanzee gestural communication that may provide interesting parallels as well as possible homologous neurological structures.

Relative brain size with respect to body weight shows parrots and corvids (such as crows, rooks, and jays) are comparable to chimpanzees, with humans topping the list; dolphins particularly, but even seals, also have high ratios. Generally that greater relative brain size is associated with advanced cognitive processing and with high levels of sociality, longevity, slow development and long parental investment as well as a large forebrain. Interestingly it is different brain structures that show these correlations. In humans and other mammals, it is the cortex; in birds it is the nidopallium, until recently not considered a homologous structure.

Forebrain size has been linked to different abilities in different species. In birds, the linkage appears to be to innovative behavior. In ungulates
and primates forebrain size is linked more closely to social dynamics\textsuperscript{41} such as intra-group co-ordination and aspects of group size; linkage may also be to the type and quality of bonding relationships.\textsuperscript{42}

In fact the most pertinent commonalities between primates, including humans, and birds, are virtually identical neuronal connections and microcircuits that have been recently identified as mediating similar behaviors.\textsuperscript{43}

Very different neural systems can subserve complex behaviors, namely that of cephalopods, particularly the octopus, likely squid, possibly cuttlefish.\textsuperscript{44–46} The octopus nervous system has three main parts: a large brain of two central masses, the arm nervous system, and optic lobes. The system consists of about 500 million neurons, in contrast to rats’ 100 million and dogs’ 600 million.\textsuperscript{47} That brain is among the largest of any invertebrate and the brain/body ratio of Octopus vulgaris is comparable to that of lower vertebrates.\textsuperscript{48} The octopus may have undergone convergent evolution with vertebrates, needing extensive memory and learning perhaps driven in part by its being a solitary hunter or exacerbated by its vulnerability due to loss of the ancestral shell.\textsuperscript{49} The mammalian hippocampus and octopus MSF-VL system in the large brain lobes are similar, specifically in architecture, physiological connectivity and the exceptionally high number of small interneurons in the learning and memory areas. Convergence is not complete, with typical invertebrate neural communication, particularly with respect to cell structure and membrane properties. However, like those in other species, activity-dependent synaptic plasticity exists in neural areas important for learning and memory.\textsuperscript{50}

In conclusion, the hippocampus and other brain structures are subserving similar and complex functions in different species. The critical aspect appears to be similar micro patterns of individual neural connections rather than the brain region per se.

**SENSING (AND INTERACTING WITH) THE ENVIRONMENT**

As emphasized in von Uexküll’s concept of Umwelt, nonhuman animals’ sensory systems differ from each other and from humans, not only in sensing capacities, but also in senses emphasized and means of gathering and utilizing the sensory information. A chimpanzee in a signing project initially learns not that the sign for flower signifies ‘flower,’ but rather the ape, presented with a flower, generalizes to associate the sign with other odors such as pipe tobacco and kitchen fumes.\textsuperscript{51,52} An elephant appears incapable of the Mirror Self Recognition test until the paradigm includes the opportunity to explore a larger mirror with the tip of its trunk.\textsuperscript{53}

The capacities can be different as in the honeybee’s detecting both polarized light, and, like many other insects, UV light. To some, UV signifies open space, not the dark nest, for the sun is the only natural source of UV. To the honeybee, UV light also allows perceiving floral patterns that provide ‘paths’ to nectar/pollen. In von Uexküll’s famous example, a tick sucks not a human, but the rock wet with butyric acid from the sweaty man no longer there. The horse’s visual system allows it to detect something very well along the horizon, but in other regions, it has somewhat reduced acuity; this is attributed to a long streak of ganglion cells across the retina which parallel the slit-like pupil of the horse’s eye.\textsuperscript{54}

What is to be constructed from the sensory systems is another matter. ‘Search image’ has been proposed as a learned and/or innate sensory pattern facilitating an organism’s finding a particular food type, especially cryptic ones. On the other hand, simply detecting change in the environment and/or from a learned sensory pattern is critically important for ‘lower’ species such as sharks and lobsters; acute sensitivity to changing odor concentration in water currents can lead the animals to the source, food.\textsuperscript{55} Cross-modal matching is achievable by horses (and other species); horses can discriminate by voice cues between a familiar and unfamiliar person, then match voice to visual/olfactory cues.\textsuperscript{56}

We likely have not yet discovered the full array of other organisms’ sensory capacities; adaptive behavior of some species before earthquakes or approaching storms suggests sensitivities we do not know.

**ANIMAL COMMUNICATION**

**Natural Animal Communication**

Animal communication encompasses a broad array of signals, including visual, acoustic, electromagnetic, vibration, and odor. The focus here will be on vocal communication, which has received extensive investigation, probably because auditory signals can readily be recorded, then used in ‘playback’ experiments.

Among the core issues are: (1) whether signals are emitted in a reflexive, emotive Groan of Pain manner as Griffin termed it,\textsuperscript{57} or via an Innate Releasing Mechanism (IRM) as earlier described by Tinbergen\textsuperscript{58} or whether some voluntary control exists. (2) the meaning of the communication. Indeed Griffin saw animal communication as ‘a window on animal minds.’\textsuperscript{52} (3) then, how to investigate these issues?
Voluntary Usage?
The issue was addressed with the concept ‘audience effect,’ which examines the impact of a particular conspecific’s presence on the likelihood of a communicator uttering a given vocalization. For example, a male might make ‘food calls’ in the presence of food and a female, but not if another male were present instead of the female.

In analyzing animal vocal communication, scientists differentiate between (1) the acoustic structure of the call, (2) the usage, and (3) comprehension, distinguishing between information that a scientist recognizes in the call and the recipient(s)’ comprehension and utilization of that information.

Many factors may impact on whether a potential vocalizer calls and whether the recipient actually responds and how. These factors, addressed already in 1977 by Smith, include past history of the organism, likely unknown to the researcher. Such concerns are not limited to ‘intelligent’ organisms; familiarity and social history have been shown to affect the signaling of Siamese fighting fish.

Meaning of Signals
Smith encouraged a ‘message-meaning analysis’ of signals, noting that the same auditory production can have different meanings, depending on recipient and context (including past history, environment, and other stored information). Thus a male bird’s springtime song may mean to another male ‘likely aggression by me if you approach’ or ‘come hither’ to a female. Messages may include information about the signaler’s behavior and probability thereof, location, individual or group identity, or external referents such as predators, food, events or other ‘things.’ Message-meaning analysis requires detailed observations about correlations with conditions and signaler and recipient(s)’ behavior, prior to, during and after the signal. It is difficult to do well.

A simpler methodology, with significant limitations, but widely adopted probably due to that simplicity, relies on ‘functional referents.’ Calls are so classified if they appear to be highly stimulus specific and if call recipients use that specificity to determine the nature of their adaptive response. This analysis sidesteps the issue of information contained in the call, requiring a ++ behavioral response as evidence for the ‘functional referent;’ it has thus been used primarily with so-called ‘food’ and ‘alarm’ calls. Concerns with this analysis and the playback experiments typically used, center on the lack of contextual information available to a recipient with which to calibrate responses, and thus a higher likelihood of a ‘default’ or fail-safe response.

Presently, scientists are attempting to fine tune their approach to studying signaling, including more studies beyond alarm and food calls. Smith’s suggested analysis, though difficult, can help elucidate signal information. Townsend and Manser, in their excellent review, suggest variants of playback experiments, including prime-probe, habituation-dishabituation and violation of expectation techniques.

Information in Alarm Calls
Most scientists agree that alarm calls contain urgency-based information (predator’s threat level). Interpretation of the referential component of calls is much more controversial. Apparent categories of functionally referential information potentially available in an alarm signal are: predator type (aerial or terrestrial, specific species), predator’s spatial location, physical qualities such as size, shape, and color, and predator behaviors such as movement (no movement, speed, kind of movement such as hawk perched, searching for prey or attacking).

Initial distinctions between calls for aerial and some ground predators were noted from astute observations of vervet monkeys (Cercopithecus aethiops) by an experienced field researcher (Struhsaker) and were then followed up by videotaped playback experiments in the field. Since then, acoustically distinctive calls for aerial and for ground predators have been found in a diverse number of species, including chickens (Gallus gallus domesticus), many species of ground squirrels (Spermophilus spp.), tree squirrels (Tamiasciurus hudsonicus), social mongooses (aka Meerkats) (Suricata suricatta), prairie dogs (Gunnison’s (Cynomys gunnisoni) and Black-tailed (Cynomys ludovicianus), and various lemurs (reviewed in Ref 84). For some species the calls appear to be quite specific in their referents, for example, the vervet monkeys have three types of calls causing differential responding, for example, looking upward and running to a nearby bush to the call for eagle-type predators, looking to the ground for snake-type calls and running up into the trees or remaining quietly there for calls for leopard-like predators. [These responses, however, are not absolutely unique to each predator type, with occasional similar responses across categories as indicated in both the original and more recent data. Recent studies also show a sex difference, with only female vervets exhibiting the distinctive responding (J. Fischer, personal communication)]. Social mongooses calls distinguish aerial versus ground predators at different urgency levels. Various species of prairie dogs appear to have both distinctive calls and appropriate responding behavior to the calls for at
least four different potential predators (coyote (*Canis latrans*), domestic dog (*Canis familiaris*), red-tailed hawk (*Buteo jamaicensis*), and human (*Homo sapiens*)) and also possibly to badgers (*Taxidea taxus*) and bats, pinnipeds, cetaceans and elephants (discussion in Ref 97). There are scattered references to refinement of usage and development of unique food calls in some species. 90 Some of the most perplexing interpretations of data are for alarm calls said to denote predator characteristics such as size, color, or shape. These distinctions have been reported for prairie dogs, but black-capped chickadees also appear to encode information about predator size, and male chickens provide graded information about aerial stimuli size, distance and speed, to which captive females respond in graded fashion in experimental situations. 95

Is some call information (e.g., size, speed, distance) merely a correlate of urgency? Slobodchikoff’s experiments argue against that interpretation, in that acoustic structure of prairie dog alarm calls varied with colors on intruders and were distinctive for certain geometric shapes (triangle vs. circle–square). 96 Slobodchikoff (pers. comm.) suggests that the geometric sensitivities may be related to the prairie dogs’ predator classes: triangular for raptors, circular–rectangular for mammalian ground predators.

**Plasticity**

Plasticity, originally thought to be the property only of human language, has been found in song birds (*Oscines*), then in hummingbirds (*Trochilidae*) and parrots (*Psittaciformes*) and then more widespread. Some species show gradual development to the adults’ more complex acoustic alarm calls (e.g., prairie dogs, meerkats). Prairie dogs have been shown to modify calls made to a human intruder if that intruder became more threatening (e.g., fired a gun). Goat (*Capra hircus*) contact calls have been shown to exhibit plasticity, affected both by kinship and membership in different social groups. 98 These differences potentially promote mother-kid recognition, individual identity, and the formation of ‘dialects’ indicative of social group membership. Growing evidence supports vocal production learning in some other mammalian species: bats, pinnipeds, cetaceans and elephants (discussion in Ref 97). There are scattered references to refinement of usage and development of unique food calls in some primate species. 99

**Further Questions**

How to conceptualize present findings in animal communication? Analysis has been greatly facilitated by the introduction of discriminant functional analysis (DFA) and other statistics, replacing some of the tedious measurement and possible subjectivity in classification. Acoustic structural differences do reliably sort calls according to descriptors such as color, size, and shape and other conditions, but, in many cases, we are unable to provide evidence, at this point, that call recipients are using that information.

Why do such complex communication systems exist in some species? The alarm systems of prairie dogs and meerkats may have resulted from evolutionary pressures deriving from their ecological conditions. For example, prairie dogs are a fixed social species, subject to the same predator individuals, with fairly set escape opportunities (bolt holes and tunnels). Some individual predators have different strategies: some coyotes rapidly charge at any prairie dogs; others wait at a well-populated burrow. It would be beneficial to recognize those individuals, perhaps aided by color or shape information. The field needs further explorations of communication complexity across species and ecological conditions.

**Caching, Episodic Memory, and Mental Time Travel**

Whether animals have episodic memory remains debated still, Tulving having claimed it to be a uniquely human capacity. Episodic memory (‘remember’) is distinguished from semantic memory (‘know’). To remember, for Tulving, includes recognizing that it is oneself in the past episode and in the present; that assertion is most difficult to establish in a nonlinguistic organism. Evidence supports close relationships between episodic memory and the ability to project oneself into the future, with shared neural systems and developmental paths. Planning for others seems to precede developmentally planning for self, a distinction Clayton suggests may be useful in animal studies. Whatever the difficulties of interpretation, there have been useful criteria established for investigating ‘episodic-like’ memory in nonhuman animals: (1) the what-where-when paradigm, and (2) the ‘unexpected question’ technique.

In a set of ingenious experiments, Clayton and colleagues, allowed scrub jays (*Aphelocoma coerulescens*) to bury larvae, a preferred food and, in a separate place, peanuts, less preferred. The birds had learned that the larvae decay and become inedible after five days, but the peanuts do not. Given a choice soon, or after five days, the scrub jays chose the appropriate spot to retrieve the food. This experiment fulfilled the what-where-when conditions. However, subsequent research indicated limited success beyond...
the food caching corvids, and only scrub jays met all the conditions the researchers set.

The ‘unexpected question’ paradigm suggested by Zentall\textsuperscript{108} tests for something that was incidental at the time of training (presumably ‘unattended’ by the animal), using a probe trial inserted within the ordinary testing trials. As Clayton et al note, a useful approach for future studies.

**PROBLEM SOLVING, TOOL USE, AND STRATEGIC BEHAVIOR SEQUENCES**

**Problem Solving**

Köhler\textsuperscript{109} set chimpanzees problems to acquire out-of-reach food, having boxes available that could be piled up or poles that could be fit together. Köhler reported that the chimpanzees solved these problems spontaneously, not by stimulus–response association or trial and error, but by a sudden insight. There are other interpretations of the chimpanzees’ behavior. Many other species were subsequently also seen to be capable of various problem solving tasks.

Some of the most remarkable understandings, interpreted as comprehending causal relations, are exhibited in Heinrich’s experiments with ravens (\textit{Corvus corax}).\textsuperscript{110} In one set, adult captive ravens with no experience with strings, after several hours, pulled up meat dangling on a meter long piece of string. They pulled up sections, stood on the captured string, and repeated this motion until reaching the meat. If startled, ordinary ravens fly off with any food in their mouth. In this experiment, a raven who was unsuccessful at pulling up the food, did try to fly away with meat on a string, but those who had pulled up the meat did not do so, even on the first staple. In other experiments with crossed colored strings, one holding a rock and the other meat, some ravens immediately pulled on the correct string. Other ravens did so after a brief tug moved the unpalatable rock. However they persisted over subsequent trials in initially pulling the incorrect string, directly under which hung the rock, then corrected and pulled the string which moved the meat. Another task, with different ravens and a looped string which ‘illogically’ required pulling down on the string to move the meat up was never successfully solved and the ravens lost interest. We do not know all causal relations or ‘physics’ the ravens understand, or the ‘rules’ they apply, but gradually, across species, we may be able to determine ecologically appropriate generalities.

**Tool Use**

In the wild, tool use has been observed in a wide array of taxa, including all great apes, some monkeys, some birds, particularly the corvids, some cetaceans, fishes, invertebrates including octopi, and, surprisingly, in only five species of nonprimate mammals. Veined octopi (\textit{Amphioctopus marginatus}) have been filmed carrying discarded coconut shells along as they walk, requiring an ungainly inefficient ‘stilt walk’ to do so, then using the shells for protective shelter as needed.\textsuperscript{111}

The mammals observed using tools in the wild are some Asian elephants (\textit{Elephas maximus}) which modify branches to swat away flies, sea otters (\textit{Enhydra lutris}) which frequently use rocks to break the shells of clams and sea urchins, some bottle nose dolphins (\textit{Tursiops} sp) using sponges to protect body parts while foraging, humpback whales (\textit{Megaptera novaeangliae}) which blow bubble curtains used to trap fish schools, and as recently observed, brown bears (\textit{Ursus arctos}) which scratch themselves with selected, barnacle encrusted rocks.\textsuperscript{112} The topic has several extensive reviews\textsuperscript{113–116} and will be mentioned only briefly here.

In captivity, various species, not observed using tools in the wild, have been taught tool use, including rooks (\textit{Corvus frugilegus})\textsuperscript{117} and wood pecker finches (\textit{Cactospiza palilida})\textsuperscript{118} or have independently demonstrated tool creation and use.\textsuperscript{118} One of the more remarkable instances of tool creation involved captive New Caledonian crows (\textit{Corvus moneduloides}). A female crow, having seen a wire hook, but never having witnessed the process of bending wire, nevertheless, bent a wire into a hook to reach food down a tube. This creation involved innovative behavior and nonnatural materials, not likely to be encountered in the wild.\textsuperscript{119}

The definition of tool use is a continuing debate, but most scientists agree that it requires the manipulation of a freely movable object on a target object to modify the target object’s physical characteristics.\textsuperscript{113} Using tools is of especial interest because it implies a goal or purpose, requires at least short-term planning (sometimes longer) and, depending on the context, can require flexible behavior. Some species can also modify their tools to be more efficient.

The definition of tool use can also be extended.\textsuperscript{111} For example, Tinbergen reported Herring gulls picking up clams (movable) and opening them to eat by dropping them onto rocks (stationary).\textsuperscript{120} A gorilla used a stick apparently to determine water depth, thus improving its access to information.\textsuperscript{121} Mike, the well known Goodall study chimpanzee, improved his display by loudly banging discarded kerosene cans, such continued usage finally resulting in a rise in his status.\textsuperscript{122}
Given the diversity of species capable of tool use and the various specialized uses, it is likely that there are different cognitive mechanisms and different ecological and social constraints/drivers underlying the capacity, as is true of many cognitive abilities.

Strategic Behavior Sequences

Introduction

Strategic behaviors exhibited by animals can reveal both cognitive complexity and intended behavior. The behaviors are relevant to issues of representation and intentionality, both in the philosophical sense of intentionality and ‘intended’ or ‘purposeful’ (included within a concept of intentionality). Several aspects of strategic behaviors are of particular interest to Cognitive Ethologists: organisms must be able to prioritize between conflicting demands, for example, courting, mating, feeding self, feeding young, protecting young, hunting, avoiding predation. Animals also often need to use spatial information, recognize and take advantage of opportunistic events, overcome obstacles, especially novel ones, learn through either actual or mental trial and error, and sometimes even deceive.

Great apes’ strategic behaviors are well documented, so I will note lesser known cases, firstly, those of an ungulate, the pronghorn antelope (Antilocapra Americana). Their complex antipredator behavior also supports evolution of a specialized intelligence, not via the social intelligence hypothesis, but rather from the driving force of predation, in the antelopes’ case, particularly on the young.

Predator Avoidance Behavior/Protecting Young: Antelopes

In general, ungulate adults avoid predation by being large bodied and/or fast runners. However, as reported by Byers, mother pronghorn antelopes hide vulnerable newborns, staying away and, before returning, run about, even for a half an hour, often staring, appearing to look for predators. The high predation pressure at Byers’ site, results in 75–100% of the fawns falling to coyotes or eagles. Byers reports a returning mother suddenly seeing two low-flying golden eagles. The doe leaves the young’s region, craning back her head, a posture used only when looking at golden eagles. She then waits 30 min, departing again when the eagles return.

With coyotes, Byers reports that the antelope mother, usually positioned far from the young (about 70 m), extrapolates from the coyote’s path, distracting only when the coyote’s path will intercept the fawns. She then flashes her large white rump patch and prances distinctly.

Protecting the Young: Injury Feigning Birds

Some ground nesting birds when having a nest or young, will perform various apparently distractive behaviors in the presence of a predator or intruder. For the Piping plover (Charadrius melodus), these include flying conspicuously in front of the intruder, vocalizing near the intruder, ‘false brooding’ (sitting fluffed out on a site where there is no nest), or the most dramatic, engaging in very awkward wing-flapping, commonly termed ‘broken-wing displays’ or ‘injury feigning.’ So ‘injured,’ the bird may display, sometimes for many minutes or for hundreds of feet, but then simply flies away. The birds give an impression of trying to lead the intruder away from the nest, though some have claimed the movements are ‘hysterical’ and others have claimed the movements are released and directed throughout by sign stimuli. Ristau investigated the possibility that the behavior is purposeful, applying what Dennett has termed a first order intentional stance, namely that ‘the plover wants to lead the intruder away from the nest/young.’ A purposeful interpretation suggests the following predictions: (1) the plover should move in a direction such that an intruder following it would move further from the nest or young, (2) the plover should monitor the intruder’s behavior, and (3) the plover should respond appropriately to changes in the intruder’s behavior.

Ristau found that in 44/45 cases the Piping plover displayed while moving in a direction that would lead the intruder away from the nest. The bird did monitor the intruder and changed its behavior if an intruder stopped following the display, including such actions as flying or walking closer to the intruder or displaying more intensely.

The bird also chose its location for display, sometimes flying, which, in all cases examined, resulted in the bird being closer to the intruder. The plovers also quickly learned to discriminate between humans who had behaved in ‘threatening’ ways and those who had not, namely those who previously had hovered over the nest and those who had simply walked by, not looking at the nest. Only one or two exposures were necessary. Others have interpreted the ‘broken-wing’ behavior of plover species in a much more minimal way. Byers, for example, contrasts the ungulates’ ‘calculated’ behavior with that of another plover species, the killdeer (Charadrius vociferous). He claims the killdeer parents display no matter what his path, dependent only on his approach distance. However, as demonstrated in the above research by Ristau with a related species, the plover’s...
display is not static, but on a path leading away from the young. Readiness to display does appear to depend on previous exposure to humans, birds initially being very wary, likely to display and doing so at greater approach distances. Ristau’s detailed sequential analysis, adopting the stance of possible purposeful behavior, does lead to a deeper appreciation of the complexity of the interactive behavior, than does simply noting approach distance. This use of the intentional stance is instrumental in nature, helpful in suggesting experimental work and meaningful kinds of observations. As various philosophers and scientists have suggested, further conceptual work is needed to better theoretically ground these and other behaviors studied/analyzed by cognitive ethologists.132

**Predatory Strategies**

Strategies are also required by the predators. Very well documented accounts show individual members of genus X overcome obstacles to reach their prey, taking long detours around, often losing visual contact with that prey. In danger themselves of predation by their prey, they are opportunistic, moving closer when such movements are disguised or the prey is distracted by other events. Some of the predator’s communication is highly similar to that used in the prey’s courtship and suffices to mislead the prey. Genus X is any of several jumping spiders, *Portia*. These large venomous spiders build their own webs to capture insects, but also specialize in preying upon other spiders by invading their webs. *Portia* plucks the strings of the prey’s web, sometimes similarly to the prey’s courtship vibrations. Signals that bring the prey closer to the web edge are continued, otherwise varied. Some signals are like those of a ruffling breeze or falling leaf. Should a breeze blow, *Portia* advances, under protection of those vibrations. Should the prey advance aggressively, *Portia* retreats. *Portia* may return, even a half an hour later, but often with a different tactic, perhaps dropping precisely from above, on a silken thread, onto the prey, killing it with a poisonous bite. In laboratory experiments, *Portia* can, on first encounter, successfully capture novel spiders, never encountered before. Critics will invent a myriad of complex modules to deal with these phenomena; others may suspect that some cognitive capacities may reside in such organisms.

**Other Aspects of Predator and Prey Behavior**

Alerting predators to one’s presence is a tactic that is used by many species, when predation appears to rely on surprise, for example, antelopes produce a high bounding gait (‘stotting’);135; hares stand bipedally.136 And prey likewise carefully monitor predator activities, seeming able to detect when predators are not dangerous, either resting at a distance or otherwise engaged.137

Some predators are capable of co-operative hunting, from simple to complex, particularly in chimpanzees and lionesses (*Panthera leo*), but observations exist also of pelicans (*Pelecanus crispus*), cormorants (e.g., *Phalacrocorax auritus*), Harris’s hawks (*Parabuteo unicinctus*), and likely other birds of prey, South American otters (*Pteronura brasiliensis*), dusky dolphins (*Lagenorhynchus obscurus*), killer whales (*Orcinus orca*), hyenas (notably *Crocuta crocuta*), and other species.138

**MIRROR SELF RECOGNITION EXPERIMENTS**

The mirror self-recognition (MSR) experiments139 are of interest for several reasons. In these, a mark is placed on an organism where it cannot be seen except by the organism’s viewing its own reflection in a mirror. The successful subject tries to explore or remove the mark. Human children pass this test between 18 and 24 months of age, other species which succeed, at later ages. Gallup and later de Waal have suggested that MSR capacity has coevolved with empathy and perspective taking.140,141 And species with those capacities have evolved with complex social group structures and/or interactions.

Although a myriad of species have been tested, from chickens and beyond, only humans, great apes, dolphins (*Tursiops truncates*),142 Asian elephants (*Elephas maximus*),143 and magpies (*Pica pica*),144 the only nonmammalian species, have succeeded. Arguments can be made for homologous evolution in humans and great apes, but would require convergent evolutionary mechanisms for the other species.

To succeed does not imply having the same capacity for self recognition that humans do; that capacity develops gradually beyond MSR. MSR entails recognition of self as a body, not self as a mind, or psychological entity existing in the past, present, and future.

When individuals pass the test, they go through several stages. Initially they (1) give ‘social displays,’ reacting to the image as an ‘other,’ often threatening, sometimes courting, then (2) physically inspect the mirror, even looking behind it, (3) test for behavioral contingencies, often passing repeatedly in front of the mirror, and (4) inspect the marking. In tests with successful species, not all individuals pass, some stopping at earlier stages or losing interest altogether,
not uncommon behavior for non-MSR tasks too. For gorillas and orangutans, some researchers report success and others failure.

Why the magpie succeeds at MSR, while parrots, a social and very cognitively advanced species, have not, is unclear. The magpie is a corvid, stores food, requiring detailed memory capacity, and remembers who has observed its storing, suggesting strong social sensitivities.144 Of five magpies tested, clear MSR evidence occurred in two birds, weaker in another and not in two.

Why do tests fail for some experiments and some species? The successful Asian elephant tests allowed the elephant to explore the mirror with its trunk, a primary appendage for assessing its environment,52 and provided a far larger mirror for the elephant to view than had earlier work.145 Interestingly, the elephant used the smaller mirror to locate hidden food; such instrumental mirror use without passing MSR has occurred in various species. The direct gaze entailed in MSR is, in many species, particularly primates, an aggressive communication and so may impact on exploration of the image. Despite some debate about MSR,146 it does appear to require advanced cognitive/social abilities and so remains a useful comparative technique.147

**MORALITY**

Morality is considered by many to have its roots in emotional and empathetic behavior. DeWaal and colleagues specifically propose roots in empathy/consolation, pro-social tendencies, and reciprocity/sense of fairness.

Preston and de Waal suggest a model for empathy divided into ultimate and proximate levels.148 De Waal149 suggests that state matching and ‘emotional contagion’ probably evolved with parental care, then generalized to other social domains such as courting and predator defense. Higher empathy levels evolved, allowing more effective support for other group members, some requiring perspective taking, an ability more prevalent in large brained species such as apes, elephants and dolphins. However, he does consider that empathy is characteristic of all mammals and likely birds, or at least some avian species. All these states would require some level of sentience.

Emotional contagion, has been demonstrated in mice (Mus musculus), whose writhing in response to the pain from an injection of acetic acid was exacerbated if they observed a cagemate similarly writhing in pain; general sensitivity to pain, even from a different source, was also increased. However social relationships mattered; this occurred only for cage-mate pairs. In fact, males, but not females, showed a counter-empathetic reaction, reducing their own pain sensitivity when witnessing the pain of unfamiliar males, presumably likely rivals.150

A sense of fairness has been investigated, specifically ‘inequity aversion,’ a term from economics theory. In seminal research with capuchin monkeys (Cebus apella), the monkeys refused to accept a piece of cucumber, a less preferred food that they had been exchanging with the experimenter for tokens, when their partner suddenly started receiving highly preferred grapes instead of cucumber.151 The results set off a flurry of controversy and research, discussed in an excellent review by Brosnan and DeWaal.152 Most research entailed non-human primates, and sometimes dogs (Canis lupus familiaris), generally indicating negative responses to continuing inequity between an animal and a social partner, with the disadvantaged often refusing to continue the task. Cleaner fish (Labroides dimidiatus) which work cooperatively, punish those not contributing to the cleaning.153 However, in experiments, they did not exhibit inequity aversion, suggesting that punishment, rather than sensitivity to equity, can maintain cooperation.154

What of the other side of injustice, the ‘advantaged inequity’ of the one receiving more. This ‘second order inequity,’ considered as deriving from the first, and weaker, does, at least sometimes with chimpanzees, lead to the advantaged individual reacting negatively or refusing to continue.

Specifically prosocial behavior has been studied, concentrating either on the choices producing inequity or on responses to inequity. Typically individual A makes choices that can lead either to reward being received only by itself or also by its partner. Prosocial choices prevail in both monkeys and apes studied, and, particularly for ‘second-order inequity,’ depend strongly on the value of the relationship.

Certain other conditions seem to be necessary for inequity aversion. Interactions should be continuing, not one-off. Partners should see each other. A task must be involved; freely given rewards produce no effect. For chimpanzees, disadvantaged inequities must occur at least 50% of the time; otherwise it is tolerated. This is reasonable, for in the natural world, inequities can even out over time and tolerance can promote cooperation. Close social relationships are essential, taking precedence over kinship. Indeed the inequity response is more common with highly socially cooperative species such as those that hunt in groups and form coalitions.
and alliances, irrespective of brain size, or social organization.149,155 Critics emphasize frustration and contrast effects as explanatory mechanisms.156,157 de Waal and colleagues stress the need for expanding research to more species and to observations of naturally occurring fairness, such as necessary in chimpanzee alliances and in the play of canids (Canidae) and other species. In play, one who plays too roughly, or doesn’t ‘apologize’ for it can be excluded from future play.158 Although no species exhibits the broad sense of fairness shown by humans, aspects are present in many species and situations.159

OTHER ASPECTS OF COGNITIVE ETHOLOGY

Cognitive Ethology is a broad field, encompassing too many areas to be dealt with here, including meta-cognition, imitation and culture, navigational abilities, animal artificial language and cognition projects, Theory of Mind, and deception. Laboratory experimentalists and field scientists can be at odds, with those who have restricted their experience to the laboratory to tend toward much more minimal interpretations of animal achievements (as in animal culture)160 than would most ethologists.161

CONCLUSION

Over the last decade, there has been enormous interest in and research relevant to Cognitive Ethology, the field begun by Donald R. Griffin. Given the evidence, perhaps particularly that from nonintrusive techniques finding similar brain activities and correlated behaviors in human and other species, a scientist is hard put to deny at least some level of consciousness to nonhuman animals or to claim that it is not a subject for scientific study. In 2012, prominent neuroscientists signed the Cambridge Declaration on Consciousness asserting that evidence could not support humans as the unique harbors of consciousness. The questions become which animals are conscious, to what levels, and what best ways to investigate the phenomena.

It is also clear that exceptional intelligences may exist for different species only in particular modular domains, as driven by ecological and social factors impacting on their evolution. Advanced cognitive abilities have been found in diverse species, including those with vastly different neural organization such as the octopus, an organism deserving of further study. Some species exhibit episodic-like memory, usually considered to be uniquely human; a strong case is made from caching abilities of some corvids. Natural animal communication studies have revealed information within some signals that appears to designate specific predator and predator classes and also descriptors such as size, shape, color, and a potential predator’s speed and behavior, some of which, however, may simply be correlates of urgency. Research has concentrated on vocal alarm calls, and should be extended to the more difficult task of understanding communication not affording such conspicuous responses to signals. Animals, often, but not exclusively, the great apes and corvids, have shown remarkable instances of problem solving and novel tool creation and use, both in the field and in controlled captive conditions. The study of behavioral strategies utilized in anti-predator activities has benefited from taking an intentional stance, thereby generating hypotheses and detailed data collection not typically gathered; the Piping plover’s use of the broken-wing display is an example. A burgeoning field of investigation into the evolutionary origins of human senses of justice and morality has shown widespread instances of concern for ‘fairness’ and ‘inequity aversion’ in the species studied, but should be extended beyond primates and dogs. The behavioral expression of such concerns depends on many factors, particularly social bonding strength and likelihood of a continuing relationship; the field is not without controversy. And controversy still exists over the definitions of many abilities, particularly as they relate to human abilities; examples include consciousness itself, episodic memory in animals, tool use, deception, and morality, among others. However, we should attempt to understand those capacities in relation to the organism’s particular ecological and social needs, not merely defining them in terms of human capacities.

Varied research efforts have underscored the importance of careful, detailed observations by experienced researchers of animals behaving in their natural environments. From these can arise the hypotheses to be further investigated by additional observations and field and laboratory experiments. When experiments in the lab contradict plausible interpretations of behavior observed in the wild, scientists must be wary. The laboratory is a highly circumscribed situation; experimental design should allow for possible advanced capabilities to be demonstrated. We need to be aware of possible unrecognized assumptions about an animal’s perceptions and goals. We must realize possible impacts of boredom, of fear, of the salience of
the organism’s sensory system. In the end, in the beginning, we must return again to von Uexküll’s admonitions to be mindful of the Umwelt of the animals we wish to understand.

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REFERENCES


46. Into the mind of an Octopus. *Phil Psych*. Submitted for publication


FURTHER READING
