

Observing Cognitive Complexity in Primates and Cetaceans

Christine M. Johnson
University of California, San Diego, U.S.A.

This paper on cognitive complexity in primates and cetaceans is a review of studies that use only observational methods. These studies include descriptive accounts, both qualitative and quantitative, of behavior-in-context in naturally-occurring and quasi-experimental settings, especially involving the micro-analysis of video. To unify this piecemeal but burgeoning literature, “cognition” is taken as embodied, largely visible, and distributed across physical and social environments. Its study involves documenting the adaptation of behavior to changing conditions, especially in ontogeny, tool-use, and social discourse. The studies selected for this review focus on the cognitive complexity that is apparent in the versatility, the hierarchical organization, and the long-term patterning of such behavioral adaptations. Versatility is seen, for example, in the substitution of different acts or objects into established routines, in the size and flexibility of action repertoires that enable variably configured and sequenced performances, and in the marked occurrence of individual differences. Hierarchical organization is seen in the substitution or iteration of a subroutine that fails to disrupt its larger routine, in the simultaneous embedding of one social interaction within the frame of another (as in “social tool” use), and in the insertion of a novel or borrowed subroutine as a tactical response, especially one that temporarily redirects an animal’s trajectory. The complexity apparent in long-term patterning includes tracking and making selective use of multiple histories (e.g., concerning kinship, rank, etc.) whose predictions and tactics may vary, responding to “market” values that change with ecological and social factors, and exploiting traditions of practice which provide social and material resources that shape engagement and learning. While this literature includes far more primate than cetacean examples, the primate work offers helpful suggestions for settings, issues, and techniques that could be adapted to the sensori-motor, ecological, and social constraints on cetacean cognition. The array of observations reviewed illustrate the utility across species of scoring such parameters as displays of attention in multiple modalities, abrupt trajectory changes, the complementarity and contingency of actions, and the resiliency of sequences, to help identify the media that matter in a given cognitive ecology. Systematic micro-analyses, in conjunction with long-term relational data that track changes in affordances and coordination, make such observational approaches a viable and valuable addition to the study of comparative cognition.

For many decades, primate cognition has been studied in the lab and in the field (see Cheney & Seyfarth, 1990, 2007; Kohler, 1927; Matsuzawa, Tomonaga, & Tanaka, 2006; Premack & Premack, 1983; Tomasello & Call, 1997). In contrast, given the significant difficulties in housing aquatic mammals or in acclimating and viewing them in the wild (although see Herzing, 2002), far fewer studies on cetacean cognition have been done (see Herman 1980a; Herman, Pack, & Morrel-Samuels, 1993; Johnson & Herzing, 2006; Pack & Herman, 2006; Schusterman, Thomas, & Wood, 1986). Nonetheless, these limited studies show that these two, otherwise diverse taxa appear to share certain key attributes. Both have relatively large brains, are keen problem solvers in the lab, and participate in complex societies in the wild. Such indicators of cognitive complexity make a compelling case for the further comparative study of their cognition, and the many dolphins currently held in captivity offer us a particularly promising opportunity.

Correspondence concerning this article should be addressed to Christine M. Johnson
Department of Cognitive Science, 9500 Gilman Drive, University of California, San Diego, La Jolla,
CA 92093-0515, U.S.A. (johnson@cogsci.ucsd.edu).

The greatest advantage that captive dolphins offer researchers interested in studying cognition is their ease of accessibility. Although most animals held for display are not available for regular participation in experimental studies, many can be readily viewed underwater. Housed communally by law, they provide daily examples of social interaction that anyone with a video camera can capture. Renowned for their curiosity and playfulness, the introduction of toys or other opportunities for enrichment can not only improve the quality of the animals' lives, but provide researchers with additional interesting interactions to record. Making use of such "naturalistic" behavior to study cognition, however, relies on the deployment of observational methods that are based on different models, and thus ask somewhat different questions, than experimental studies typically do.

Observational studies of human cognition have made significant headway, in recent years, in describing how cognition happens in everyday life (e.g., Grannot & Parziale, 2002; Goodwin, 2000; Hutchins, 1995a, 2001; Resnick, Levine, & Teasley, 1991). Plus, developmental studies of cognition have long relied on observational methods (e.g., Piaget, 1952; Vygotsky, 1978; for contemporary work see especially Fogel, 1993; Rogoff, 1990; Thelen & Smith, 1994). In both cases, naturalistic (as opposed to experimentally constrained) behavior, observed in a real-world setting, is the main focus of analysis. Such studies maximize ecological validity and provide insights into how even complex human cognition can be observed.

Observational methods are most compatible with embodied models of cognition. These models take cognition as developing through engagement with the world, and so motivate an ontogenetic analyses of what bodies do under varying environmental constraints. As a result, the comparative researcher can begin by documenting the nature of a species' interface with the world - what can be discriminated, what is salient, what arouses, as well as the range of possible motoric responses. But cognition is more than just perception and action. It is the conditional change in sensory-motor activity - the adaptiveness of behavior - that characterizes an event as cognitive. Thus we say that learning, or problem solving, or coherent discourse occur when there is an observable improvement in the "fit" between behavior and conditions. Those conditions can include physical structures in the environment, as well as the behavior of other individuals. And cognitive work, from this view, is largely visible, especially during development, in the way that these activities and conditions "come into coordination" (Hutchins, 1995a, 2001).

The task of observing cognition, then, involves documenting the development of conditional relationships - how changes in behavior fluctuate with changes in setting. Experimental approaches operate on a similar premise, in that they involve the controlled manipulation of settings aimed to test for predictable changes in behavior. However, these approaches tend to reside in a different theoretical framework. In that view, cognition is seen as a capacity or representation inside the head of the individual, which is taken as the source and driver of behavior. It is this invisible structure, then, that must be inferred by the researcher based on the conditional relationships observed (see Johnson, 2001). In

contrast, observational methods focus not on the “product” of learning, or on the “producer” of adaptive behavior, but on the *process* itself (see Johnson, 1993). By studying the nature of that process - how fit is accomplished, how constraints interact, how the trajectory of experience limits and supports what is possible - an observer can, through the systematic description of interaction, discover the regularities and requirements of cognition.

This observational approach to cognition can be applied to any species, including the simplest of organisms in congress with their worlds. But in this paper we are concerned with cognitive complexity. As we shall see from the many examples to follow, that complexity will be apparent in the length, variability, and embeddedness of behavioral sequences and in the elaborate and sometimes time-displaced nature of the relevant conditions that can come into play. (For discussions of complexity in nonhuman cognition, see Byrne, Corp, & Byrne, 2001a; Connor, 2007; Parker, 2004; Russon & Galdikas, 1993; Sambrook & Whiten, 1997; de Waal & Tyack, 2003).

Some models of embodied cognition discuss complexity in terms of the sophistication of the mental representations that are implicated by a subject’s performance. For example, these might include embodied simulations, across-domain mappings, schemata, and even amodal abstractions (see Barsalou, Simmons, Barbey, & Wilson, 2003; Fauconnier & Turner, 2002; Lakoff & Nunez, 2000). But in this paper, the focus will remain on what bodies-in-context do, and especially on how they organize over time. Naturalistic observations are advantageous for this, since data are collected *in situ* and both behavior and conditions are readily tracked. As a result, a number of examples of complexity in action have accumulated. Thus, while not denying that invisible mental processes - memory, inference, expectation, etc. - are involved, this methodological review aims to test the limits of the observational approach by determining how much cognitive complexity can be accounted for through a description of visible events alone (see Johnson, 2002). Inasmuch as this proves successful, we will have calibrated a powerful tool for further investigating cognitive complexity.

The studies reviewed here are, for the most part, rigorous, quantitative analyses of naturalistic behavior. Most involve the micro-analysis of videotaped interactions, and almost all emphasize change over time. But such observational studies of cognition are in fact rather scarce, even for nonhuman primates (and almost nonexistent for cetaceans!). Scattered over a range of sub-disciplines, they make use of a variety of techniques, and often define their terms in different ways, especially concerning their models of cognition. One goal of this paper, then, is to use a distributed, embodied model of cognition to unify this disparate literature, and show how a coherent set of methods emerges from this work that can become the basis for future observational studies of these and other cognitively complex species.

Observational Studies

Research on animal cognition using observational methods is of two main types - qualitative and quantitative, with various sub-divisions within each. These approaches share many features, but are also distinct in the type of data they collect and the way those data are analyzed. All types will be included in this review, but the emphasis will be on micro-ethology - the quantitative analysis of moment-by-moment interactions in a naturalistic setting.

Qualitative

Qualitative accounts (e.g., Goodall, 1971; King, 2004; Russon & Galdikas, 1993, 1995; Savage-Rumbaugh & Lewin, 1994; Shanker & King, 2002; Tayler & Saayman, 1973; de Waal, 1982; Whiten & Byrne, 1988) tend to involve detailed narrative descriptions of a small number of particular events. These events may be chosen as typical of the animal in a given situation or stage of development, or they may be rare, even one-time events that the authors see as telling. These accounts stress a multi-scalar approach, promoting the interpretation of the events by situating them in their larger social and historical contexts. For primates and cetaceans, such studies offer a sense of the range of the animals' cognition, frequently including examples selected to exemplify complexity. Given, as we shall see below, the role of innovation and variability in complex cognitive systems, such qualitative accounts offer the advantage of providing a way to capture novel events - events that can sometimes be lost in more quantitative approaches.

On the other hand, compared to quantitative methods, qualitative descriptions are at a disadvantage in being (potentially) less reliable or generalizable as sources of information. The main risk in selective descriptions is that sufficient additional sampling could reveal a very different distribution of activity that would alter which model is the most appropriate for the behavior. Plus, such analyses are often written by people with many years of experience observing and interacting with their subjects. This, on the one hand, may distort, with entrenched biases, their descriptions of what has occurred, but, on the other, may be the source of important theoretical and behavioral insights. The difficulty for the reader of such accounts is to determine which is the case, and for the potential researcher to avoid the pitfalls. Descriptions that emphasize specific, physical actions and conditions often seem more reliable than those that involve higher-level descriptors. As we shall see, however, studying cognitive complexity complicates matters, since it may, in fact, require some type of higher-order descriptions. Grounding these in systematic observation will help to justify the interpretations that are generated.

Quantitative

Quantitative observational methods include quasi-experiments and purely ethological approaches. Quasi-experimental studies are those in which the researchers modify the subjects' environment in some way, but, unlike in classic experiments, do not constrain the range of responses that the animals can make to that change. To keep the focus on the process of adaptation, studies of this sort that are included in this review will be those that report detailed accounts of the animals' behavior under the altered circumstances, rather than those in which one reaction versus another is predicted *a priori*. The other type of quantitative approach does not involve manipulating the animals' environment in any way, but rather recording and analyzing their everyday activity. In these ethological studies, a context is often chosen (e.g., feeding, tool-use, play) providing some regularity of environment relative to which behavior is assessed. Many studies are developmental, with the participants' behavior scored repeatedly over an extended period of time. Unlike the qualitative studies outlined above, the quantitative nature of these studies demand both well-specified scoring criteria, rigorously applied (including inter-observer reliability ratings), and a high sampling rate.

Some quantitative studies work to maximize the number of subjects sampled (e.g., Call & Tomasello, 2007; Hopkins et al., 2005). Such studies have the advantage of being able to directly extrapolate statistically significant findings to the community or species at large. Often in these studies, relatively unitary features or factors are recorded - such as whether the subjects gestured, or looked, or imitated, or not. These data are then pooled and perhaps correlated with categorical conditions, such as the presence or absence of food, tools, conspecifics, etc. However, because their high "N" precludes detailed analyses, such studies typically provide only limited information on cognitive *processes*. For example, the great majority of contemporary research on gesture in nonhuman primates is done in this way, with checklists of gesture types compiled for sizable numbers of chimpanzees, orangutans, gorillas, etc. (see Call & Tomasello, 2007). The fact of the occurrence of such gestures, in and of itself, tells us little about cognition. Even so, findings such as a difference in the variability of repertoires across different species, or the fact that the attentional state of the non-gesturing animal matters to the type of gesture used, do offer hints to the cognitive processes that may be involved.

To assess incidents of gesturing as cognitive events, we would need to see how those actions *fit* in the adaptive process in which they occur. To actively study such processes, a shift to an intensive focus on how interactions unfold is required. Given the constraints of painstaking micro-analyses, such studies often involve only a few individuals. In this case, it is the large number of examples of a given type of interaction that provide the sample sizes that permit statistical analyses. But this focus on the particulars of behavior in a limited number of subjects does alter the population to which any statistical generalizations can be applied. That is, the data cannot be used to justify claims that a species or community of the animals studied would all tend to produce the same observed pattern. Instead, the data

support claims that the pattern does reliably occur in the particular animals studied, and in that way, demonstrate that at least some members of this species are capable of the observed cognition. Nonetheless, rigorously showing what even one animal is capable of, does tell us something about the range of capabilities of the species as a whole, and of the conditions with which they engage.

Micro-ethology

Both qualitative and quantitative observational approaches employ the methods of micro-ethology. Micro-ethology - the frame-by-frame analysis of interaction - has become an increasingly prominent technique, given the current prevalence and ease of digital video recording. In the wild, remote motion-sensitive cameras can be used to detect and record activity at feeding or nesting sites (e.g., Markham & Altmann, 2008; Sanz, Call, & Morgan, 2009). In captivity, animals on display for the public are readily filmed, and hours of video can be stored, edited, and carefully reviewed with commonly available software. The more this approach is practiced, the more we are learning about its potential and limitations.

While similar to traditional ethology (e.g., Lorenz, 1982; Tinbergen, 1952), the practice of micro-ethology differs in some critical respects. Traditional ethological analyses tend to document macro-level behavioral categories (e.g., grooming, aggression, food sharing) and often involve pooling data across subjects. Those tallies are then frequently correlated with gross ecological or demographic parameters. As discussed above, this can provide necessary background information for interpreting cognitive events and is, in fact, an important part of a multi-scalar approach. But in addition, micro-ethology - by zeroing in on the particulars of embodied adaptations and how they change - provides a direct look at the “contents” of distributed mind (Hutchins, 1995b, 2001).

Micro-analytic studies vary in the level of detail they choose to score. This can range from the activity of individual muscle groups that produce a facial expression (Parr, Winslow, Hopkins, & de Waal, 2000; Vickel et al., 2007), to postural and locomotory moves that may take many seconds, or even minutes, to perform (e.g., Forrester, 2008; Johnson & Oswald, 2001; for discussion, see Byrne et al., 2001a). The appropriate level for a given study depends, of course, on the questions being addressed. In fact, in such studies, it is the choice of ethogram - the set of criteria for scoring behavior - that functions as the hypothesis being tested. That is, by selecting the criteria they do, the researchers test whether those are indeed the ‘media that matter.’ If those parameters vary in regular, specifiable ways in the pertinent interactions, they are presumed to be mechanisms of the adaptation being studied. For example, Johnson (2004) scored the relative timing and direction of head turns in a triad of bonobos as a test of the hypothesis that such moves were contingent upon one another. The emergence of reliable patterns of contingency, under certain conditions (see details below), served as evidence

that head orientation, including that of third parties, was indeed tracked and responded to in these animals.

It is important to remember, however, that studying cognition as adaptive engagement demands a distributed unit of analysis. It is not types of acts, but types of *interactions*, that are most useful here. Moves by only one part of the body (head, hand, etc) often profit from being scored in terms of their coordination with other parts (see Forrester, 2008), and relative to objects of attention in the environment (see Goodwin, 2000; Hutchins, 2005). Similarly, in the social domain, a look toward another animal would be considered one type of event if the other animal is looking back, but a very different event if the other is turned away. As a result, researchers sometimes record individual acts, but only while tracking them in relation to other concurrent acts or environmental events (see Forster, 2002). Such interactions can include relationships in time such as contingency or synchrony, in space such as proximity, in form such as similarity or complementarity, and in dynamic force such as manipulation, collaboration, or opposition. We shall see examples of all of these relationships in the discussion of cognitive complexity, below.

A focus on interaction also raises the issue of “affordances”, the constraints on fit (Gibson, 1979). Proximity, for example, affords certain kinds of access to the bodies of others that a greater distance does not, and objects that are detached and fit in the hand afford manipulating in a way that anchored or outsized ones do not. Learning is visible, for instance, when an animal changes the type of act it directs to a particular object, revealing affordances of that object not exploited earlier. Furthermore, tracking such affordances over time creates a trajectory of “co-regulation” (Fogel, 1990; King, 2004). For example, as a subject manipulates a tool during a task, that very activity changes the affordances of the situation, which in turn make new manipulations adaptive. Similarly, social co-regulation is a venerable notion, especially in development, where co-participants in an activity shape one another’s options (e.g., Harlow, Harlow, & Hansen, 1963; Hinde, & Simpson, 1975; see also Goodwin & Kyratis, 2007; Rogoff, 1993; Shanker & King, 2002). It is these relative descriptors - affordance, fit, co-regulation - that come into play in describing changes in the efficiency or the smoothness of a routine, in the co-attunement of attention, or in the social coordination or obstruction of action.

Not everything that nonhuman primates and cetaceans do is complex. As in humans, their cognition is undoubtedly an amalgam of simple and more complicated processes. As a result, the following review does not aim to characterize the full array of cognitive processes in these taxa, or even to consider all the observational studies that have been done. Instead, particular studies that exemplify types of complexity, and methods of addressing them, are selected to illustrate the key concepts and approaches involved. It is hoped that they will provide a guide for the design of future observational studies.

Observing Cognitive Complexity in Primates

Interactions with objects

Manipulating objects - whether food, toys, or tools - is not, in itself, necessarily complex. It meets that criterion only to the extent that it displays versatility, hierarchical organization, and the influence of long-term behavior patterns.

Versatility in object use is revealed in a number of ways. One advantage of studies that do not pool data across individuals is that they do not treat individual variation as “measurement error” (Lee & Karmilov-Smith, 2002; see Fogel, 1990; Johnson, & Karin-D’Arcy, 2006). As a result, high levels of individual differences in tool use and other food processing interactions are routinely reported in observational studies. For example, individual differences in component acts that serve to accomplish similar ends are reported in plant processing in gorillas (Byrne & Byrne, 1993), insect fishing (Humble, 2006) and nut cracking in chimpanzees (e.g., Biro, Sousa, & Matsuzawa, 2006) and leaf-wrapping in capuchin monkeys (Perry et al., 2003). Differences in object use can also be seen across the lifetime of a given individual, not just in terms of proficiency but also as the “problem set” changes for an animal as it changes in size and strength (see Russon, 2006). An infant orangutan, for example, in attempting to forage on a date palm, has only certain object manipulations open to it; however, as it matures, not only can it accomplish new acts, but those acts then give it access to new parts of the plant, which in turn restructures the techniques used to forage on it. Versatility in object use is also apparent in the length of elaborate routines, sometimes involving different objects at different stages of the process. In the imitative play of rehabilitant orangutans, for example (Russon & Galdikas, 1993, 1995), the extended sequences of activities involved in fire-making, bridge building, boat launching, laundry washing, etc. are repeated and varied in subtle and developing ways.

Such elaborations arise, in part, as a function of the size of an animal’s repertoire of component motor outputs, which provide multiple options for configural and sequenced performance. A creature with subtly articulated parts, like the grasping hands of a primate, is thereby afforded a wide range of possible moves. The extent to which these are exercised and coordinated in these animals provides a ready measure of complexity. Byrne and colleagues (Byrne & Byrne, 1993; Byrne, 1999; Byrne et al., 2001a), for example, have conducted detailed micro-analyses of videotape of wild gorillas manipulating thistles and other difficult-to-process foods. They found that those gorillas engaged in more bi-manual coordination than do the other apes (see also Hayashi, Takeshita, & Matsuzawa, 2006), and show a remarkable division of labor, across subsets of fingers on a given hand, in a particular task (Byrne, Corp, & Byrne, 2001b). Such dexterity enables them to generate complex sequences that can give this, the most herbivorous of the apes, exceptional access to nutritious, but well-defended, plant

foods. In their micro-analysis, Byrne and colleagues have documented over 100 such components, combined in population-wide as well as idiosyncratic ways.

Another source of complexity arises in the hierarchical organization of this food-handling activity. When the sequences documented by Byrne and colleagues are re-analyzed in terms of their functional stages - prepare, gather, support, tidy, remove debris, and eat - a hierarchical relationship is evident between those stages (Byrne, 1999; Byrne et al., 2001a). For example, different subroutines can be substituted for others in any number of larger routines (e.g., for processing other types of foods), depending on the local conditions, and the level of expertise of the practitioner. Similarly, some stages will loop until a criterion is met (e.g., gather until hand is full; remove debris until bundle is clean). Whether completion of that subroutine requires only one, or many repeated iterations, when that criterion is ultimately met, the system reliably moves on to the next stage. A similar pattern is seen in the use of termite-fishing tools in west African chimpanzees (Sanz, Call, & Morgan, 2009). These chimpanzees modify stems by pulling the tip through their teeth to form a “brush” which is more efficient in collecting the termites. However, as these brushy ends are dipped into holes in the termite mound, they become disarrayed, and the chimps will sometimes perform, and repeat, a repair subroutine to smooth the tip, before resuming fishing.

Byrne and colleagues (e.g., Byrne & Russon, 1998; Byrne et al., 2001a) argue that if these feeding routines were linearly organized, confusion could be expected to follow such variable patterns of iteration. But if the iterated subroutine is a modular event, embedded in the larger routine, such a hierarchical organization would allow it to vary without disrupting the overall order of events. Parsing of such sequences, they argue, is probably facilitated by regularities within each module, as well as by the sequence of accomplished states (“sub-goals”) that are typically produced. These may be evident to observers, including other apes, in part through the differential impact of interruptions (Byrne et al., 2001a). Presumably, interruptions that occur within a subroutine will engender that subroutine starting over, while those occurring at the transition between subroutines would be more readily followed by the next subroutine in the sequence. In all, then, such hierarchical constraints on the way that these interactions unfold represent a complex organization of the cognition involved.

Substituting one subroutine for another, or substituting elements within a subroutine, are hallmarks of flexible cognitive systems. Rehabilitant orangutans, for example, in imitating human activities, sometimes substitute different objects into familiar routines and attempt different routines on similar objects (e.g., Russon & Galdikas, 1993, 1995). For example, they might paddle a boat with sticks, floor boards, or plastic dippers (instead of real paddles, even if available) and may use a wiping motion to spread, clean up, or cover over spilled paint. Recognizing the various affordances of a single object, and shifting between them appropriately, involves a similar flexibility. The chimpanzees above who fray one end of a stem to termite fish, will sometimes flip the stick over and use the stiffer, un-frayed end to widen hole in the mound, and then return to dipping the modified end (Sanz et al., 2009). Behaviors seem particularly complex when subroutines are imported

into novel contexts. Savage-Rumbaugh (1986), for example, describes the human-enculturated chimpanzee Austin having difficulties seeing into his throat in a mirror. As Putney (2007, p. 216) put it, Austin “exited to the flashlight retrieval subroutine” and, once retrieving it, shined the light down his throat for the first time while observing it in the mirror.

While some of the complexity described above may involve individual innovation, it is important to recognize that adaptations are necessarily situated. Cognitive models that focus on individual abilities tend to characterize cognition as either being subject to “local conditions” or not. But, nearly all cognition, even the most complex, is subject to such conditions (Goodwin, 2000; Hinde, 1987; Hutchins, 1995a,b). This is why characterizing cognition as “adaptation” requires specifying the conditions being adapted to. What varies, in this view, across different types of cognition, is HOW interactions with those conditions proceed. In fact, given the way conditions shape activity, they can be considered active participants in the cognitive process. This is particularly obvious when the relevant conditions are social, but even the inanimate world is a co-creator of cognition. The maneuvers the gorillas develop are as much “selected by” the spikey thistles as they are by the gorillas’ sensory-motor systems. Charting how such dialectical processes emerge and change over time is just what provides observable sources of cognitive complexity (see Lave, 1984).

Documenting such processes isn’t a simple matter, however. Consider the excellent attempt by Inoue-Nakamura and Matsuzawa (1997). These researchers provisioned wild chimpanzee feeding sites with nuts and with rocks that could be used, as hammer and anvil, to crack those nuts. They did micro-analyses of videotape of three infants learning the technique of nut cracking, sampled at .5 years, 1.5 years, 2.5 years and 3.5 years of age. They identified a set of “fundamental actions” directed at the stones and nuts, as well as higher-order classes of activity based on the number of acts, objects, and degree of coordination involved. They assessed the duration, order, and frequency of these activities over the three years. They also looked at changes in the conditional probabilities of the six “basic actions” involved in successful nut-cracking.

As a result, Inoue-Nakamura and Matsuzawa (1997) were able to substantiate a number of observable patterns in these infants’ learning to use stone tools. They found, for example, that all the “basic acts” of nut-cracking were in the animals’ repertoires by 1.5 years, but did not become coordinated until 3.5 years of age. They also found that this development moved through successive but overlapping stages of relationship between act and object: single act on a single object, successive acts on a single object, successive acts on multiple objects, simultaneous, unrelated acts on multiple objects, and coordinated acts on multiple objects, including, finally, successful, if inexperienced, nut-cracking. Furthermore, their conditional probabilities (see Inoue-Nakamura & Matsuzawa, 1997, Fig. 6, p. 171) suggest that, at 1.5 years, the infants often picked up, independently, both stones and nuts, and even put nuts on an anvil. At 2.5 years, they repeatedly placed the nut on the anvil, and were first seen to then hit the nut with their hand. By 3.5 years, they put the nut on the anvil, and then diverted their hand to pick up the

hammer before bringing it back to hit the nut, thus inserting the already well-practiced 'stone retrieval subroutine' into the 'setup-and-hit' sequence. As a result, like with the gorilla's plant processing, we see sequential embedding, this time as a part of the gradual ontogeny of a complex, multi-stage technique.

Interestingly, ineffectual act-and-object interactions, as well as a number of "unrelated" actions, continued to occur throughout this learning period. The authors also briefly noted that frequent "reverse" and "short cut" sequences occurred during these learning processes. While the authors' efforts were prodigious and informative, the sequential micro-analysis of a number of 'runs' at those objects, at various ages, that included non-basic actions, could have provided critical information on *how* these coordinations eventually developed. It may be, for example, that events like reversals and short cuts, rather than detracting from learning, can be conducive to it by providing examples of both more and less effective activity, enabling the system to more rapidly stabilize on an efficacious pattern (for discussion, see Byrne & Russon, 1998; Kuczaj & Trone, 2001).

Further analysis of the continuing process of expertise could also be informative. Several studies report the canalization of tool-use techniques in adult practitioners, as their activity becomes increasingly stereotyped, and often increasingly efficient, over time (e.g., Biro, Sousa, & Matsuzawa, 2006; Byrne & Byrne, 1993). But careful scrutiny of even these stereotyped sequences might reveal how subtle differences become more pertinent with increased expertise. For example, perhaps expert nut-crackers are more likely to react to a slight wobble in their anvil stone. Increased attention to such newly-pertinent details seems likely to lie behind the emergence of the well-known innovation of a "meta-tool" (Matsuzawa, 1994, 1996) - the occasional use of a third rock to support and steady the anvil. Inserting an object into an opening is a sub-routine to which chimpanzees are particularly disposed (see Hayashi & Matsuzawa, 2003), but perhaps it was only once the principal components of the larger nut-cracking routine were well established, that this tactic could emerge as an embedded subroutine. That is, this use of a tool (the small rock) to modify a tool (the anvil) may have been brought about by a shift in the problem, and its affordances, that became salient against the regularities of expertise.

The other set of conditions in which such object use is situated is, of course, social. This is often true both immediately and historically. That is, for example, all of the above activity involving infants learning to crack nuts occurs in the presence of their mothers and others in their group. Inoue-Nakamura and Matsuzawa (1997) included data that showed that the infants often observed their mothers, and later others, cracking nuts and, especially early on, scrounged nut kernels from both (see also Biro et al., 2006; Hirata & Celli, 2003). But it is striking how, as they grew older, they persisted in manipulating the nuts and stones while in these nut-cracking groups even though literally years went by without their succeeding at cracking a nut. Clearly something in the activity itself - perhaps just participating in the group event? - was sufficient to motivate them to persist. Interestingly, although tolerating scrounging, the mothers were never observed to actively intervene in the infants' learning process (Hayashi & Matsuzawa, 2003;

Hirata & Celli, 2003; although see Boesch, 1991; see also more on cetacean teaching, below).

The infants' activity was, however, scaffolded in yet another way. Historically, this particular group of chimpanzees (at Bossou, Guinea) is well known for using rocks to crack nuts (Sugiyama & Koman, 1979). It is the fact of this cultural tradition that assured the researchers that the chimpanzees would exploit the affordances of the rocks that were provided; rocks laid out in the vicinity of nut trees in the territory of chimpanzees that do *not* use rocks to crack nuts would not have engendered the same organized group behavior. Such traditions in primates are well-documented, with subgroup and population-level differences seen in a variety of foraging and social behaviors (e.g., Bard et al., 2005; Fragaszy & Perry, 2003; McGrew, 1992; Whiten et al., 1999). The extent to which such traditions affect what and how individuals attend to certain features of their worlds, organize their behavior, and thus shape what and how they learn, is another example of how conditions co-create cognition (see Hutchins, 2008; Perry, 2006).

Triadic interactions

In the social domain, one type of interaction long characterized as complex involves tactical engagements between three or more individuals (e.g., Humphrey, 1976; Kummer, 1967). Where most social interactions in animals are dyadic, adding an additional individual or two disproportionately complicates matters. These interactions are “tactical” in the sense that concerted effort over time, by a given individual, is compatible with an outcome of benefit to that individual. It has been argued that such triadic interactions were a critical development in the evolution of primate cognition (see Byrne & Whiten, 1988; Tomasello & Call, 1997; de Waal, 1986a; de Waal & Tyack, 2003). The micro-analysis of such polyadic interactions is a promising source for evidence of hierarchical complexity.

Micro-analysis can be used, for example, to establish when multiple animals in one another's vicinity are, in fact, simultaneously engaged with more than one others. Johnson (2004) and colleagues, for instance, analyzed videotape of a triad of adolescent bonobos in a captive setting. These three animals - two females and a male - spent a great deal of time in one another's vicinity, more often as a triad than a twosome, and frequently groomed, peered, contacted, and had sex with one another (see Johnson, 2004). Even when no other obvious interaction was occurring, they were highly attentive to one another. The focus of this study was the relative timing of head moves that gave the animals better or worse visual access to one another. In particular, they assessed events (the first in each 2 minute interval) in which one animal turned its head toward one of the other two, and recorded the latency until the next head move by any animal, while noting all three animals' access to the others. They found, for example, that if animal A turned to B, the best predictor of whether A would linger with that access or quickly turn away was not B's access to A, but C's. That is, if the third party had

direct visual access to A's turn to B, and A could see that, A was much more likely to quickly look away than if C had little or no access. One weakness of this study was that by only focusing on one modality (head turns), and not tracking the other relevant media (such as proximity, relative body orientation, compatibility of movements, etc.) they were unable to predict which animal would be likely to initiate or respond to such events under which conditions. Nonetheless, while the authors do not claim that the tactic of avoiding being caught looking at another was typical of bonobos in general, their work does support that a bonobo can mediate its gaze interaction with one conspecific based on its gaze interaction with another.

Embedding is even more obvious in the triadic interactions typically labeled "social tool" use. Although the participants and contexts vary, a social tool interaction is generally one in which one individual, the "user," engages with another, the "tool," to in some way impact upon a third, the "target." These interactions include a number of collaborative activities captured by (sometimes colorful) terms such as "recruit," "protected threat," "buffer," "passport," "alibi," "slander," and "fall guy." (e.g., Byrne, 1995; Kummer, 1967; Packer, 1977; Smuts, 1985; Strum, 1987; Whiten & Byrne, 1988). In these and other types of social tool interactions, the user is often connoted as insincere, or at least as exploitative. Such interactions are often associated with the argument for "Machiavellian intelligence" (Byrne & Whiten, 1988; Whiten & Byrne, 1997) - involving competitive, often deceptive tactics - as a key primate cognitive adaptation. Modeling the cognition involved in these interactions in terms of attributed intentions provoked stimulating controversy (e.g., Heyes, 1993; Povinelli, 1994; Povinelli & Vonk, 2003; Whiten, 1991), and some real progress has been made by looking closely at the behaviors¹ involved (see Strum, Forster, & Hutchins, 1997).

Johnson and colleagues (Johnson & Oswald, 2001), for example, did micro-analysis of two dozen social tool interactions in captive bonobos, and as many dyadic interactions in the presence of a passive third party. The social tool interactions were of four types: "recruit" (user solicits tool in agonism against target), "buffer" (user employs tool as a kind of shield or deterrent, relative to an aggressive target), "passport" (user affiliates with tool, gaining access to tool's affiliate, target), and "alibi" (user maintains visual attention on tool while target solicits or harasses user). They scored the precise timing of changes in proximity, contact, and relative head and body orientation for all three animals in both the social tool and dyadic contexts. Of particular interest were the differences between the users' interactions and those of the dyad initiators. In the latter, proximity, along with all of the initiator's attentional resources, were directed at, and responsive to, the dyad partner. But in the social tool interactions, the user's attention was divided. The user's proximity was highest with the tool, but its body orientation was most often 'open' to both others at once, and changes in its head orientation were significantly more contingent upon moves by the target, than upon moves by the tool. The authors suggest that it may be this tight contingency

¹Experimental work on relevant behaviors such as gaze following, pointing, and strategic inhibition, has likewise contributed much to this endeavor (see Itakura, 1995; Pack & Herman, 2006; Tomasello, Call, & Hare., 1998).

between the head moves of the user and target despite the user's ostensible engagement with the tool, that prompts the typical characterization of the user's behavior as "shifty" or "insincere" relative to the tool.

Complexity in this study could be observed in the regularities of relative positioning and orientation of the three bodies involved (Fig. 1, below). The proximity of the user and the tool, along with their similar or complementary body orientations, formed familiar patterns in these episodes, very like commonplace dyadic performances of grooming, peering, contact, play, etc. (see dotted ovals in Fig. 1). In the same episodes, as described above, the contingency of gaze (head orientation) between the user and the target established that some kind of engagement was going on between that pair as well (solid ovals in Fig. 1). The resulting configuration embeds the user:tool interaction pattern within the user:target one. That is, under the user's initiation, the user:tool pattern is physically embedded in the user's interaction-space with the target. In this study, recruit, buffer, and passport all showed this feature of one dyadic interaction embedded in another, as would most social tool interactions. Alibi could sometimes show an additional level of embedding (Fig. 2), as when an adolescent female did an elaborate show of attention towards a distant animal, and away from the baby with whom she was just playing, when the mother approached. Note that the simultaneous embedding of one social subroutine in another is somewhat different from the sequential embedding of iterated loops in the object-use routines discussed above. Here, each participant has continuous access to the multiple routines, and not only the individuals but the routines themselves can interact.

The sequential embedding of one social routine within another can also occur. This is apparent, for instance, in polyadic engagements between two individuals and one or more objects of mutual interest. Based on the pioneering study by Menzel (1974), for example, Hirata and Matsuzawa (2001) analyzed video of pairs of chimpanzees moving about their enclosure after one of them (the "witness") had been shown the hiding place of a treat that the other (the "witness of witness") was not shown. Scored at a somewhat more macro level than the above frame-by-frame analysis, these authors created a precisely timed, systematic narrative tracking actions such as threaten, fight, seek treat, pursue other, and wait. They also recorded all looks to the partner, and all changes in direction of travel relative to one another and to the treat. Besides recording these individual behaviors, they also classified interactions based on changes in the direction of travel of one animal, following it's having watched the direction of travel of the other. These interactions were classified as neglect (go a different way than the other), adjust (change to following other), pursue (gain/maintain close proximity while following other), and neutral (no change in behavior).



Figure 1. Social Tool use: User's interaction with Tool (dotted oval) is embedded in User's interaction with Target (solid oval), in "Recruit" (top frame) and "Buffer" (bottom frame).



Figure 2. Social Tool use: Complex embedding in "Alibi." When Target (mother, right) approaches, User (adolescent female, center) stops looking at/touching mother's infant (left) and looks off at Tool/Alibi (distant animal, offscreen). Ovals indicate one possible type of embedding that might apply here (see text).

In this study, one particular pair of chimpanzees - the subordinate Chloe and the dominant Pendesa - provided a representative example of the sort of pattern that often develops in such studies (see also Cousi-Korbel, 1994; Menzel, 1974; Mitchell & Anderson, 1997; Woodruff & Premack, 1979). At first, when Chloe was the knowledgeable “witness”, she went directly to the food without interference or even attention from Pendesa. However, after Pendesa had the opportunity to play the role of witness, she began to threaten Chloe when Chloe again played the witness. Effectively intimidating her subordinate, this allowed Pendesa to search, without competition, for the food. After Pendesa’s second round as witness (during which, as ever, she went directly to the food without interference from Chloe), her tactics changed once again. This time when Chloe became the witness, Pendesa began to monitor and adjust to Chloe’s behavior, following her to the baited container. At first, Chloe was successful at beating the observant but lagging Pendesa to the treat, but over subsequent trials, Pendesa pursued her and began to run ahead of her once the baited container became evident along their common path. As Chloe began to lose the treat to this tactic, her behavior then shifted. Being subordinate, she could not use the threat tactics that Pendesa had, to keep herself from being followed. But she could exploit Pendesa’s aroused attention and acquisitional activity to promote being followed elsewhere. In the next trials, Chloe began moving toward an empty container, and only after Pendesa had tracked and passed her to examine that container, would Chloe divert to the actual hiding place. Thus, Pendesa became another type of “social tool,” engaged by Chloe as an embedded subroutine in her own acquisitional activity, to clear a circuitous path to the hidden food. However, after a few sessions of this, Pendesa again altered her behavior, now maintaining close proximity to Chloe and frequently adjusting to her trajectory. In doing so, Pendesa was often able to retrieve the reward, leading Chloe to “lose the motivation” to seek the treat when Pendesa was the witness-of-witness. Interestingly, on subsequent “control” trials in which neither animal was first shown the hiding place, when they were released into the compound, none of these behaviors - monitoring, following, or misleading - were observed; the animals just separately searched for the hidden food.

In this lovely example of co-regulation, the dyad cycles through multiple adaptations to one another’s maneuvers through the compound. As they do, they provide clear illustrations of substitution and embedding. In the case, for example, of Chloe “misleading” Pendesa to the unbaited container, Chloe has substituted the unbaited for the baited container in her ‘approach container’ subroutine. That is, she does not veer randomly from her original course, but directs her trajectory to another container’s position. Chloe also embeds this modified routine sequentially into her own treat-seeking behavior. When she notices Pendesa attending to her, Chloe shifts to the modified trajectory. However, as soon as Pendesa passes, Chloe abruptly resumes a direct course to the baited container, just as Byrne’s gorillas moved on, after iterated cleaning loops, to the next phase of thistle processing. Chloe’s abrupt trajectory change at the moment of Pendesa’s move to the unbaited container, stands as behavioral evidence that Pendesa’s behavior satisfied Chloe’s

subgoal of eliminating the competition, freeing her to move on with her original sequence. This was presumably the result of Chloe's recent experience, in which Pendesa's passing was the penultimate phase of a ballistic trajectory that would invariably take Pendesa to the nearby container. Chloe was able to adapt to this short-term change in the predictability of Pendesa's behavior to mark a profitable insertion point for her next subroutine.

As Whiten and Byrne (1988) noted, tactical shifts in attentional access often characterize "deceptive" events. Turning away, moving to block a mutual line of sight, moving in a subdued non-salient way, temporarily redirecting the attention of others, etc. are all common tactics of Machiavellian primates. Such moves often continue only so long as they are being watched, followed by an abrupt shift in trajectory. The abruptness of Chloe's shift from heading to the unbaited to the baited container is remarked by the authors (Hirata & Matsuzawa, 2001), and is a common feature of qualitative accounts of "deceptive" behavior (e.g., Byrne & Whiten, 1990; Savage-Rumbaugh & McDonald, 1988; de Waal, 1986b). These abrupt changes are often interpreted as a "release" from the self-inhibition presumed to be involved, for example, in preventing oneself from approaching a contested resource (Cousi-Korbel, 1994; Mitchell & Anderson, 1997). Sudden, radical changes from one type of organization to another are typical when dynamical systems re-organize (see Fogel, 1990; Thelen & Smith, 1994). A tight contingency between a shift in attentional access and a redirected trajectory, makes these sorts of abrupt changes a boon to observers, providing behavioral evidence that a reorganization of a cognition system has occurred.

Surprise - a combination of the sudden disruption of previous activity, often an alert frozen posture, and orientation to the surprising event - is likewise a useful embodiment. Cheney and Seyfarth (1990, 2007), in their array of playback studies in the field, have long used the extent of such changes in attention displayed by their monkeys as measures of the valence of the calls that they have played to them. Other apparently 'information-seeking' behavior - in the form of approaching, arching the neck to look, moving to see around barriers, or reaching to manipulate with the hands - can also be particularly telling (see Chance, 1962, 1967; Johnson & Karin-D'Arcy, 2006). In these cases, behavior that changes the animals' access from unimodal (e.g., just hearing, just seeing) to multi-modal is clearly adaptive, garnering perceptual resources to deal with a new, unusual state of affairs. In the "social referencing" literature on nonhuman primates, just as in humans, infants often look to their mothers when presented with novel or otherwise disturbing stimuli (e.g., Itakura, 1995; Russel, Adamson, & Bard, 1997; Uneo & Matsuzawa, 2005). Similarly, Hirata and Morimura (2000) observed, in their studies of the development of tool use in chimpanzees, that naive animals were most likely to look to nearby experts when they experienced failure in their own attempts. Information-gathering behaviors like these are observable cognitive events that can serve as reliable indicators of important transition points in ongoing interactions.

A sensitivity to the attentional states of others can also be used in cooperative contexts. As mentioned above, the observational data on gesture shows

that the attentional state of the non-gesturing animal can alter the timing, orientation, and modality of any signals produced in primates (Call & Tomasello, 2007; Gomez, 1991; King, 2004). In fact, embedding a general-purpose attention-getting subroutine - such as touching another, or moving into view - is often a tactic that develops before a context-specific gesture routine can proceed. Hutchins and Johnson (2009) for example, describe the development of gestural requests -to-be-carried that arose in captive bonobos. In the later stages of such behavior, an infant was repeatedly seen on her mother's body, in the appropriate position to be carried, but with the mother remaining stationary. The infant would then climb off her mother to perform a request routine in a position where the mother could better see it, and where that routine would afford her mother the easiest access, if she were to take that first step, to picking up her daughter on the way.

Large-scale cognition

The claim is often made that effective participation in polyadic interactions, like the social tool examples above, requires that a participant "knows" not only about its own relationships with its protagonists, but about the relationships between the others as well (e.g., Tomasello & Call, 1997). Observational methods have been the primary source of the large-scale evidence that is used to support such claims. In particular, studies that include long-term data on social interactions - such as proximity, contact, pro-and anti-social signaling, etc. - document the history of interactions in a given group. When such histories predict currently observed behavior, one can argue, by assuming the existence of memory along with access to the historic patterns, that those patterns played a role in the observed cognition.

For example, in their important array of playback studies conducted over the past 30 years with vervet monkeys and baboons, Cheney and Seyfarth (1990, 2007) repeatedly revealed the role of social history. They have observed, for instance, that when these primates hear the alarm call of a potentially unreliable infant (Cheney & Seyfarth, 1988), or the distress calls of another animal's sister (Cheney & Seyfarth, 1999), they often look toward a member of that animal's family. Reacting to others as members of a given "family" arises from long experience observing a number of kin-typical interactions, such as proximity, nursing, grooming, supporting, and consoling. The pace at which family members interact - slow to be perturbed, quick to reconcile - as well as the relative unlikelihood of certain behaviors such as aggression, also tend to mark these kin interactions. Subgroups of individuals would tend to cluster, then, in their probability of co-engaging in such interactions, and it is this distribution, over time, that is necessary for both the savvy monkey, and the human researcher, to observe.

Rank interactions likewise occur with typical patterns of activity and timing. In fact, behaviors involved in rank-based interactions - such as agonism and mating - because of their reproductive importance and potentially high risk, are often exaggerated and highly ritualized, and thus especially easy to recognize.

Primates have been shown to recruit allies that not only outrank themselves but also outrank their opponents (e.g., Silk, 1999), and to support the higher-ranked of two opponents in an ongoing fight (e.g., Perry, Barrett, & Manson, 2004). These behaviors require that the animals can recognize individuals, have observed the histories of rank interactions between others over time, and have participated in such interactions themselves. As a result, certain features of events become salient (e.g., a violation of a standing regularity, an opportunity to alter a balance of power) and certain motivations are piqued to use that information to engage adaptively. In humans, this sort of development, arising from a history of engagement with a community of practices, has been called “professional vision” (see Goodwin, 1994): the ability to “see” the world in a way peculiar to proficient practitioners in that community.

What can make such interactions particularly complex is that different histories can be relevant in different situations. In Cheney & Seyfarth’s (2007) work, for example, playbacks to wild baboons showed that listeners responded to the same calls based on both rank and kinship factors. Rank was determined through the documentation of dyadic displacements from a resource, such as food or mates, as well as based on who typically performed the dominant, and who the subordinate, displays in all possible pairings. Members of a family tended to be closely but distinctly ranked, and families were also ranked relative to other families. Recording interactions over an extended period, these researchers were able to collect the dominant and subordinate call from nearly every individual in the group. They then recombined those calls to broadcast, from a visually hidden speaker, the sound of both commonplace, and anomalous, interactions. In an anomalous pairing, for example, if animal B was ranked above C, the researchers might play C’s dominant call in conjunction with B’s subordinate one. They found that if the vocal roles of animals adjacent in rank were switched, that switch had a greater impact on the listener if the animals were from different families, than if the reversal occurred within the same family. Reversals within a family also got a reaction, greater than playbacks of typical pairings, but were apparently less motivating than across-family rank violations. This differentiated response by the listener shows that multiple histories can be pertinent.

To further complicate matters, histories are not static (see Barrett & Henzi, 2006). Some fluctuations, such as the cycle of a female baboon’s sexual swelling, indicating changes in her receptivity to mate, can have a significant impact on what kinds of interactions tend to take place between whom, as well as on the value of opportunities to participate. For example, Cheney and Seyfarth (2007) report that when a female’s call and the grunt of a male which whom she had been associating were played from widely separated speakers, listeners took more notice when the female was at the peak of her cycle. Similarly, fluctuating ecological factors can interact with rank, as when females baboons extend their grooming networks when resources are scarce and thus more easily defensible by high ranking individuals. Henzi and Barrett (2002) found, in chacma baboons, that in years when the number of infants was high, the amount of grooming of the mother that was required to gain access to an infant was lower than in years when infants were in short supply.

Even so, higher-ranking mothers could always demand more grooming for access to their infants. Thus, in these societies, both fluctuating and more stable patterns can be relevant simultaneously.

The cycles of sexual receptivity, the seasonal availability of infants or other resources, the friendships and rivalries that develop, etc., are more than just large scale changes in activity. They are also changes in the distribution of risk, in the costs of getting things done, and the benefits to be accrued within that society. Such motivational dynamics are apparent in the amount of effort (e.g., grooming time) or arousal (e.g., stepping up when recruited for a fight) that different individuals are willing to invest at different times. In addition, patterns like reciprocity (e.g., de Waal & Brosnan, 2006) and reconciliation (e.g., Aureli, Cords & van Schaik, 2002) reveal that social debt (obligation) is another such dynamic at play in these groups. Furthermore, relationships vary in their value to the participants, observable in what those players are willing to sacrifice or demand (e.g., Cords & Thurnheer, 1993; Manson, 1999). As Barrett and Henzi (2006) suggest, such societies can be modeled as “biological markets” where commodities - like grooming or aid in agonism - are exchanged, and factors like supply and demand can alter the values of those commodities. While such market models probably apply to a wide range of social creatures (e.g., Dussutour, Denneubourg, Beshers, & Fourcassie, 2009; see Noe & Hammerstein, 1994), it is when these markets involve multiple, simultaneous forces, detectable in multiple, long-term patterns of interaction, that they become indicators of cognitive complexity (see also Barrett, Henzi, & Dunbar, 2003).

In tracking the histories of social interactions, these long-term patterns can develop a regular structure even when the individuals involved in them change (see Hinde, 1987). Mother and offspring, dominant and subordinate, friend and rival, are each embodied as configurations of behavior that group with and predict other types of behavior over time. It is these “roles” that an animal immigrating into a group of strangers can respond to, in its tactical efforts to integrate. And it is these roles that constitute the set of options that an individual integrated in a given society can potentially embody. The experience of roles as the individual matures is also variable, especially in a long-lived species who passes through a number of stages (such as infant, juvenile, adolescent, young adult, and elder, Goodall, 1986; Russon, 2006). At each stage, the animal participates in different social routines, sometimes with the same players, sometimes with new ones, and thus has access to a range of embodied, as well as observed, roles. As Parker (2004; following Kummer, 1967) suggests, the number of roles in an interaction or group - along with the flexibility in how they can be instantiated - can provide yet another basis for assessing cognitive complexity.

Consider cooperative hunting of colobus monkeys by West African chimpanzees. Boesch and Boesch (1989) report that these chimpanzees show a higher likelihood of success when hunting in greater numbers, and have been seen to call for ‘backup’ when they discover monkeys while alone. As more chimpanzees converge in the monkeys’ vicinity, an apparent division of labor “opportunistically” emerges in which the chimpanzees assume different roles -

such as “driver,” “blocker,” and “catcher” - some of which, for example, depend on stealth while others involve being noisy and conspicuous. The coordination of these different but complementary acts does seem, as the authors suggest, more complex than the confluence of similar behaviors seen in the more ‘free-for-all’ hunting style of east African chimpanzees (see also Stanford, 1999). Occurring as it does, in dense jungle habitat, observing and recording the details of this behavior is extremely difficult. Nonetheless, knowing more about who plays which roles, how different individuals move through the roles over time, and how that experience affects how, or how well, they play each role, would tell us a great deal about the cognition involved in these collaborations.

Another context in which multiple roles may be involved is in “games”. A game is organized play, play with a history. Certain features of the activity become canalized (e.g., jumping off the rock) while others are allowed to vary (e.g., head first, feet first, cart-wheeled, etc.). In social play, such regularities can emerge through a process of “ontogenetic ritualization” (Gomez, 1991; Tomasello, Gust, & Frost, 1989) in which aspects that are salient and responded to, especially in imitative or complementary ways, become the signature moves in those players' games. Perry et al. (2006) suggest that the resultant idiosyncrasy of such games demands a flexible conformism. And the fact that a game can “outlive” its inventor, as it is picked up and played by others in the group, again highlights how cultural traditions shape the cognition of their practitioners. In addition, in multi-player games, turn-taking enables players to switch roles, and gain relevant and potentially valuable experience from a different perspective. (As we saw in the “witness-of-witness” study [Hirata & Matsuzawa, 2001] above, Pendes's behavior changed radically after she had an opportunity to play Chloe's role of “witness”). The emergent structure of a game also allows a particular act to be treated not only as that act, but as a ‘move’ in the game. A slap can be a move of compliance in a slapping game, while that same behavior might be a move of resistance in a game where slapping is not characteristic. Once again, it is the large-scale cognition that allows us to differentiate these two “meanings”, where meaning is taken as *relevance* to the long-term patterns observed.

In everyday life, many of the roles that adult animals play relative to particular others do not tend to change. If A is dominant to B, he will most likely continue to play that role. Alliances may change, especially in the more “Machiavellian” systems, but such changes can come with serious costs. Of somewhat lower risk, if still cognitively costly, is the role modification that can arise in “fission/fusion” societies (Barrett, Henzi, & Dunbar, 2003; Johnson, 1990). In these societies - seen, for example, in chimpanzees (Goodall, 1986; Nishida, 1979) and spider monkeys (Symington, 1990) - subgroup membership varies, such that individuals spend their days with a shifting set of others selected from the larger community. In this circumstance, triadic interactions might involve A, B and C on one day, and A, B and D on another. “Audience effects,” as described above, could result in A’s role relative to B shifting, depending on whether C versus D is present. An animal adept at flexible role-playing could probably gain advantages in these shifting social circumstances. Long-term data on who has access to whom,

what they do on first contact after separations, and how roles are impacted by subgroup membership, could help capture the complexity here.

Polyadic audience effects can happen even in coherent social groups (e.g., baboons, above), but in fission/fusion groups, these effects interact with new affordances that also arise over time. Unlike in many animals who travel, feed, and socialize in one coherent group, animals in a fission/fusion society may not have the opportunity to see important social events (e.g., rank or resource disputes) that occur between others in their community. The resulting differential distribution of access to events sets up a market in social information². This can be exploited not only by suppressing or demonstrating behavior depending on who may observe it, but also by generating a motivation to seek out information and develop strategic criteria for doing so. This may be evident in certain “testing” behaviors (see Perry, et al., 2006; Zahavai, 1977) for not only assuring that your own relationships remain stable, but also to assess the relationships of others. For example, the potentially costly “eye poking” games reported among allies in capuchin monkeys (Perry et al., 2006), or the aggression toward the allies of others, presumably to determine the willingness of their supporters to defend them, in chimpanzees (de Waal, 1982), could provide crucial information to which the actors might not have, otherwise, had access.

Differential access to information may also play a role in the emergence of abilities that enable individuals to respond to invisible circumstances. For example, Menzel (1999) describes captive chimpanzees watching their caregivers walk out of sight with an apple and a banana, to routinely hide them for the chimps to find. If the human returns eating a banana, the chimp, once released into the compound, will work to find the (presumably) hidden apple, but not bother to seek the (presumably) eaten banana. At this level of complexity, it is clear that multiple large-scale patterns, as well as the detailed specifics of a given interaction, will be necessary to detect and account for such cognitive events.

It is interesting to note that even though observational methods depend on observable behavior, we have seen a number of examples, like the above, in which *absent* activity or individuals are relevant. In any goal-oriented behavior, for example, in which an individual acts in a manner consistent with an (eventual) outcome, during most of that behavior, the outcome is absent. An infant gestures to request being picked up only in the absence of its being carried. And yet, characterizing the gesture in terms of the currently unobservable (and potentially failing-to-happen!) behavior is reasonable because of the history of that interaction. It is these patterns that warrant the claim that what is not observed - or rather, what is observed not to be present - matters.

²It may have been just such a market in which the value of *hearsay* was a major selective payoff for the evolution of human language.

Observing Cognitive Complexity in Cetaceans

While considerably fewer observational studies have been done on dolphin cognition, examples of complexity similar to those reported for primates can be found. A marked versatility can be seen, for example, in the adaptability of dolphin imitation. In an extraordinary act of innovative imitation, a juvenile bottlenose dolphin, described by Tayler and Saayman (1973), was seen to release a mouthful of its mother's milk in mimicry of a cloud of cigarette smoke exhaled by an oceanarium visitor. In this same paper, Tayler and Saayman also describe an adult dolphin mimicking a diver scraping algae from the sides of its tank. In this case, the dolphin reproduced the pertinent object relationships - scraping one object along the surface of another - by holding the object in its mouth (unlike the diver, who held his tool in his hand). But these animals can also produce approximations of the limb and body movements of other species. For example, these same authors describe a bottlenose dolphin who imitated the swimming movements of a seal in her tank - forelimbs stroking, while the rest of the body passively followed. This is very different from dolphin locomotion, in which the forelimbs are used for steering and propulsion is provided by strokes of the tail. Bottlenose dolphins can also imitate human actions (e.g., Harley, Xitco, Roitblat, & Herman, 1998; Herman, Morrel-Samuels, & Brown, 1989; Xitco, 1988; see Herman, 2002; Kuczaj & Yeater, 2006) in which pectoral fin movements map to human hand/arm movements, and fluke movements to feet/leg movements. As Tayler and Saayman (1973) note, "the clumsiness with which the dolphins execute these movements emphasized their unnaturalness" (p. 289) and, we might add, the animals' remarkable versatility in producing them.

Vocal imitation is likewise flexible in these animals. Vocal imitation is rare in (nonhuman) mammals - if common in some bird species - but is well-documented in the cetaceans (see Reiss & McCowan, 1993; Rendell & Whitehead, 2001; Tyack, 2000). It plays a role, for example, in the development of pod- or community-specific dialects, in coalition-specific whistles, and in breeding-site songs. In the best-studied and most elaborate of these songs (Payne & Payne, 1985), all the male humpback whales in a given area have been observed to sing the same song, which might last for 15 minutes and include some 40 phrases repeated in a specific order. New phrases may be introduced, while others are altered or dropped out, as the mating season progresses, and all the singers in the area keep up with the changes. A flexibility of vocal imitation has also been repeatedly reported in captive dolphins (e.g., Caldwell & Caldwell, 1972; Eaton, 1979; Herman, 1980b; Lilly, 1965; Pryor, 1975). These animals have been described as imitating human voices, as well as other environmental sounds, including trainer whistles, diver bubbles, and tank cleaning.

There are also a number of reports of the versatile use of objects by cetaceans. In the wild, they are occasionally seen to play with a bit of kelp or other flotsam, for example letting it slip from their pectoral fin to catch it on their flukes (e.g., Herzing, 2002; Johnson & Norris, 1994). In Shark Bay, Australia, a few animals in a large resident population of bottlenose dolphins appear to practice

some kind of foraging with the aid of a marine sponge (Smolker, Richards, Connor, Mann, & Berggren, 1997) and have apparently passed this unusual technique to their offspring (Kreutzen et al., 2005; Mann & Sargeant, 2003). While the manipulation of objects is, of course, much more prevalent in the "handy" primates, captive cetaceans in particular are regularly exposed to an assortment of human tools, toys, and refuse, which they often manipulate (e.g., Kuczaj et al., 2006; McBride & Hebb, 1948; Pryor, 1975). For example, in the above report a bottlenose dolphin imitating a diver's scraping algae, the mimicking dolphin used such objects as a feather, a fish, a seaslug, a stone, and paper (Tayler & Saayman, 1973). Kuczaj, Makecha, Trone, Paulos, and Ramos (2006), in their quantitative analysis of play in captive dolphin calves, include similar descriptions of object substitution in established play routines, as well as variability in acts directed to a single object. In one particularly nice example of co-regulation between an object and an individual, they describe a dolphin's adaptation to one ball's novel affordances. The dolphin had repeatedly performed a play routine of "dribbling" balls (also seen at other oceanarium, personal observation). To do this, a dolphin generally grabs the ball in its mouth, takes it below the surface, and then forcibly "throws" it down. The buoyancy of the ball makes it rise again quickly, and the dolphin catches it in its mouth, and then begins another iteration. In this case, the interesting adaptation occurred when the dolphin attempted this routine with a water-filled ball that sank rather than floated. Upon finding that its dribbling technique was ineffective, the dolphin developed a new routine of dropping the ball and then maneuvering below it to catch it with different parts of its body.

Play is an inherently versatile activity, distinguished by its novelty and flexibility. It is a common part of the lives of both primates and cetaceans, and persists, especially in the latter, into adulthood. Following Piaget (1952), Kuczaj and colleagues suggest that the activity generated in play is often "moderately discrepant": a combination of familiarity and novelty that unthreateningly challenges the player to adapt, and provides opportunities for innovation (Kuczaj & Trone, 2001; Kuczaj et al., 2006). As a result, they suggest that play may, in fact, have evolved to "enhance the ability to adapt to novel situations" (Kuczaj et al., 2006, p. 234). And, as we have seen in both taxa, above, such adaptations can be quite complex, involving the substitutions of objects or actions and the embedding of subroutines (see also Pryor, Haag, & O'Reilly, 1969).

The complex embedding of subroutines into other routines was particularly apparent, in the primate examples, in cases of social tool use. However, while it is sometimes suggested that "Machiavelian intelligence" should be expected in some cetaceans (e.g., Connor & Mann, 2005) there are no observational studies (to my knowledge) that document the details of social tool use in these animals. Similarly, these same dolphin species are reported to live in fission/fusion societies in the wild (e.g., Connor, Wells, Mann, & Read, 2000; Herzing & Brunnick, 1997; Wells, Irvine, & Scott, 1980; Wursig & Wursig, 1977), which means they may be subject to the same sort differential access to information that has led some primates to develop the complex information-seeking, misleading, and bond-testing interactions discussed above. Clearly, these

animals are excellent candidates for such sophisticated social practices, and much research is needed on how they organize and co-regulate their behavior.

There is evidence, however, that some cetaceans do show the sort of sensitivity to the attention of others that is characteristic of such complex social interactions. For example, dolphins, like primates, appear to solicit following by fluctuating between facing the destination (with both body and head), and facing potential followers (often only by head) (see Gomez, 1991; Maestripieri, 1995; Xitco, Gory, & Kuczaj, 2001). This activity enacts aspects of two different trajectories - reaching the destination and engaging with a conspecific - and can serve to both draw the followers and highlight a potential path. This can be seen, for example, in Xitco and colleagues' (2001) account of captive dolphins leading the way to a baited site, while followed by divers that assist them in harvesting the food. The dolphins would commonly swim toward the container, and then pause and remain with their bodies oriented to the bait while their heads turned to and from the approaching diver. These dolphins would never perform this behavior when there was no attentive diver in the water (see also Xitco, Gory, & Kuczaj, 2004), leading those authors to propose that what the dolphins were doing might be considered "spontaneous pointing." But data on the preconditions of the dolphins' behavior, while necessary, are insufficient to document "pointing" if the latter is taken as the accomplishment of showing. The fact that the dolphins' activity was effective in enabling the humans to come and assist, confounds the humans being *shown* where to go, with their being anticipated to help. Future studies might aim to watch for situations in which showing alone - that is, provoking a reorientation by the other - appears to satisfy the pointing individuals.

A stronger case for "showing" in these animals arises in one of the most complex types of collaborative attention - teaching. In the teaching observed in some cetaceans (e.g., Bender, Herzing, & Bjorklund, 2009; Guinet & Bouvier, 1995; see Rendell & Whitehead, 2001), showing becomes the elaborate modification of a pre-existing routine. Bender et al. (2009), for example, analyzed video of wild spotted dolphin adults foraging with and without their calves nearby. (Alloparenting in this species provides opportunities for mothers to sometimes feed on their own while their infants are tended by others: Miles & Herzing, 2003). In this study, the researchers focused on the foraging technique called "crater fishing" (see Herzing, 2002) in which a dolphin roots in the sand for buried fish. Once she stirs up the fish from its hiding place, a mother working alone only spends, on average, less than three seconds chasing and capturing such prey. In contrast, when her infant was nearby and watching, chase time was many times longer (mean: 22 s), and repeated reorientations to the fish were performed, accompanied by prolonged echolocation. Plus, while the mothers generally ate the fish themselves, the some 10% of cases in which they did not, all involved an observing infant who was allowed to pursue and eat the prey. To test if it was the presence of their calves as a distraction that made the moms less efficient at capturing the prey, the researchers assessed the difference in the mothers' performance when the calves were nearby but not attending, versus when the calves were in the "observation position" - hanging vertically in the water with their

heads oriented to the foraging activity. It was only in the latter case that the significant differences in the mother's activity arose.

That the mothers iterated and exaggerated the chase process while being attended by their infants shows the versatility of that subroutine, as well as its adaptability to the attention of others. It prolongs the amount of time the calves have to observe the hunting process, and gives them a more salient model to imitate. While this presumably would facilitate learning, this study does not, unfortunately, provide data on the development of the calves' technique. But such data could be collected, even in a captive setting involving other demonstrated behaviors, by video sampling the infant's progress over time. Observational studies of apprenticeship in humans (see Lave & Wenger, 1990), in which such interactions are analyzed as cases of the "guided participatory appropriation" of skills (Rogoff, 1990), offer helpful precedents in dealing with such rich, real-world, videotape datasets (see also Matsuzawa, 1994; Parker, 2004).

Interestingly, in contrast to the above, in nonhuman primates the modified performance of expert foraging practices in the presence of novices is rarely if ever seen (e.g., Hayashi & Matsuzawa, 2003; Hirata & Celli, 2003; Inoue-Nakamura and Matsuzawa, 1997; although see Boesch, 1991). That is, while novice primates attend to and ultimately reproduce the behavior of experts, the experts do not generally attend to or help structure the novice's performance. A marked exception to this involves human-enculturated apes who, after considerable experience as novices being actively taught by their human caregivers, are commonly seen to engage in active interventions in the learning processes of others (e.g., Fouts, Fouts, & Van Cantfort, 1989; Savage-Rumbaugh & Lewin, 1994; Shanker & King, 2002). A sign-language trained chimpanzee, for example, paused in her routine of signing "food" in anticipation of a treat, to shape her offspring's hand, and move it to his mouth to perform the sign, just as she herself had been taught to do (Fouts et al., 1989). This finding again attests to the critical role played by social context in the scaffolding and shaping of cognition. That teaching may occur in cetaceans even without human enculturation, suggests that this could be a particularly fruitful area to look for examples of complex embedding.

It may be that the occurrence of teaching in cetaceans is just another aspect of a generalized tendency to collaborate. In marked contrast to most primates, for example, collaborative foraging is commonplace in cetaceans (see Mann, Connor, Tyack, & Whitehead, 2000; Norris & Dohl, 1980). This is likely the result of the ecological pressures and opportunities presented by the aquatic environment. For instance, dolphins working as a group can easily control a school of prey fish that a single individual simply cannot. The tendency to work together is also reflected in the importance of synchrony in these animals. Synchronized activity is observed from early infancy, where it facilitates infant locomotion by allowing it to slipstream on the mother's movement through the water, as well as provides opportunities to learn from shared attention and co-activity (Norris & Dohl, 1980; see Fellner, Bauer, & Harley, 2006). Among older animals, synchrony is a common pro-social practice (e.g., Johnson & Norris, 1986, 1994; Pryor, 1990; Tavolga, 1966) and can be seen, for example, in the tandem displays of male

coalition partners in bottlenose dolphins (Connor, Smolker, & Bejder, 2006). The fact that social collaborations can even appear between dolphins of different species (see Herzing & Johnson, 1997) suggests a level of flexibility and context sensitivity that is consistent with cognitive complexity. Clearly, collaborative activity in cetaceans is an area much in need of detailed cognitive analyses. Even in captivity, situations requiring collaboration could be fairly easily arranged to observe how the animals adapt.

Finally, just as in primates, a systematic look at the large-scale cognition - the observable history of social patterns in a particular group - can also provide sources of complexity. Cultural traditions, for example, are evident in the large-scale variability of cetacean foraging techniques and social structures, compared across different groups of a given species in the wild (Mann et al., 2000; Rendell & Whitehead, 2001). For example, killer whales in some areas noisily pursue fish as prey, while those in other waters silently hunt marine mammals. Similarly, bottlenose dolphins in Florida tend to form coalitions of two males, while in Australia they more often form coalitions of three, and in Scotland the males are not seen to form coalitions at all. Regardless of the effect of ecological constraints on these differences, in each case the animals are showing behavioral adaptations shared by their community that shape their challenges and options for response.

Long-term observations also indicate that, like in primates, particular "roles" arise in the patterns of kinship, rank, and coalitional interactions. Biological markets, involving exchanges that show altruism, reciprocity, and reconciliation (e.g., Caldwell & Caldwell, 1966; Connor & Norris, 1982; Weaver, 2003), are likewise operating in some species. Shifts in the value of social and ecological commodities, especially in the fission/fusion societies seen in certain dolphins, would add yet more patterns for these animals, and their human observers, to track. The roles that arise in such interactions, and that no doubt change over development in these long-lived animals, would clearly contribute to the complexity of cognition in these species.

Probably the most complicated roles for which we do have evidence in cetaceans occur in "second-order" coalitions. In these interactions, seen in Indian Ocean bottlenose dolphins (Connor, Heithaus, & Barre, 1999; Connor, Smolker, & Richards, 1992), two triadic coalitions work together against a third for access to a reproductive female. Such coalitional behavior - including herding females, engaging in synchronous displays with allies, and antagonizing rivals - can involve a multiplicity of roles. These can be simultaneously embedded, as when a male dolphin plays one role in his coalition (high fidelity, long-term supporter), while playing another in relation to the second coalition (temporary ally), and yet others with respect to the third coalition (competitor) and to the herded female (potential mate). The micro-analysis of these interactions could go a long way toward developing our understanding of the cognition involved in these interactions, how it develops, and by what acts, and relationships between acts, it is mediated.

For future research

As this paper shows, observational methods can yield a wide range of useful data on the complexity of cognition in primates and cetaceans. Several sources of complexity emerged in these quantitative and qualitative studies of activity-in-context. They include the versatile substitution of acts and objects into existing subroutines, the embedding, simultaneously or sequentially, of subroutines into larger routines, and the multiplicity of long-term patterns that come into play.

While different from the experimental approaches often used to study animal cognition, the observational methods reviewed in this paper offer a viable, productive alternative. In the micro-analyses of engagements with objects and social others, this work focused on the predictability and elaboration of event sequences, on contingencies between shifts in especially attentional behavior, and on the tactical timing of changes in subroutine. It demonstrated the utility of analytic techniques such as tracking audience effects, identifying dyadic interactions embedded in other dyadic interactions, characterizing the insertion points for iterated subroutines, and noting the abruptness of changes in behavioral trajectories as an indication of subroutine satisfaction. It provided warrants for attributing value to certain outcomes, for discerning the problem-set changes associated with growing expertise, and for treating the achievement of multi-modal access as information-seeking behavior. It also showed how large-scale data can reveal patterns of interaction that shape the animals' options, and how the roles that individuals play socially develop, alternate, and overlap. In particular, it showed how creatures that are responsive to multiple market forces, especially while living in a fission/fusion society, can develop a particular sensitivity to the attentional states of others, can learn from switching roles, and can even strategically respond to the absence of critical information. Finally, from a theoretical perspective, this approach showed that a focus on the dialectic - on the co-regulation between the thistle and the gorilla, between the chimpanzee its rocks and its nut, between the misleader and the misled, or between the infant requesting to be carried and the mother with whom she negotiates - allows us to document cognition as it transpires. By tracking how affordances change as interactions proceed, and by assessing behavior in terms of its relative features like synchrony, complementarity, or accessibility, it allows us to do direct cognitive analyses of the activity we see. The complexity that emerges is thus grounded in visible behavior, and so is consistent with, and gainfully informs, embodied models of distributed mind.

As the above array of research illustrates, there is great potential in this approach for the study of cognition in captive cetaceans. Videotape (with audio!) of these animals, interacting with one another and their surroundings, could provide rich observational data on cognition-in-action. Many of the questions and techniques seen in the work on primates could be readily translated to investigate these aquatic mammals, adapted to their particular sensory-motor constraints, their avid sociality, and their penchant for synchrony and play. Contexts like learning, imitation, object use, social tool and other triadic interactions, collaboration,

teaching, games, and shifts in the social marketplace all could be investigated. As long as the analyses include both long-term and micro-analysis, the cognitive processes involved could be systematically documented. As has hopefully been demonstrated here, this multi-scalar approach can constitute a rigorous and revelatory method for the comparative study of cognitive complexity.

References

- Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in gregarious animals: A predictive framework. *Animal Behaviour*, *63*, 1–19.
- Bard, K. A., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., Costall, A., & Matsuzawa, T. (2005). Group differences in the mutual gaze of chimpanzees (*Pan troglodytes*). *Developmental Psychology*, *41*, 616-624.
- Barrett, L., & Henzi, S. P. (2006). Monkeys, markets and minds: Biological markets and primate sociality. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 209-232). New York: Springer.
- Barrett, L., Henzi, S. P., & Dunbar, R. I. M. (2003). Primate cognition - from what now to what if. *Trends in Cognitive Science*, *7*, 494-497.
- Barsalou, L. W., Simmons, W. K., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Science*, *7*, 84-91.
- Bender, C. E., Herzing, D. L., & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition*, *12*, 43-53.
- Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bousou, Guinea: Case studies in nut-cracking and leaf-folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 476-508). Tokyo: Springer-Verlag.
- Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*, 530-532.
- Boesch, C., & Boesch, H. (1989). Hunting behavior in wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, *78*, 547-573.
- Byrne, R. W. (1995) *The thinking ape*. Oxford: Oxford University Press.
- Byrne, R. W. (1999). Imitation without intentionality. *Animal Cognition*, *2*, 63-72.
- Byrne, R. W., & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. berengei*): Variability and standardization. *American Journal of Primatology*, *31*, 241-261.
- Byrne, R. W., Corp, N. & Byrne, J. M. E. (2001a). Estimating the complexity of animal behaviours: How mountain gorillas eat thistles. *Behaviour*, *138*, 525-557.
- Byrne, R. W. Corp, N., & Byrne, J. M. E. (2001b). Manual dexterity in the gorilla: Bimanual and digit role differentiation in a natural task. *Animal Cognition*, *4*, 347-361.
- Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, *21*, 667-721.
- Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence*. Oxford: Cambridge University Press.
- Byrne, R. W., & Whiten, A. (1990). Tactical deception in primates: The 1990 database. *Primate Report*, *27*, 2-101.

- Caldwell, M. C., & Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology*, 9, 1-8.
- Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. Mahway, NJ: Erlbaum.
- Chance, M. R. A. (1962). An interpretation of some agonistic postures: The role of “cut-off” acts and postures. *Symposia of the Zoological Society of London*, 8, 71-89.
- Chance, M. R. A. (1967). Attention structure as the basis of primate rank orders. *Man*, 2, 503-518.
- Cheney, D. L., & Seyfarth, R. M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, 36, 477-486.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago: University of Chicago Press.
- Cheney, D. L., & Seyfarth, R. M. (1999). Recognition of other individuals’ social relationships by female baboons. *Animal Behaviour*, 58, 67-75.
- Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics: The evolution of a social mind*. Chicago: University of Chicago Press.
- Connor, R. C. (2007). Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B*, 362, 587-602.
- Connor, R. C., Heithaus, R. M., & Barre, L. M. (1999). Super-alliance of bottlenose dolphins. *Nature*, 371, 571-572.
- Connor, R. C., & Mann, J. (2005). Social cognition in the wild: Machiavellian dolphins? In S. Hurley & M. Nudd (Eds.), *Rational Animals* (pp. 329-367). Cambridge: Oxford University Press.
- Connor, R. C., & Norris, K. S. (1982). Are dolphins reciprocal altruists? *The American Naturalist*, 119, 358-374.
- Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour*, 72, 1371-1378.
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, 89, 987-990.
- Connor, R. C., Wells, R., Mann, J., & Read, A. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. Connor, P. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of whales and dolphins* (pp. 91-126). Chicago: University of Chicago Press.
- Cords, M., & Thurnheer, S. (1993). Reconciliation with valuable partners by long-tailed macaques. *Ethology*, 93, 315-325.
- Cousi-Korbel, S. (1994). Learning to outwit a competitor in mangabees (*Cercocebus torquatus torquatus*). *Journal of Comparative Psychology*, 108, 164-171.
- Dussutour, A., Denneubourg, J-L., Beshers, S., & Fourcassie, V. (2009). Individual and collective problem-solving in a foraging context in the leaf-cutting ant *Atta colombica*. *Animal Cognition*, 12, 21-30.
- Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore*, 2, 22-23.
- Fauconnier, G., & Turner, M. (2002). *The way we think*. New York: Basic Books.
- Fellner, W., Bauer, G. B., & Harley, H. E. (2006). Cognitive implications of synchrony in dolphins: A review. *Aquatic Mammals*, 32, 511-516.
- Fogel, A. (1990). The process of developmental change in infant communicative action: Using dynamical systems theory to study individual ontogenies. In J. Colombo &

- J. Fagan (Eds.), *Individual differences in infancy* (pp. 341-358). Hillsdale, NJ: Erlbaum.
- Fogel, A. (1993). *Developing through relationships*. University of Chicago Press, Chicago.
- Forrester, G. S. (2008). A multi-dimensional approach to investigations of behavior: revealing structure in animal communication signals. *Animal Behaviour*, *76*, 1749-1760.
- Forster, D. (2002). Consort turnovers as distributed cognition in Olive baboons: A distributed approach to mind. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 163-171). Cambridge, MA: The MIT Press.
- Fouts, R. S., Fouts, D. H., & Van Cantfort, T. E. (1989). The infant Loulis learns signs from cross-fostered chimpanzees. In R. A. Gardner, B. T. Gardner, & T. E. Van Cantfort (Eds.), *Teaching sign language to chimpanzees* (pp. 280-292). Albany, NY: State University of New York Press.
- Fragaszy, D. M., & Perry, S. (2003). *The biology of traditions*. Cambridge: Cambridge University Press.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Gomez, J. C. (1991). Visual behavior as a window for reading the mind of others in primates. In A. Whiten (Ed.), *Natural theories of mind* (pp. 195-208). Oxford: Basil Blackwell.
- Goodall, J. (1971). *In the shadow of man*. Boston: Houghton Mifflin.
- Goodall, J. (1986). *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.
- Goodwin, C. (1994). Professional vision. *American Anthropologist*, *96*, 606-633.
- Goodwin, C. (2000). Action and embodiment within situated human interaction. *Journal of Pragmatics*, *32*, 1489-1522.
- Goodwin, M. H., & Kyratis, A. (2007). Children socializing children: Practices for negotiating the social order among peers. *Research on Language and Social Interaction*, *40*(4), 279-289.
- Granott, N., & Parziale, J. (2002). *Microdevelopment: Transition processes in development and learning*. Cambridge: Cambridge University Press.
- Guinet, C., & Bouvier, J. (1995). Development of intentional stranding techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology*, *73*, 27-33.
- Harley, H. E., Xitco Jr., M. J., Roitblat, H. L., & Herman, L. M. (1998). *Imitation of human models by bottlenose dolphins*. The Napoli Social Learning Conference, Naples, Italy.
- Harlow, H. F., Harlow, M. K., & Hansen, E. W. (1963). The maternal affectional system of Rhesus monkeys. In R. H. Rheingold (Ed.), *Maternal behavior in animals* (pp. 254-281). New York: Wiley.
- Hayashi, M., & Matsuzawa, T. (2003). Cognitive development in object manipulation by infant chimpanzees. *Animal Cognition*, *6*, 225-233.
- Hayashi, M., Takeshita, H., & Matsuzawa, T. (2006). Cognitive development in apes and humans assessed by object manipulation. In T. Matsuzawa, M. Tomonoga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 395-410). Tokyo: Springer-Verlag.
- Henzi, S. P., & Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour*, *63*, 915-921.

- Herman, L. M. (1980a). *Cetacean behavior: Mechanisms and functions*. New York: John Wiley & Sons.
- Herman, L. M. (1980b). Cognitive characteristics of dolphins. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 363-430). New York: John Wiley & Sons.
- Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In C. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 63-108). Cambridge, MA: MIT Press.
- Herman, L. M., Morrel-Samuels, P., & Brown, (1989). *Behavioral mimicry of live and televised models by bottlenose dolphins*. The 30th Annual Meeting of the Psychonomic Society, Atlanta, GA.
- Herman, L. M., Pack A. A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. R. Roitblat, L. M. Herman, & P. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 273-298). Hillsdale, NJ: Erlbaum.
- Herzing, D. L. (2002). *The wild dolphin project: Long-term research of Atlantic spotted dolphins in the Bahamas*. Jupiter, FL: Wild Dolphin Project.
- Herzing, D. L., & Brunnick, B. J. (1997). Coefficients of association of reproductively active female Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, 23, 155-162.
- Herzing, D. L., & Johnson, C. M. (1997). Interspecies interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. *Aquatic Mammals*, 23, 85-99.
- Heyes, C. M. (1993). Anecdotes, training, trapping and triangulating: Do animals attribute mental states to others? *Animal Behaviour*, 46, 177-184.
- Hinde, R. A. (1987). *Individuals, relationships and culture: Links between ethology and the social sciences*. Cambridge, UK: Cambridge University Press.
- Hinde, R. A., & Simpson, M. J. A. (1975). Qualities of mother-infant relationships in monkeys. CIBA Foundation Symposium. *Parent-infant interaction* (pp. 39-67). Amsterdam: Elsevier.
- Hirata, S., & Celli, M. (2003). Role of mothers in the acquisition of tool use behaviours by captive infant chimpanzees. *Animal Cognition*, 6, 235-244.
- Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (*Pan troglodytes*). *Animal Cognition*, 4, 285-295.
- Hirata, S., & Morimura, N. (2000). Naïve chimpanzees' (*Pan troglodytes*) observation of experienced conspecifics in a tool-using task. *Journal of Comparative Psychology*, 114, 291-296.
- Hopkins, W. D., Russell, J., Freeman, H., Buehler, N., Reynolds, E., & Schapiro, S. J. (2005). The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychological Science*, 16, 487-493.
- Humle, T. (2006). Ant dipping in chimpanzees: An example of how micro-ecological variables, tool use, and culture reflect the cognitive abilities of chimpanzees. In T. Matsuzawa, M. Tomonoga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 439-451). Tokyo: Springer-Verlag.
- Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303-317). Cambridge: Cambridge University Press.
- Hutchins, E. (1995a). *Cognition in the wild*. Cambridge, MA: MIT Press.
- Hutchins, E. (1995b). How a cockpit remembers its speed. *Cognitive Science*, 19, 265-288.

- Hutchins, E. (2001). Distributed cognition. *International Encyclopedia of the Social and Behavioral Sciences* (pp. 2068-2072). Oxford: Elsevier Science Ltd.
- Hutchins, E. (2005). Material anchors for conceptual blends. *Journal of Pragmatics*, 37, 1555–1577.
- Hutchins, E. (2008). The role of cultural practices in the emergence of modern human intelligence. *Philosophical Transactions of the Royal Society B*, 363, 2011-2019.
- Hutchins, E., & Johnson, C. M. (2009). Modeling the emergence of language as an embodied collective cognitive activity. *Topics in Cognitive Science*, 1, 523-546.
- Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 111(2), 159-173.
- Itakura, S. (1995). An exploratory study of social referencing in chimpanzees. *Folia Primatologica*, 64, 44-48.
- Johnson, C. M. (1993). Animal communication via coordinated cognitive systems. In P. P. G. Bateson, N. Thompson, & P. Klopfer (Eds.), *Perspectives in ethology, Volume X: Variability in behavior* (pp. 187-207). New York: Plenum Press.
- Johnson, C. M. (2001). Distributed primate cognition: A review. *Animal Cognition*, 3, 167-183.
- Johnson, C. M. (2002). The Vygotskian advantage in cognitive modeling: Participation precedes and thus prefigures understanding. *Behavioral and Brain Science*, 25, 628-629.
- Johnson, C. M. (2004). The micro-ethology of social attention: “Brightness” in bonobos. *Folia Primatologica*, 75(suppl 1), 175.
- Johnson, C. M., & Herzog, D. L. (2006). Primate, cetacean and pinniped cognition compared: An introduction. *Aquatic Mammals*, 32, 409-412.
- Johnson, C. M., & Karin-D’Arcy, M. R. (2006). Social attention in nonhuman primates: A behavioral review. *Aquatic Mammals*, 32, 423-442.
- Johnson, C. M., & Norris, K. S. (1986). Delphinid social organization and social behavior. In R. J. Schusterman, J. A. Thomas, & F. G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 335-346). Hillsdale, NJ: Erlbaum.
- Johnson, C. M., & Norris, K. S. (1994). Social behavior. In K. S. Norris, B. Wursig, R. S. Wells, & M. Wursig (Eds.), *The Hawaiian spinner dolphin* (pp. 243-286). Berkeley, CA: University of California Press
- Johnson, C. M., & Oswald T. M. (2001). Distributed cognition in apes. In J. D. Moore & K. Stenning (Eds.), *Proceedings of the 23rd Annual Conference of the Cognitive Science Society* (pp. 453-458). University of Edinburgh, Scotland: Human Communication Research Centre.
- King, B. J. (2004). *The dynamic dance: Nonvocal communication in African great apes*. Cambridge, MA: Harvard University Press.
- Kohler, W. (1927). *The mentality of apes*. New York: Vintage.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. (2005). Cultural transmission of a foraging strategy involving tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences*, 102, 8939-8943.
- Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology*, 19, 223-240.
- Kuczaj, S. A., & Trone, M. (2001). Why do dolphins and whales make their play more difficult? *Genetic Epistemologist*, 29, 57.

- Kuczaj, S. A. & Yeater, D. B. (2006). Dolphin imitation: Who, what, when and why? *Aquatic Mammals*, 32, 413-422.
- Kummer, H. (1967). Tripartite relations in Hamadryas baboons. In S. A. Altmann (Ed.), *Social communication among primate* (pp. 63-72). Chicago: University of Chicago Press.
- Lakoff, G., & Nunez, R. (2002). *Where mathematics comes from*. New York: Basic Books.
- Lave, J. (1984). The dialectic of arithmetic in grocery shopping. In B. Rogoff & J. Lave (Eds.), *Everyday cognition* (pp. 67-94). Cambridge, MA: Harvard University Press.
- Lave, J., & Wenger, E. (1990). *Situated learning: Legitimate peripheral participation*. Cambridge, UK: Cambridge University Press.
- Lee, K., & Karmiloff-Smith, A. (2002). Macro- and micro-developmental research: Assumptions, research strategies, constraints and utilities. In N. Granott & J. Parziale (Eds.), *Microdevelopment: Transition processes in development and learning* (pp. 243-268). Cambridge: Cambridge University Press.
- Lilly, J. C. (1965). Vocal mimicry in *Tursiops*: Ability to match numbers and durations of human vocal bursts. *Science*, 147, 300-301.
- Lorenz, K. (1982). *The foundations of ethology*. New York: Springer-Verlag.
- Maestripieri, D. (1995). Maternal encouragement in nonhuman primates and the question of animal teaching. *Human Nature*, 6, 361-378.
- Mann, J., Connor, R. C., Tyack, P. L., & Whitehead, H. (2000). *Cetacean societies: Field studies of dolphins and whales*. Chicago: University of Chicago Press.
- Mann, J., & Sargeant, B. (2003). Like mother, like calf: The ontogeny of foraging traditions in white Indian ocean bottlenose dolphins. In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 236-266). Cambridge, UK: Cambridge University Press.
- Manson, J. H. (1999). Infant handling in wild *Cebus capucinus*: Testing bonds between females? *Animal Behaviour* 57, 911-921.
- Markham, A. C., & Altmann, J. (2008). Remote monitoring of primates using automated GPS technology in open habitats. *American Journal of Primatology*, 70, 495-499.
- Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R. Wrangham, W. McGrew, F. de Waal, & P. Heltne (Eds.), *Chimpanzee cultures* (pp. 351-370). Cambridge, MA: Harvard University Press.
- Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 196-209). Cambridge, UK: Cambridge University Press.
- Matsuzawa, T., Tomonoga, M., & Tanaka, M. (2006). *Cognitive development in chimpanzees*. Tokyo: Springer-Verlag.
- McBride, A. F., & Hebb, D. O. (1948). Behavior of the captive bottlenose dolphins, *Tursiops truncatus*. *Journal of Comparative and Physiological Psychology*, 41, 111-123.
- McGrew, W. (1992). *Chimpanzee material culture*. Cambridge, UK: Cambridge University Press.
- Menzel, C. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology*, 113, 426-434.
- Menzel Jr., E. W. (1974). A group of young chimps in a one-acre field. In A. Schrier & F. Stollnitz (Eds.), *Behavior of non-human primates: Modern research trends* (pp. 83-153). New York: Academic Press.

- Miles, J. A., & Herzing, D. L. (2003). Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquatic Mammals*, 29, 363-377.
- Mitchell, R. W., & Anderson, J. R. (1997). Pointing, withholding information and deception in capuchin monkeys (*Cebus appella*). *Journal of Comparative Psychology*, 111, 351-361.
- Nishida, T. (1979). The social structure of chimpanzees in the Mahale Mountains. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 72-122). Menlo Park, CA: Benjamin/Cummings.
- Noe, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, 35, 1-11.
- Norris, K. S., & Dohl, T. (1980). The structure and function of cetacean schools. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 211-262). New York: John Wiley & Sons.
- Pack, A. A., & Herman, L. M. (2006). Dolphin social cognition and social attention: Our current understanding. *Aquatic Mammals*, 32, 443-460.
- Packer, C. (1977). Reciprocal altruism in *Papio anubis*. *Nature*, 265, 441-443.
- Parker, S. T. (2004). The cognitive complexity of social organization and socialization in wild baboons and chimpanzees: Guided participation, socializing interactions and event representation. In A. E. Russon & D. R. Begun (Eds.), *The evolution of thought: Evolutionary origins of great ape intelligence* (pp. 45-60). Cambridge, UK: Cambridge University Press.
- Parr, L. S., Winslow, J. T., Hopkins, W. D., & de Waal, F. B. M. (2000). Recognizing facial cues: Individual recognition in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, 114, 47-60.
- Payne, K. B., & Payne, R. (1985). Large-scale changes over 19 years in the songs of humpback whales in Bermuda. *Zeitschrift fur Tierpsychologie*, 68, 89-114.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K., et al. (2003). Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. *Current Anthropology*, 44, 241-268.
- Perry, S., Barrett, H. C., & Manson, J. H. (2004). White-faced capuchin monkeys exhibit triadic awareness in their choice of allies. *Animal Behaviour*, 67, 165-170.
- Perry, S. E. (2006). What cultural primatology can tell anthropologists about the evolution of culture. *Annual Review of Anthropology*, 35, 171-190.
- Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Louis, J., Jack, K., Mackinnon, K. C., et al. (2006). Traditions in wild white-faced capuchin monkeys. In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 391-425). Cambridge, UK: Cambridge University Press.
- Piaget, J. (1952). *The origins of intelligence in children*. New York: International Universities Press.
- Povinelli, D. J. (1994). Comparative studies of animal mental state attributions: A reply to Heyes. *Animal Behaviour*, 48, 239-241.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Science*, 7, 157-160.
- Premack, D., & Premack, A. (1983). *The mind of an ape*. New York: Norton.
- Pryor, K. (1975). *Lads before the wind: Adventruers in porpoise training*. New York: Harper & Row.
- Pryor, K. (1990). Non-acoustic communication in small cetaceans: Glimpse, touch, position, gesture, and bubbles. *NATO ASI Series*, 196, 537-544.

- Pryor, K. Haag, R., & O'Reilly, J. (1969). The creative porpoise: Training for novel behavior. *Journal of the Experimental Analysis of Behavior*, *12*, 653-661.
- Putney, R. T. (2007). Willful apes revisited: The concept of prospective control. In D. Washburn (Ed.), *Primate perspectives on behavior and cognition* (pp. 207-220). Washington, D.C.: American Psychological Association.
- Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology*, *107*, 301-312.
- Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*, 309-382.
- Resnick, L. B., Levine, J. M., & Teasley S. D. (1991). *Perspectives on socially shared cognition*. Washington, D.C.: American Psychological Association.
- Rogoff, B. (1990). *Apprenticeship in thinking: Cognitive development in social context*. New York: Oxford University Press.
- Rogoff, B. (1993). Children's guided participation and participatory appropriation in socio-cultural activity. In R. Wozniak & K. Fischer (Eds.), *Development in context* (pp. 121-153). Hillsdale, NJ: Erlbaum.
- Russel, C. L., Adamson, L. B., & Bard, K. A. (1997). Social referencing by young chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*, 185-193.
- Russon, A. E. (2006). Acquisition of complex foraging skills in juvenile and adolescent orangutans (*Pongo pygmaeus*): Developmental influences. *Aquatic Mammals*, *32*, 500-510.
- Russon, A., & Galdikas, B. (1993). Imitation in ex-captive orangutans. *Journal of Comparative Psychology*, *107*, 147-161.
- Russon, A. E., & Galdikas, B. M. F. (1995). Constraints on great apes' imitation: Model and action selectivity in rehabilitant orangutan (*Pongo pygmaeus*) imitation. *Journal of Comparative Psychology*, *109*, 5-17.
- Sambrook, T., & Whiten, A. (1997). On the nature of complexity in cognitive and behavioral science. *Theory and Psychology*, *7*, 191-213.
- Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, *5*, 293-296.
- Savage-Rumbaugh, E. S. (1986). *Ape language: From conditioned response to symbol*. New York: Columbia University Press.
- Savage-Rumbaugh, E. S., & Lewin, R. (1994). *Kanzi: The ape at the brink of the human mind*. New York: John Wiley & Sons.
- Savage-Rumbaugh, E. S., & McDonald, K. (1988). Deception and social manipulation in symbol-using apes. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence* (pp: 224-237). Oxford: Oxford University Press.
- Schusterman, R. J., Thomas, J. A., & Wood, F. G. (1986). *Dolphin cognition and behavior: A comparative approach*. Hillsdale, NJ: Erlbaum.
- Shanker, S. G., & King, B. J. (2002). The emergence of a new paradigm in ape language research. *Behavioral and Brain Sciences*, *25*, 605-656.
- Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, *58*, 45-51.
- Smolker, R. A., Richards, A. F., Connor, R. C., Mann, J., & Berggren, P. (1997). Sponge-carrying by Indian Ocean bottlenose dolphins: Possible tool-use by a delphinid. *Ethology*, *103*, 454-465.
- Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine.
- Stanford, C. (1999). *The hunting apes*. Princeton, NJ: Princeton University Press.

- Strum, S. S. (1987). *Almost human: A journey into the world of baboons*. New York: Norton.
- Strum, S. C., Forster, D., & Hutchins, E. (1997). Why Machiavellian intelligence may not be Machiavellian. In A. Whiten & R. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 50-85). Cambridge: Cambridge University Press.
- Sugiyama, Y., & Koman, J. (1979). Tool-using and making behavior in wild chimpanzees at Bossou, Guinea. *Primates*, 20, 513-524.
- Symington, M. M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology* 11, 47-61.
- Tavolga, M. C. (1966). Behavior of the bottlenose dolphin (*Tursiops truncatus*): Social interactions in a captive colony. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 718-730). Berkeley, CA: University of California Press.
- Taylor, C. K., & Saayman, G. S. (1973). Imitative behaviour by Indian Ocean Bottlenose Dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, 44, 286-298.
- Thelen, E., & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action*. Cambridge, MA: MIT Press.
- Tinbergen, N. (1952). "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology*, 27, 1-32.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55, 1063-1069.
- Tomasello, M., Gust, D., & Frost, G. T. (1989). The development of gestural communication in young chimpanzees: a follow up. *Primates*, 30, 35-50.
- Tyack, P. L. (2000). Functional aspects of cetacean communication. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 270-307). Chicago: University of Chicago Press.
- Uneo, A., & Matsuzawa, T. (2005). Response to novel food in infant chimpanzees: Do infants refer to mothers before ingesting food on their own? *Behavioral Processes*, 68, 85-90.
- Vick, S.-J., Waller, B. M., Parr, L. A., Smith Pasqualini, M., & Bard, K. A. (2007). A cross species comparison of facial morphology and movement in humans and chimpanzees using FACS. *Journal of Nonverbal Behavior*, 31, 1-20.
- Vygotsky, L. S. (1978). *Mind in society: The development of higher psychological processes*. Cambridge, MA: Harvard University Press.
- de Waal, F. B. M. (1982). *Chimpanzee politics*. New York: Harper and Row.
- de Waal, F. B. M. (1986a). Dynamics of social relationships. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 421-430). Chicago: University of Chicago Press.
- de Waal, F. B. M. (1986b). Deception in the natural communication of chimpanzees. In R. W. Mitchell & N. S. Thompson (Eds.), *Deception: Perspectives on human and nonhuman deceit* (pp. 221-244). Albany, NY: State University of New York Press.
- de Waal, F. B. M., & Brosnan, S. F. (2006). Simple and complex reciprocity in primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 85-105). New York: Springer.
- de Waal, F. B. M., & Tyack, P. L. (2003). *Animal social complexity: Intelligence, culture and individualized societies*. Cambridge, MA: Harvard University Press.
- Weaver, A. (2003). Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, 19, 836-846.

- Wells, R. S., Irvine, A. B., & Scott, M. D. (1980). The social ecology of inshore Odontocetes. In L. M. Herman. (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 263-318). New York: John Wiley & Sons.
- Whiten, A. (1991). *Natural theories of mind*. New York: Oxford University Press.
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*, 233-274.
- Whiten, A., & Byrne, R. W. (1997). *Machiavellian intelligence II: Extensions and evaluations*. Cambridge: Cambridge University Press.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in chimpanzees. *Nature*, *399*, 682-5.
- Woodruff, G., & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, *7*, 333-362.
- Wursig, B., & Wursig, M. (1977). The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *198*, 755-756.
- Xitco Jr., M. J. (1988). Mimicry of modeled behaviors by bottlenose dolphins. Unpublished master's thesis, University of Hawaii, Honolulu.
- Xitco, M. J., Gory, J. D., & Kuczaj, S. A. (2001). Spontaneous pointing by bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *4*, 115-123.
- Xitco Jr., M. J., Gory, J. D., & Kuczaj II, S. A. (2004). Dolphin pointing is linked to the attentional behavior of a receiver. *Animal Cognition*, *7*, 231-238.
- Zahavai, A. (1977). The testing of a bond. *Animal Behaviour*, *25*, 246-247.