
Equivalence Classification as an Approach to Social Knowledge: From Sea Lions to Simians

RONALD J. SCHUSTERMAN, COLLEEN REICHMUTH
KASTAK, AND DAVID KASTAK

Despite the fact that no other living species has communication skills that rival human language, the Cartesian position that nonhuman animals lack cognitive abilities can no longer be defended. On the contrary, many species show varying degrees of proficiency at forming abstract concepts and manipulating symbols. Indeed, the past quarter century has seen a wealth of research on learning, memory, and concept formation, demonstrating that animals as diverse as sea lions and simian primates are able to solve abstract problems. Strong evidence of complex cognitive skills can be found in the laboratory and in the field when circumstances require an animal to form representations of its earlier experiences.

Recently there have been several findings indicating that animals not only classify objects along physical dimensions, but can also classify them according to their function. Thus, dissimilar stimuli can be perceived as constituting an equivalence class. An equivalence class is defined by equivalence relations that emerge between dissimilar stimuli that share common spatio-temporal or functional contingencies. These stimuli can include signals, individuals, objects, behavioral events, and reinforcers. Relations among the

stimuli comprising an equivalence class enable individuals to apply similar meaning to structurally disparate class members. Thus, stimulus equivalence, or more simply, equivalence, allows animals to rapidly form natural categories.

The behavioral theory of equivalence relations developed from research dealing with reading comprehension in human subjects. Thirty years ago, Sidman (1971) reported the emergence of reading comprehension in a severely retarded teenage boy. Through reinforcement training with a procedure called matching-to-sample (MTS), the boy was taught to select pictures of objects and printed names of objects upon hearing spoken object names. Following this training he spontaneously related the written words to the corresponding spoken English words as well as the objects they represented. The critical node or link in this paradigm was the spoken word; it allowed the boy to spontaneously connect the printed names and pictures of objects with one another even though he had not been able to relate them before.

Equivalence as a conceptual process has some of its historical roots in the notion of mediated generalization, in which different stimuli become related to one another through their connection with a common element. For example, various food items may be rapidly generalized, not on the basis on their physical similarity, but rather, on the basis of a common response, "salivation," that mediates the relationships among the different foods (see for example Pearce 1994, p. 128). Similarly, with respect to language, humans tested via galvanic skin response show greater generalization between the printed words "urn" and "vase" than the printed words "urn" and "earn." In this case, common linguistic meaning, rather than structural similarity, serves to mediate the relationship between the different words (Riess 1940).

A revised model of equivalence, as developed by Sidman (1994), is particularly useful for describing the symbolic behavior of verbally competent subjects. However, the formation of equivalence relations is far from being the sole province of humans. There is now accumulating evidence that at least some nonhuman primates, marine and terrestrial mammals, and birds form equivalence classes in natural as well as laboratory studies.

In this chapter we will explain how equivalence relations are established in the laboratory as well as in the field. We will describe how stimulus equivalence phenomena show that associative learning mechanisms, far from being simplistic, can account for novel and complex behaviors. This approach provides a useful framework for understanding how a variety of animals organize

information about social groups as well as social relationships involving themselves and others.

Equivalence in the Animal Laboratory

Sidman's original formulation of equivalence classes relied on the integration of experimental results and mathematical theory. This led to a behavioral definition of equivalence that was based on the demonstration of three emergent pairwise stimulus relations (reflexivity, symmetry, and transitivity) from a subset of directly trained relations. Procedurally, this meant that a formal demonstration of equivalence class formation could take place only within the context of MTS. Such an MTS procedure involves the training of conditional discriminations, or "if-then" rules, between stimuli by requiring the subject to select one of two or more comparison stimuli as the correct match to a sample stimulus. A given comparison stimulus is thus selected conditionally upon the presentation of a particular sample (Carter & Werner 1978). Based on the formulation by Sidman and Tailby (1982), equivalence relations can be demonstrated following MTS training of the two relations $A \rightarrow B$ and $B \rightarrow C$ (that is, if stimulus A is the sample, select stimulus B as the comparison; if B is the sample, select C as the comparison). The reflexive relationships $A \rightarrow A$, $B \rightarrow B$, and $C \rightarrow C$, symmetrical relationships $B \rightarrow A$ and $C \rightarrow B$, transitive relationship $A \rightarrow C$, and symmetry/transitivity combination $C \rightarrow A$ should all emerge without further training. These emergent relationships demonstrate that the three stimuli have become equivalent, or substitutable, for one another. This procedure is especially suited to studies of linguistic behavior because verbal labels, pictures of objects, and printed words can easily be designated as sample and comparison stimuli.

Potential members of an equivalence class in an experimental setting can be arbitrary shapes, sounds, or any one of a variety of different stimuli; however, some psychologists view the ability of human subjects to form equivalence classes a result of linguistic competence (see, e.g., Horne & Lowe 1996, 1997 and associated commentaries). This view is not supported by recent research showing that verbally deficient humans, and even humans lacking basic linguistic skills, can form equivalence relationships between items in their environment (e.g., Carr et al. 2000). Thus, equivalence classification, rather than being a cognitive by-product of linguistic competence, is more likely a basic ability that underlies or structures complex human behaviors such as

language. Given this perspective, the issue of how nonhuman animals organize perceptual information into meaningful categories takes on new comparative significance.

An example of an MTS procedure adapted for use with nonhuman subjects is shown in Figure 7.1, which illustrates a sea lion matching visual stimuli. Animals have had some success in demonstrating the properties of equivalence within the context of MTS procedures. Reflexivity, or generalized identity matching, has been convincingly demonstrated experimentally by sea lions (Kastak & Schusterman 1994), bottlenose dolphins (Herman et al. 1989), and common chimpanzees (Oden et al. 1988). Symmetry and transitivity have been more difficult to demonstrate in MTS procedures (but see results of D'Amato et al. 1985; review by Zentall 1998). Thus far, only a single sea lion has shown all the emergent properties of equivalence relations (Schusterman & Kastak 1993). Further, the same sea lion subsequently transferred her knowledge of the equivalence relations from MTS to a two-choice simple discrimination task (Schusterman & Kastak 1998). The success of the sea lion in the original MTS study (Schusterman & Kastak 1993) can be attributed to several factors, including the large sample size of stimulus sets, exemplar training with a subset of those stimulus sets, and the subject's experience performing identity matching prior to symmetry and transitivity testing. Rather than being an isolated case of success, we expect that, given the same extensive and appropriate training and testing methodology, many other taxa will also show evidence of equivalence classification, or what could also be termed classes or categories of object relations.

This view is bolstered by a variety of studies with animals showing categorical behavior in experimental procedures other than MTS. For example, Schusterman and Gisiner (1997) have suggested that the grammatical sequences of gestural signs or lexigrams used in animal language research may lead to the formation of functionally equivalent classes (see also Herman et al. 1984). In studies with language-trained sea lions, referential signs of a given type (e.g., objects, actions, or modifiers) could be interchanged without disrupting the resulting performance of the animal. For example, any sign representing an object, whether a "ball," "cone," or "cube," or even a novel object, generated an object-oriented response when placed in the correct position in an instructional sequence. However, if the signs for an object and an action were transposed in a sequence, the sea lion often balked. Schusterman and Gisiner cited the apparent substitutability of signs sharing a common sequence position as evidence of functional class formation, with

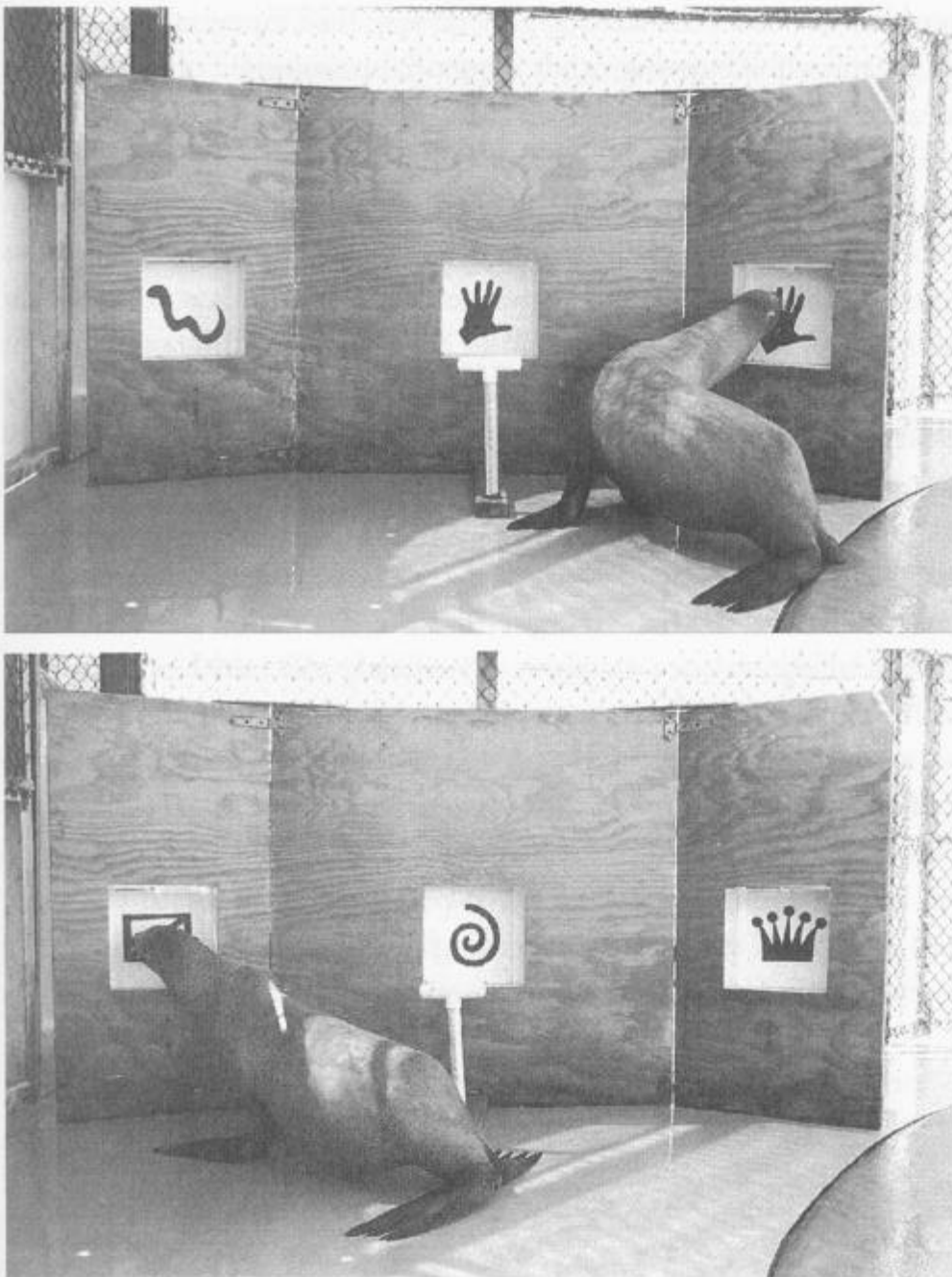


Figure 7.1. A California sea lion relating stimuli in the context of a matching-to-sample procedure. The subject positions her head at the station in front of the center panel, views the sample stimulus (*center*) and two comparison stimuli (*sides*), and then selects one of the comparison stimuli by touching it with her nose. The upper photograph shows an identity match ($A \rightarrow A$, or in this case, $\text{hand} \rightarrow \text{hand}$). The lower photograph shows an arbitrary match ($A \rightarrow B$, or in this case, $\text{spiral} \rightarrow \text{rectangle}$). The procedure can be extended to allow for testing of symmetrical and transitive relations.

the different stimuli in a class sharing general response topographies that do not extend to stimuli occupying other sequential positions. Further support for the idea that functional classes can arise from sequential procedures in nonhuman animals comes from studies with rhesus monkeys showing a transfer of function between stimuli sharing the same ordinal positions in different stimulus sequences (Chen et al. 1997). After learning to organize multiple sets of stimuli into desired sequences, a rhesus monkey can immediately organize a recombined set of stimuli (drawn from different stimulus sets) into the correct order on the basis of their prior ordinal positions. Figure 7.2 illustrates this finding with a hypothetical example showing how sequence training can generate emergent equivalence classes based on common ordinal positions. Both sea lions and simians understand that disparate stimuli appearing in a given sequential position are related to one another.

Vaughan (1988) was the first to argue that the distinction between functional classes and equivalence classes was artificial, and based primarily on differences in procedure. He trained pigeons on a discrimination reversal procedure in which the subjects were presented with a sequence of 40 different slides of trees that were divided into two arbitrary sets of 20 slides each. The pigeons were conditioned to peck at any of one set of slides, designated as positive, and to withhold pecking when presented with any of the other set of slides, designated as negative. Following learning of the positive set, the reinforcement contingencies were reversed, and responses to members of the

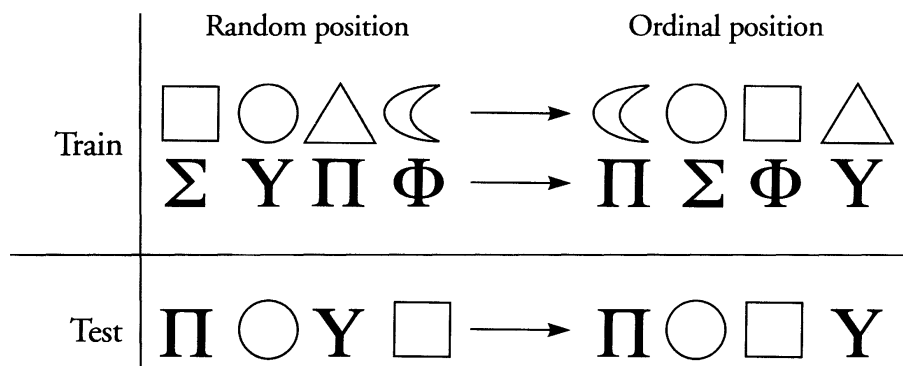


Figure 7.2. An illustration demonstrating how, hypothetically, sequence training can generate emergent equivalence classes based on shared ordinal positions. In the *training* phase, the animal learns to place four randomly assorted geometric shapes or Greek letters into appropriate ordinal positions. Afterward, in a *test* phase, the animal demonstrates that it can spontaneously substitute a geometric shape for a Greek letter and vice versa by placing the stimuli presented into the four appropriate ordinal positions.

formerly negative set were reinforced as positive. After repeatedly shifting the reinforcement contingencies between the two sets of stimuli, the pigeons began changing their responses to all members of a set after being exposed to the reversed contingency with just a few. Thus, the reversed contingency for slides presented at the beginning of a session predicted reversed contingencies for slides presented in the remainder of the session. Although the stimuli in each set were not physically similar or directly related, they became interrelated through their common behavioral functions. Vaughan concluded that the functional classes formed by his pigeons in the context of a simple discrimination/reversal procedure were the same as equivalence classes demonstrated in MTS procedures. However, his interpretation was not widely accepted because he failed to determine if the two functional classes formed by his pigeons would transfer to equivalence classes as demonstrated by MTS.

Sidman and his colleagues (1989) replicated and expanded Vaughan's procedure to determine if human subjects would show transfer to MTS. In this experiment, the functional classes formed by human subjects in a simple discrimination/reversal procedure transferred immediately to conditional discriminations in a MTS procedure. Further, the functional classes were expanded through traditionally defined equivalence relations. Thus, for human subjects, functional classes and equivalence relations do appear to comprise the same behavioral processes (Sidman 1994).

Recently, we adapted Sidman and colleagues' (1989) procedure to test whether functional classes formed by another nonhuman species, the California sea lion, in a simple discrimination/reversal procedure would also generate traditionally defined equivalence relations (Reichmuth Kastak et al. 2001). Using a repeated reversal procedure with stimuli designated "letters" and "numbers," we first documented the formation of functional classes in two California sea lions. This was accomplished through training on two-choice discrimination trials where a number was always presented with a letter. Once each subject consistently responded to the letter class, the reinforcement contingencies were reversed, and subsequently, only selections of number stimuli were rewarded. Following many reversals in reinforcement contingencies from one positive class to the other, we found that the sea lions began to treat all of the stimuli in a class alike; that is, the responses established for one class member immediately transferred to all other members of that class (see Figure 7.3). We next tested our sea lions to determine if class membership would transfer across procedures to an MTS context. We found

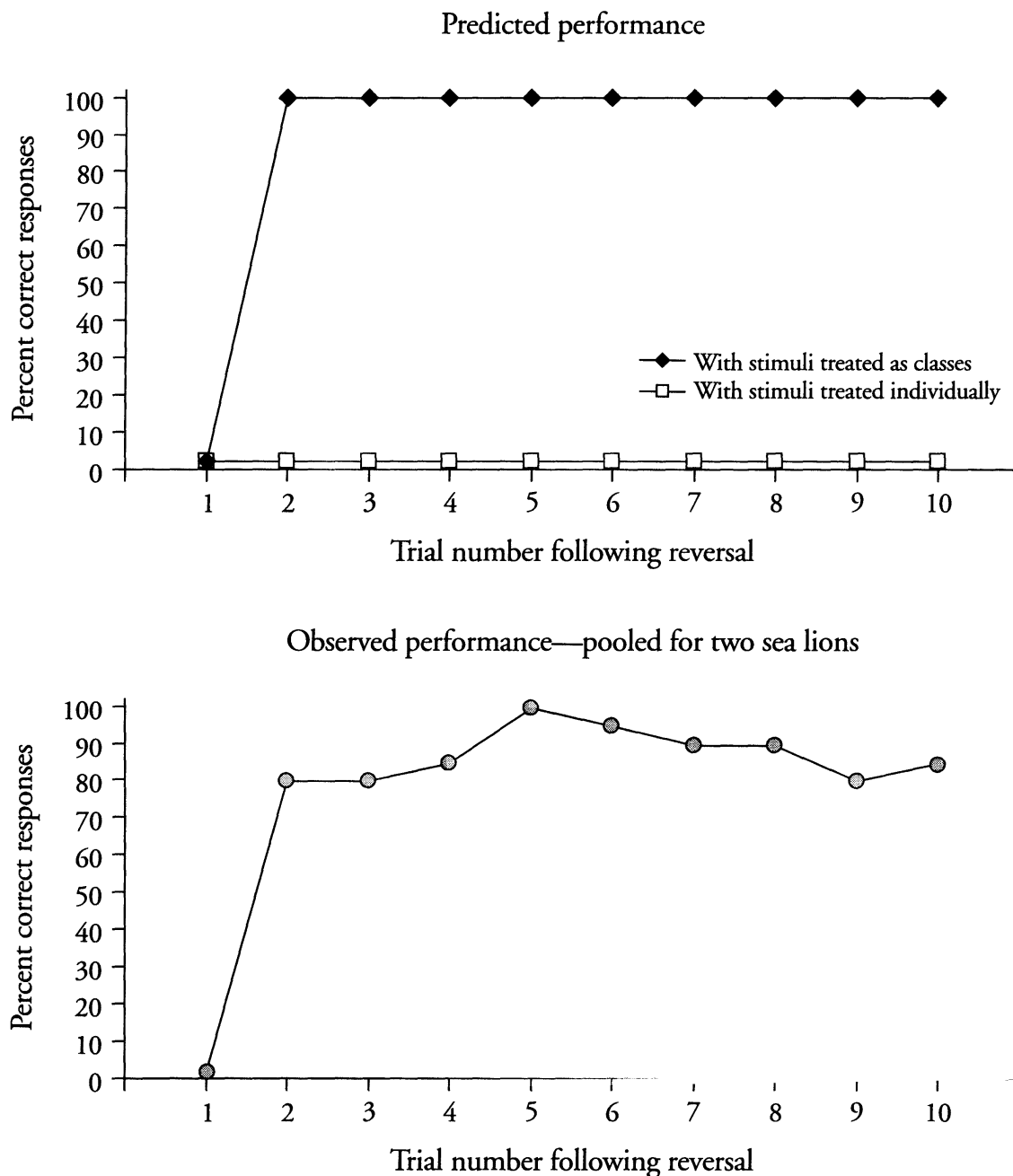


Figure 7.3. Predicted and observed performance showing equivalence classes emerging within a repeated reversal experiment. Two sea lions were trained with 20 dissimilar stimuli divided into two sets of 10. Two-choice simple discrimination trials were presented with one stimulus from each set, with stimuli from the same set always reinforced as correct choices. Following acquisition of responses to one set, reinforcement contingencies were repeatedly alternated between sets. The upper panel shows predicted performance on the 10 unique trials following a set reversal with subjects treating the stimuli either as individual problems or as members of a class. The lower panel shows the observed performance pooled for two sea lions, which is strikingly consistent with the model based on equivalence classification.

that the sea lions immediately related the letters and numbers into class-consistent conditional discriminations; that is, given three stimuli, the sea lions matched the sample stimulus (either a letter or a number) to the comparison stimulus belonging to the same class. Further, we found that these classes could be expanded through equivalence relations. Once a new stimulus was related to an existing class member, new relationships emerged between the new stimulus and all the other members of the class without further training. In all of these experiments, appropriate within-class responding produced class-specific food reinforcers, that is, correct responses to the letter class were followed by one type of fish reinforcement (herring), whereas correct responses to the number class were followed by an alternate type of fish reinforcement (capelin). These results show that equivalence classes can be readily formed when stimuli are related to the same biological reinforcer. Further, these findings show that the functional classes formed by our sea lions were the same as equivalence classes. Whether this result would be obtained with pigeons remains to be determined.

Although the majority of laboratory experiments investigating abstract classification in animals have not been conducted with an equivalence model in mind, the results of many of these studies also describe new relationships emerging from directly trained relationships (see Zentall 1998 for a partial review). These studies include operant procedures and classical conditioning paradigms, as well as complex categorical problem-solving tasks (see, e.g., Savage-Rumbaugh et al. 1980; Wasserman et al. 1992). The sum of what we presently know about relational learning in a range of animals leads us to believe that relational learning abilities are not unique to any single animal taxa studied in experimental contexts. Whether this ability extends to more natural and complex social situations is the central theme explored in this paper.

Equivalence and Contextual Control

Even the expanded model of equivalence, which includes relations based on function, responses, and reinforcers, may not, at first glance, appear to account for the flexibility with which some animals classify stimuli in their environment. To facilitate an understanding of how equivalence applies to complex behaviors seen in the field, in this section we introduce the ideas of contextual control and behavioral contingencies, which are important in determining equivalence class membership under a variety of conditions.

According to the mathematical definition, an equivalence relation satisfies

the properties of reflexivity, transitivity, and symmetry. As described earlier, this definition is restrictive in both a theoretical and an experimental sense. However, Sidman more succinctly described an equivalence relation as “defined by the emergence of new—and predictable—analytic units of behavior from previously demonstrated units” (1994, pp. 387–388). Thus, after training $A \rightarrow B$ and $B \rightarrow C$, the relation $C \rightarrow A$ emerges without training. This may also occur when members of a potential class share a common reinforcement history, temporal or spatial contiguity, or a common response. The colloquial definition of the word “equivalence” is similarly restrictive. In lay terminology, equivalence implies that members of a class are the same, or at least treated as such. Such misunderstandings likely stem from the idea of mutual substitutability or interchangeability and can lead to confusion of equivalence with failure to discriminate. This type of confusion has resulted in only limited acceptance of equivalence as a useful model for describing social relations (Connor et al. 2001; Seyfarth & Cheney in press).

Ideas regarding applications of equivalence in a social setting would be nearly useless if not for contextual control, which allows the content of an equivalence class to change based on context, or the environmental conditions that share some spatial, temporal, or situational contingency with the class members themselves. For example, in one context, a hammer and a screwdriver might be members of the class “tools,” defined by a common general function. These tools might also be related by spatial contiguity (e.g., they occupy the same drawer in a toolbox), or shared association with a third stimulus (e.g., they were manufactured by the same company). However, in a new context, based on specific function, these two tools occupy different classes (i.e., one is used to drive nails, the other is used to turn screws). Thus, the idea of contextual control allows equivalence classes to be both flexible (class membership can change based on context) and hierarchical (stimuli can belong to more than one class at the same time).

In operant terminology, the equivalence relation and contextual control can be exemplified by a four-term behavioral contingency, conditional stimulus—discriminative stimulus—response—reinforcer (see Sidman 2000 for a review of the relation between four-term contingencies and equivalence relations). The three-term part of the contingency (discriminative stimulus—response—reinforcer) describes generally understood operant behavior in which the discriminative stimulus sets the occasion for a particular response, which is then reinforced. The response is strengthened, but only in the presence of the appropriate discriminative stimulus. The four-term contingency

adds contextual control to the three-term contingency in the form of the conditional stimulus. In the presence of one conditional stimulus, a given discriminative stimulus occasions the appropriate response. In the presence of a second conditional stimulus, a different discriminative stimulus becomes relevant, and thus a different response is reinforced. In every case, the conditional and discriminative stimuli, appropriate response, and contingent reinforcer become members of a class, and the defining equivalence relation includes each stimulus pair as well as each pairing of stimulus and reinforcer.

Connor and colleagues (1999; Case Study 4B) have described the formation of super-alliances and shifting alliance partners in bottlenose dolphins. A hypothetical example of a four-term contingency inspired by this observation of alliance formation is shown in Figure 7.4. In this example, a male dolphin chooses alliance partners based on their usefulness in helping to obtain access to two types of resources: food and ovulating females. The presence of either food or ovulating females determines the salience of one group of male dolphins or another. If ovulating females are present (conditional

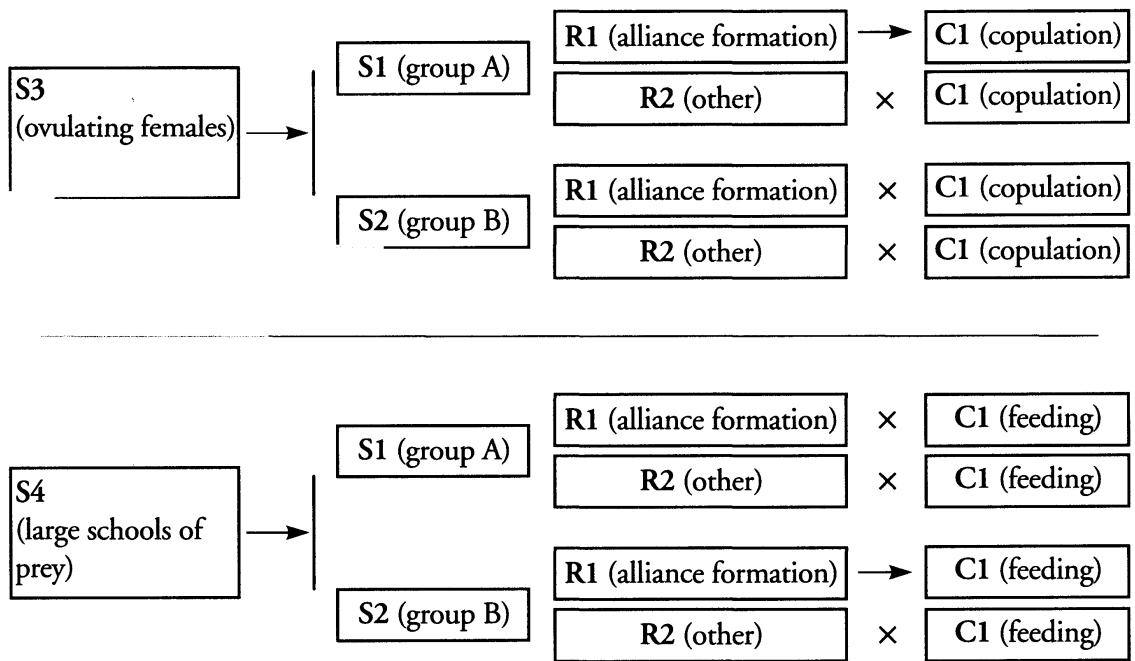


Figure 7.4. Four-term behavioral contingencies as applied to Connor et al.'s (1999) descriptions of alliance formation in bottlenose dolphins. The presence of a conditional stimulus, related to a given discriminative stimulus, occasions an appropriate response that leads to a specific reinforcing consequence. In each of the two cases depicted, the conditional and discriminative stimuli, appropriate response, and contingent reinforcer become members of an equivalence class.

stimulus 1), the male may form an alliance (response 1) with the first group (discriminative stimulus 1), leading to copulation (reinforcer 1). If schools of prey are present (conditional stimulus 2), the male may form an alliance (response 1) with the second group (discriminative stimulus 2), leading to successful foraging (reinforcer 2). Other factors, specifically the motivational state of the male dolphin, will enter the contingency as additional conditional cues and determine which stimuli and responses are appropriate for a particular context. When the concept of conditional control is considered, equivalence becomes a powerful and flexible paradigm within which a variety of very complex social relations in animals may be studied. Further, if an understanding of ordinal rank in social settings is superimposed as an additional contextual control, hierarchical preferences of association can emerge, dramatically increasing the number of pairwise or dyadic relations possible. As discussed earlier, sea lions and monkeys readily understand ordinal position in laboratory tasks, suggesting that they can form concepts of rank relations among individuals in social settings. These concepts allow an understanding of where another animal fits in with respect to all other members of the group.

Another criticism of the equivalence model is that it fails to account for "learning without reinforcement" (Seyfarth & Cheney in press). This criticism appears especially valid given the incorporation of behavioral units into the definition of equivalence, and Sidman's position that "The establishment of equivalence relations is, then, one of the outcomes of reinforcement contingencies" (1994, p. 387). Thus, distinctions between behaviors demonstrated in the laboratory, under controlled conditions of food reinforcement, and those that occur in the field, with no observable or explicit reinforcement, seem to be valid. However, this argument is countered by the examples of classical conditioning leading to emergent relations that satisfy the revised definition of equivalence (reviewed in Zentall 1998). Classical conditioning establishes associations between biologically neutral events and biologically significant events. Consider a vervet monkey observing an unknown, unrelated monkey who is grooming a third monkey, with whom the first monkey has recently had an aggressive encounter. The spatiotemporal contiguity of the unknown monkey, the known enemy, and the aversion, aggression, or stress response of the first may be sufficient to condition a similar response to the unknown monkey in the absence of explicit reinforcement. Thus, equivalence classification readily explains how relations between many pairs of individuals can be learned and remembered.

Experiments with humans and nonhuman animals, and theoretical treatments of equivalence (e.g., Sidman 2000) have spawned novel ideas resulting in a broader view of what equivalence classification means. As equivalence theory continues to develop, the reinterpretation of previous laboratory and field studies and the design of future experiments will likely generate a more parsimonious approach to a wide array of behavioral phenomena, including complex social behavior by nonhuman animals.

Approaches to the Study of Social Knowledge

The model of equivalence relations was developed to better understand a variety of behavioral phenomena, including 1) how symbols acquire meaning, 2) how novel behavior occurs in the absence of explicit reinforcement, and 3) how an individual classifies perceptually dissimilar items into the same category. We have applied the model of equivalence in order to better understand how animals living in social groups may benefit by forming categories, which include not only recognizable individuals but also relationships between individuals.

Primatologists have often observed that the behavior of individual animals may be influenced by the behavior of other individuals with whom they have previously associated; these interactions can be further influenced by the participants' mutual interactions with other individuals. For example, individuals may be more likely to interact positively with their siblings, in part because of their previous positive interactions and in part through their mutual interactions with their mothers. More complicated cases of social knowledge occur when the information acquired by an individual is gained through observations of others interacting, rather than by direct interactions. Thus, the attitudes and behaviors of animal A in relation to animals B, C, or D may be affected by A's observation and evaluation of the interactions and outcomes involving B and C, B and D, C and D, and so on. This type of social knowledge, which requires an animal to observe, classify, and evaluate interactions between other recognizable individuals, has been termed "triadic awareness" by de Waal (1982; Chapter 9), "non-egocentric social knowledge" by Cheney and Seyfarth (1990; see also Chapter 8), and "knowledge of third party relationships" by Tomasello and Call (1997). The latter investigators have hypothesized that this is an exclusive ability of simian primates (Tomasello & Call 1997; Tomasello 2000).

The ability of primates to perceive triadic relationships among classes or

groups of conspecifics was first noted in the 1950s by Japanese primatologists and European ethologists. For example, Kawai (1958) observed that a juvenile Japanese macaque might be aggressed against by nonrelatives when it was alone, but that such behavior was rarely observed when its mother, who was dominant to the aggressive individuals, was present. However, the presence of other dominant adults near the juvenile did not have the same inhibiting effect. Kawai concluded that the potential aggressors recognized that only the dominant mother, and not the dominant nonrelatives, would protect the juvenile offspring. Similarly, Kummer (1967) observed that hamadryas baboons displayed knowledge about third-party relationships in the context of dominance interactions. He describes a situation in which a male is dominant to two females, A and B. Female A threatens female B, blocking the latter's access to the male while she simultaneously appeases the male by sex presenting. Female A then keeps herself between the male and female B, so that any return threat by B would also be directed toward the male. According to Kummer, this demonstration of a triangular or tripartite relationship, or what he also terms the "tactic of protected threatening" (1995, p. 41), indicates that the threatening female evaluates the relative ranks of the individual that is threatening as well as the one that she is soliciting. Further, experimental evidence shows that an adult male hamadryas baboon will not challenge a rival male for access to a female if he has previously observed the rival interacting positively with the female (e.g., in a grooming interaction), but this same male will frequently fight the rival male if he has not seen them together (Bachman & Kummer 1980). This suggests that the male's decision to engage his rival in an aggressive encounter is based on his evaluation of the strength of the social bond between the rival and the female.

Tomasello and Call (1997) list a number of complex interactions showing that different primates have an understanding of third-party social relationships. One of these interactions was originally described by Cheney and Seyfarth (1986, 1989) as "complex redirected aggression." An individual from one kin group witnesses a member of its matriline in an aggressive encounter with an individual from another matriline. After observing this encounter, the focal animal is likely to act aggressively toward a relative of its kin's opponent. Not only did Cheney and Seyfarth (1989) find that relatives of two opponents were significantly more likely to display aggression toward each other following a fight than during a matched control period, but they also noted that the vervet monkeys reconciled following fights, not only with their former opponents, but with the kin of their former opponents as well.

Cheney and Seyfarth (1999) documented similar trends in aggressive behavior from free-ranging baboons that “observed” fights between relatives and control subjects by listening to sequences of prerecorded calls that simulated aggressive interactions. Thus, these field observations suggest that members of a kin group, or even more generally perhaps, the members of a nongenetic alliance (see Connor et al. 2001), recognize others as equivalent members of the same category (friends) or not (foes) as hypothesized by Schusterman and colleagues (2000). This hypothesis suggests that equivalence classification constitutes a general learning process that is the basis of the coding of social relationships in many species. In this manner, an animal may learn to combine individuals of the same matriline because they have a common history of shared spatiotemporal interactions and functional relations. These equivalence judgments may be made on the basis of one’s direct past interactions with other individuals or by observing the social encounters of others. Thus, when an individual reconciles after a fight, not with a former opponent, but with the kin of a former opponent, it does so because members of the same matrilineal group or alliance have become functionally interchangeable.

Recently, Seyfarth and Cheney (in press; Chapter 8) have proposed that the social knowledge of monkeys and baboons is more complex and hierarchically structured than either conventional associative theories of learning or our current version of equivalence theory can account for. Rather, Seyfarth and Cheney propose that simian primates organize information about their social companions into two-level nested hierarchies based on matrilineal kinship and rank; they emphasize important contextual or evaluative aspects of social knowledge, a point also made by de Waal (1982). It is important to note that the presence of nested hierarchies does not preclude an analysis based on the equivalence model. In this paper and elsewhere (Schusterman & Kastak in press) we have shown how context and the affective state of the perceiver can control equivalence classification. Unlike the many descriptive behavioral terms discussed in this section, this mechanism can explain how animals form flexible categories as reflected in complex social behavior.

Social Knowledge in Sea Lions

As reviewed earlier, the best evidence of equivalence classification in the laboratory comes not from simian primates but from sea lions. Sea lions are pinnipeds, a group of flipper-footed mammals that give birth on land or ice

and forage at sea. They comprise three taxonomic families derived from a bear-like ancestor: the true seals, or phocids (for example, elephant seals and harbor seals), the eared seals, or otariids (fur seals and sea lions), and the odobenids (walruses). In contrast to both simian primates and fully aquatic dolphins, the pinnipeds are smaller-brained, shorter-lived, and show less complex social and coordinated behaviors. Nevertheless, there is good observational evidence showing that most if not all pinnipeds are capable of using social knowledge in ways that are somewhat comparable to highly social taxa such as simian primates, cetaceans, and terrestrial carnivores.

Our laboratory experiments with sea lions suggest that their cognitive skills allow them to organize streams of sensory input from several modalities into categories of meaningfully related items. Similar mechanisms are probably at work when sea lions try to solve social problems in nature.

Sea lions and fur seals, the otariid pinnipeds, are colonial breeders whose social structure is usually characterized by moderate to extreme polygyny with groups of females densely aggregated and with males highly territorial. In contrast to the brief but intense maternal care and attendance in phocids, the maternal behavior of fur seals and sea lions more closely resembles that of terrestrial mammals; that is, female otariids routinely leave their pups to forage at sea during a relatively protracted lactation period in which the pup is not weaned for about 6 to 24 months of age (Reidman 1990). Prior to weaning, females and their pups repeatedly reunite by calling to one another over some distance and then confirming their mutual recognition by visual, olfactory, and tactile cues at short range. Indeed, it is likely that older pups recognize their mothers by voice, smell, gait, posture, and facial expression. Thus, early in the pup's development, it acquires multimodal input and begins forming meaningful representations. These repeated mother-pup reunions undoubtedly play a key role in both parties learning to recognize each other's vocal characteristics at great distances and under a wide variety of environmental and behavioral conditions. Furthermore, females apparently learn about the gradual and subtle changes that must occur during the maturation of their pups' voices. Indeed, Insley (2000) has shown, in playback experiments to northern fur seals on St. Paul Island in Alaska, that despite not interacting with one another for nearly eight months, females and their pups were still responsive to one another's vocal playback. Moreover, Insley tested a few mature females returning four years after weaning and they still remained responsive to the playbacks of their mother's calls, which had been

recorded while they were still pups. This study provides strong evidence that there is the potential for long-term social relationships in otariid pinnipeds.

There is a good deal of other evidence that suggests that there are long-term interactions among related female otariid pinnipeds. Some of this evidence stems from their tendency toward natal philopatry. Although offspring tend to return to the same breeding sites as their parents, there is little known about whether parents and offspring meet and interact throughout their lifetimes. However, given several factors relating to their known social behavior, it seems likely that maternal kin do establish social relationships with one another. These factors include 1) strong site fidelity, 2) very slow and gradual weakening of bonds between mothers and their offspring, 3) the overlap in maternal care sometimes observed between offspring born in successive years, 4) the fact that many otariids remain at their breeding grounds the majority of the year or even all year, and 5) observational and experimental evidence showing individual recognition (for reviews see Trillmich 1996; Insley 2001).

Two additional pieces of evidence collected in captive settings provide further support for the idea that these pinnipeds may establish long-term social bonds. With respect to the bonds between mothers and their pups, experimental demonstrations of filial imprinting with captive sea lion pups show that sea lions form strong attachments to human surrogate mothers that last for three or more years, well beyond weaning (Schusterman et al. 1992a,b). In terms of relationships with other maternal kin, observations of association patterns within a colony of captive California sea lions showed females interacting affiliatively with their kin and more aggressively with nonrelatives (Hanggi & Schusterman 1990). These relationships lasted over several years and involved mature breeding daughters associating preferentially with their mothers and each other. On the basis of these findings with California sea lions, Trillmich (1996) suggests that interactions between matrilineal kin may be a major factor influencing the social organization of these animals in the field. Mature daughters, for example, may potentially benefit from their interactions with their mothers. Such interactions may provide them with some degree of protection as they rear their young. Indeed, in an often overlooked study, Sandegren (1970) reports that on Lewis Island, Alaska, some Steller sea lion females maintain a social bond with their subadult offspring that is just as strong as the bonds they form with their newborn pups. He also reports that despite aggressive competition for preferred nursing sites,

some females with their own pups are extremely affiliative toward other females with young pups. Are these adult individuals from the same matriline? If so, then perhaps pinnipeds aggregating in a particular site may be more closely related than expected by chance. Given this possibility, female social relationships and the role of female mate choice may be far more important in structuring pinniped sociality than had hitherto been realized (Trillmich 1996).

There is also increasing evidence that males, like females, have long-term social interactions spanning three or more years. For example, it has been found that the most reproductively successful Steller sea lion males were those that had at least three seasons of experience maintaining the same territorial site and interacting with many of the same neighboring opponents (Gisiner 1985). The classifying of rivals into "familiar" and "novel" groups appears critical to the success of experienced territorial males. Such males do not waste energy interacting aggressively with familiar rivals, but these established males will aggress against newcomers with alacrity and authority. The "dear enemy" effect in the context of habituation is not sufficient to account for these patterns of aggression because the decrease in aggressive sensitivity toward a territorial neighbor persists over successive breeding seasons without any apparent recovery effects.

Although territorial male otariids may not act in a cohesive and well-coordinated fashion to drive out newcomers, several territorial males will frequently come together where their territorial borders meet and simultaneously attack any rival that is situated at the area of territorial boundary convergence, as shown in Figure 7.5a. During such skirmishes, all males in the vicinity are aroused, and will cross territorial boundaries on their way to the fight (Peterson 1968; Gisiner 1985). These multimale fights (Gentry 1970) frequently gain the attention of females who may be resting nearby (see Figure 7.5b). The motivational mechanism for the convergence of territorial males attacking a newcomer is consistent with the classic idea of social facilitation (Zajonc 1972) and the more recent notion of social enhancement (Galef 1996). In this case, the presence of the original combatants in a particular area may energize or prime nearby territorial males to exhibit similar aggressive behavior toward the intruder. Although observing the fights of neighboring males may spur an observer to join in the aggression, male observers sometimes seem to simply monitor the outcomes of these interactions. Following their observation of a rival in combat, Steller sea lions are more likely to attack while their territorial rival is still fatigued. In this way,

experienced territorial males may capitalize on “windows of opportunity” by initiating fights when they have the greatest chance of success (Gisiner 1985).

During the breeding season of California sea lions, nonterritorial subadult males also exhibit behaviors indicating that they are sensitive to how their own aggressive actions might affect a territorial bull (R. Schusterman, personal observation). For example, if a sexually motivated subadult moves alone through a territory, he will invariably move stealthily and silently; sometimes the young male will even hide behind a boulder, looking out in the direction of the resident male in a very surreptitious fashion. Once the resident male has been alerted to the presence of the intruder (frequently by the vocalizations of nearby females), the young male, remaining silent, immediately shows submissive behavior toward the bull and usually escapes into the water, and on at least one occasion, into the blind of the observers. Sometimes two or more nonterritorial males will slink through a bull’s territory in a coordinated fashion. Once detected by the bull, they race off together, charging side by side out of the territory (Figure 7.5c). Similar observations of males modulating their behavior in the presence of territorial bulls have been made in captivity (Schusterman & Dawson 1968).

In the context of triadic relations, male sea lions frequently respond to females squabbling on their territories (Eibl-Eibesfeldt 1955; Peterson & Bartholomew 1967; Sandegren 1976; Gisiner 1985). From the standpoint of proximate and ultimate causes, why do they do this? The male invariably intervenes during these female fights by vocalizing and then moving between the females, thereby separating them. Such “pacifying” interventions by these males in the fights of females appear similar, at least superficially, to those observed in chimpanzees, when a third party breaks up a fight by pulling the combatants apart and standing between them to prevent further fighting (de Waal 1982). In chimpanzees, and of course in humans as well, such a tactic is understood to relate to coalition formation and reciprocity (de Waal 1992). However, in the case of male sea lions intervening in female fights on their territories, the motivation for the behavior can be described in a different way. The proximal cause of the bulls’ intervention behavior likely depends on loud female vocalizations that capture the attention of the sexually motivated male and direct his behavior to the female interactions. The ultimate cause of the male interventions is most likely related to factors involved in reproductive success. Gisiner (1985) suggests that breaking up female fights puts males into contact with pre-estrous females more often than random ol-

a.



b.





Figure 7.5. Territorial male California sea lions driving out newcomers. *a)* Two males converge upon their territorial boundaries to simultaneously bark at and bite an intruder (*far right*) who had entered the rookery a bit earlier. *b)* One of the territorial males (*left*), in the act of attacking the newcomer (*right*), is in a “dominance” posture; the newcomer is displaying a submissive posture and facial display and is sidling away to retreat from his adversary. Neither sea lion is vocalizing and the females in the background are observing the fight. *c)* A territorial male discovers that two subadult males have entered his territory; he begins barking and the two young males gallop away without producing any vocalizations. Note the resting females on the male’s territory.

factory inspection of females normally would. This finding is further supported by Gisiner’s data showing that, in one year at Año Nuevo Island, California, male intervention in female fighting preceded nearly a third of 61 copulations observed. Clearly, the intervention behavior of sea lions, unlike that of chimpanzees, has little to do with peacemaking per se. Instead, this behavior appears related to the fact that sexually motivated males are sensitive and hyper-vigilant to female aggressive behaviors that are correlated with sexual receptivity. If this is true, and social cognition plays a role, then one might expect to find that more experienced territorial males might show more intervention behavior than less experienced territorial males. However, it is as yet unknown if this is the case.

The question arises as to whether male otariids, like nonhuman primates, dolphins, and some terrestrial carnivores, form coalitions during the breed-

ing season in order to increase their reproductive success. Campa \tilde{n} a and colleagues (1988) observed that subadult male Southern sea lions come together in groups to make what has been termed "group raids" on breeding areas containing resident territorial males and aggregations of females and pups in order to secure females for copulation. Although these raids are frequent and sometimes successful, Campa \tilde{n} a and colleagues suggest that, rather than being coordinated activity among group members, the apparent synchrony of the raiding group is due to social facilitation among sexually motivated males. However, the fact that the composition of these raiding parties is frequently similar suggests that there is some degree of durable relationships within the group.

Like males, female sea lions rely on their experiences and observations to categorize individuals in their environment. Sexually mature females appear to divide males into one of two groups: experienced and familiar males, or inexperienced and novel males. Both Steller sea lion and California sea lion females, while avoiding territorial sites occupied by males in their first or second year of tenure, tend to approach and copulate on similar territorial sites that have been occupied by the same male for three or more seasons (Gisiner 1985; Heath 1989). Thus, the reproductive success of males and mate choice by females likely depends on learning to recognize individuals and on placing those individuals into meaningful categories or groups.

Although these observations of sea lions fall short of the myriad of complex behaviors produced by nonhuman primates and dolphins, they do suggest a level of social complexity that depends on monitoring and categorizing their own relationships with others. At this time, it is unclear whether these cognitive processes extend to interactions that sea lions observe occurring between other individuals. However, it is important to note that the social behavior and social complexity of otariid pinnipeds has not as yet been investigated to the same extent as that of larger-brained, longer-lived species.

Social Knowledge in Other Animals

Alarm and Food Calling

As we pointed out earlier, there is a growing body of evidence suggesting that nonhuman primates, marine and terrestrial mammals, and birds are capable of equivalence classification in natural as well as laboratory settings. Since the original laboratory experiments on mediated generalization and equivalence

were spurred by attempts to analyze symbolic meaning in humans, it is not surprising that when animal language research peaked in the late 1970s and early 1980s there were numerous examples suggestive of equivalence formation. The evidence came from studies in which great apes and parrots were taught to label things symbolically, either with gestures, icons of various types, or vocally (for reviews see Pepperberg 1986; Schusterman & Kastak 1993; Dube et al. 1993; Cerutti & Rumbaugh 1993; Sidman 1994). Similarly, there have been classic field studies analyzing the symbolic nature of the alarm calls responded to by vervet monkeys (see Cheney & Seyfarth 1990 for a review). These studies showed that individual monkeys respond to acoustically discriminative calls with different types of anti-predator responses, even when the predator is not visually present. As the upper panel of Figure 7.6 indicates, the monkeys that perceive these calls place the structurally different alarm vocalizations of conspecifics and extraspecifics into the same category of predator. Thus, the meaning of a neighbor's call to a predator bird and a starling's call to a raptor are the same; in other words, the calls, although structurally different, are functionally equivalent. The critical evidence that the vervet monkeys are responding to the symbolic meaning or common referent of the alarm calls and not to the emotional intensity or other structural characteristics of the sound comes from playback experiments. For example, a monkey that has habituated to the playback of an alarm call dishabituates only when the meaning of the call is changed and not when the structure of the alarm call is changed (Cheney & Seyfarth 1990).

Recently, Zuberbühler's (2000a,b; Case Study 13A) research with Diana monkeys can be closely compared to that just described for vervet monkeys. This study is particularly interesting from the standpoint of applying the equivalence model to social knowledge because it brings into play the idea that categories are subject to contextual control, that is, the composition of a class can shift with the motivational or emotional state of the individual doing the classifying. As shown in the lower panel of Figure 7.6, Diana monkeys learn to classify at least five different events into a "leopard" equivalence class. Two of these events include alarm calls, "SOS" screams, and "waa" barks given by chimpanzees, which are also subjected to leopard predation. Thus, in one context, that of defense against predation by leopards, Diana monkeys respond to chimpanzee calls with conspicuous alarm-calling behavior that functions to warn conspecifics and to signal the leopard predator that it has been detected. On the other hand, chimpanzees also prey on Di-

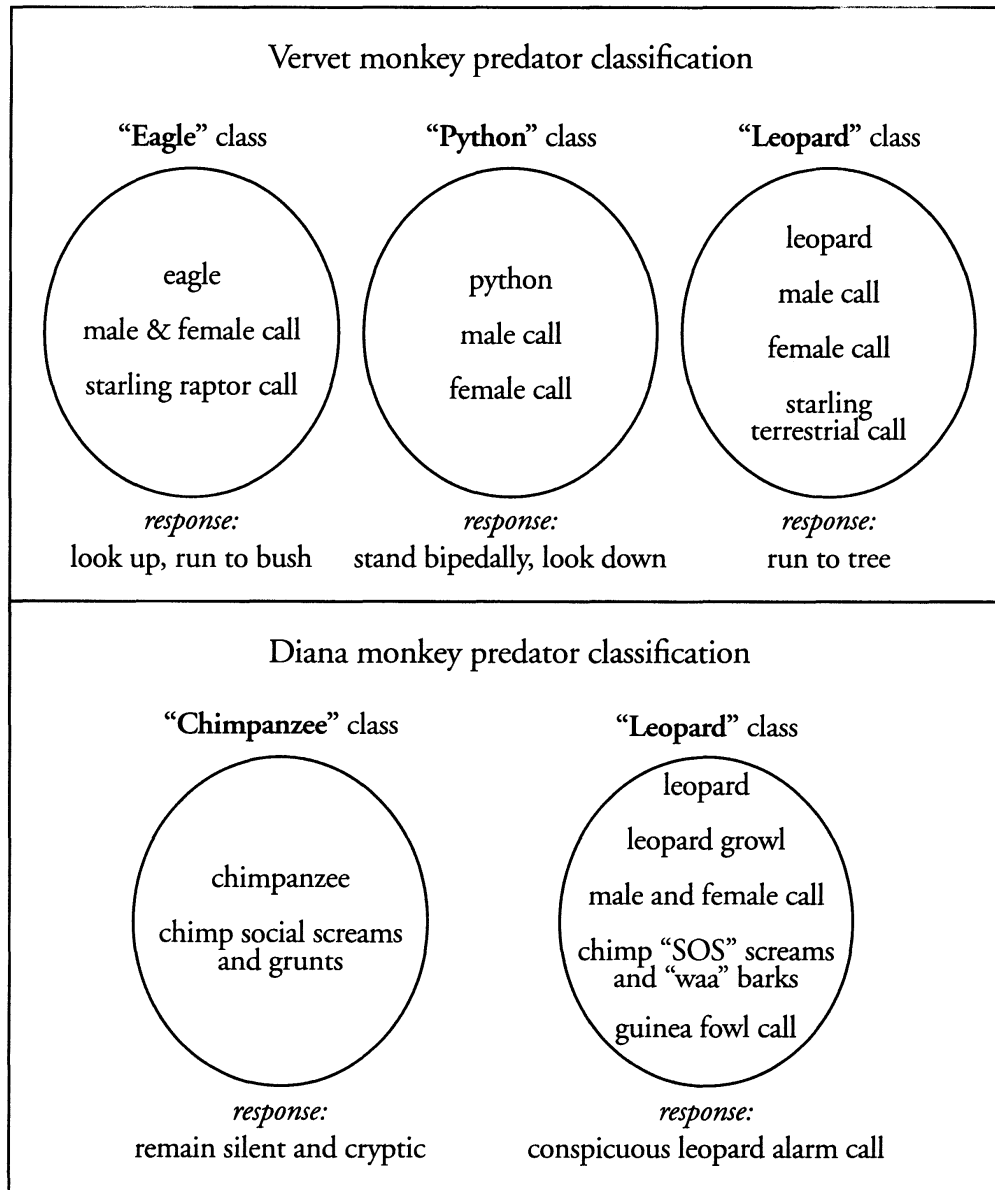


Figure 7.6. Examples showing the cues and alarm calls representing the same predator and eliciting the same behavioral response in vervet monkeys (*upper panel*) and Diana monkeys (*lower panel*). It is likely that the cues comprising each predator class and their associated response are related by equivalence.

ana monkeys. In the context of defense against predation by chimpanzees, two other chimpanzee vocalizations, social screams and grunts, receive a response from the Diana monkeys as an equivalence class; upon hearing the social calls of chimpanzees, the monkeys respond cryptically rather than conspicuously. Alarm call playback experiments involving vervet monkeys and Diana monkeys show how dissimilar events can take on the same meaning

and elicit a similar, appropriate, and context-dependent response. Thus, in a manner similar to the linguistic performance described earlier, in which a boy connects a printed word with a corresponding object on the basis of their mutual relationship with a spoken word (the nodal link), the monkeys connect conspecific alarm calls and extraspecific calls to the sound and sight of a predator (the nodal link).

Playback experiments in the field dealing with food calling in rhesus monkeys in Cayo Santiago, Panama, are comparable to those just described concerning alarm calling in other simian primates. Briefly, Hauser (1998), by means of habituation experiments, found that rhesus monkeys place three distinctive calls (warbles, harmonic arches, and chirps) into the class “high quality, rare food” and two other distinctive calls (coos and grunts) into the “low quality, common food” class. Hauser found that his monkeys responded to the meaning of the food calls rather than the structure of the individual calls, and therefore the calls within each class were interchangeable in terms of function.

Mothers and Their Offspring

The most basic experimental observation of triadic relationships in simian primates is one in which the scream of a juvenile vervet monkey is played through a concealed speaker to a group of females; the typical result is that the control females immediately look to the mother of the juvenile, sometimes before she reacts to the cry of her offspring (Cheney & Seyfarth 1980). Thus, the adult female monkey formed an equivalence class comprising the *juvenile*, its *scream*, and its *mother*. Although some primatologists view this behavior as “uniquely primate” in nature (Tomasello & Call 1997) the scant experimental evidence from similar playback experiments conducted with nonprimate species has generated conflicting findings. In a rarely cited study, Porter (1979) observed that when the cries of an infant leaf-nosed bat were played back to its creche, harem males and some neighbor males behaved as if they recognized the relation between the *infant*, its *cries*, and its *mother*. Upon hearing the playback of an infant’s cries, harem males frequently crawled directly to the mother of that particular infant and pestered her until she reacted to the voice of her offspring by flying to the speaker. Conversely, in a field playback experiment with spotted hyenas, Holekamp and colleagues (1999) found that whereas hyena mothers were likely to orient to-

ward the speaker from which the “whoop” calls of their pups was being played, control females were no more likely to look to the mother than to any other control females.

Coalitions

Undoubtedly, the best example of complex social behavior in animals comes from Jane Goodall's (1986) observations of male common chimpanzees involved in territorial wars in Gombe Stream National Park in Tanzania (Goodall 1986). Over a period of many years, she and her colleagues observed the development of two large male cohesive groups, one from the Kasekela community and one from the Kahama community. These groups had strong identities that were cemented through mutually reinforcing events such as reciprocal grooming, food sharing, and reconciliation behavior. Aggressive interactions between the two groups escalated over time, and resulted in violent behavior being directed by the stronger Kasekela community toward the weaker Kahama community. This violent behavior was directed not only toward the individual males allied with the Kahama community, but also toward the females and offspring associated with them, and even their abandoned nests. The end result of these “chimpanzee wars” was the extermination of every male individual in the Kahama community (see Figure 7.7).

Goodall's observations suggest that the members of these groups, whose internal relationships were unequal with respect to dominance, age, status, kin relatedness, and friendships, were able to reconcile their individual differences within the context of a broader category, that is, their community identity. Thus, although each group was composed of very different individuals, the members of each group were virtually interchangeable with respect to their aggressive attitudes toward their adversaries. An equivalence model explains why empty nests were viciously attacked as if they were the members of the opposing group, as well as why females and infants were attacked during patrols. Additionally, this model explains why the patrolling Kasekela males hunted down *any* individual belonging to the Kahama group, suggesting that the “search image” of the Kasekela males was for the Kahama group as a category and not for the individual males being hunted. This view is supported by the fact that the killing of Kahama males continued well past the point of any reasonable retaliation. Sniff, the last Kahama male killed, posed little threat to the coalition of eight aggressive Kasekela males; al-

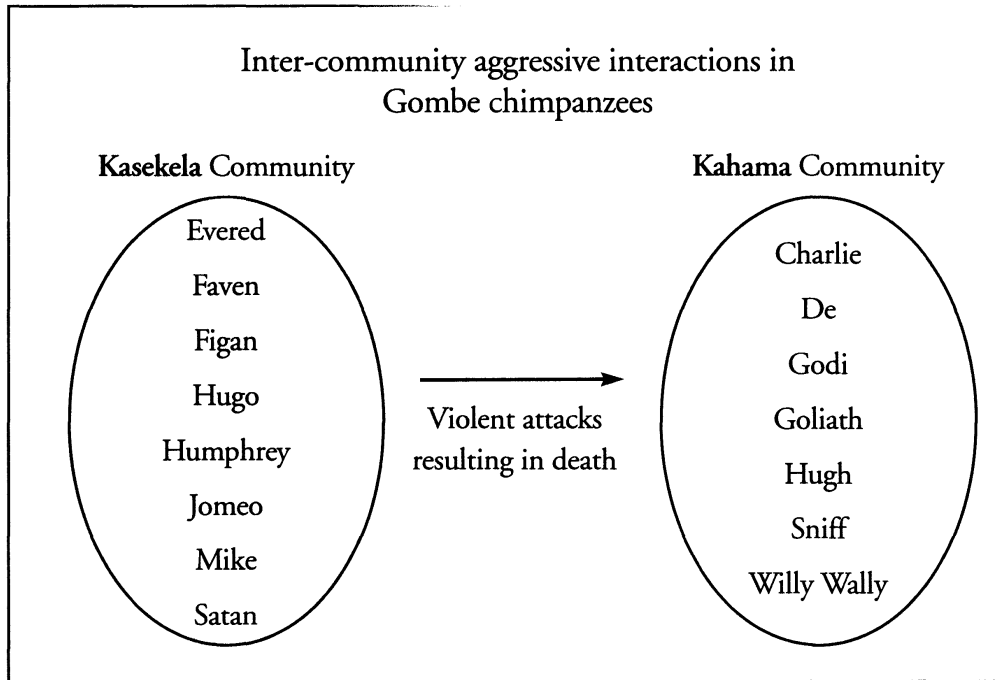


Figure 7.7. Schematic depiction of inter-community aggression between groups of male chimpanzees observed by Goodall (1986). There is a strong sense of identity within each of the communities and individuals clearly distinguish between those who “belong” to their group and those who do not. Before the division of the Gombe chimpanzees into two communities, the members of the Kahama community had enjoyed close and friendly relations with members of the Kasekela community. Once the Kahama community formed, however, the individuals in the Kasekela community no longer treated them like group members; rather they treated the Kahama males like prey animals, who were systematically hunted and killed.

though he had played with many of the Kasekela males as a youngster, he was nonetheless killed, presumably on the basis of his former association with the Kahama group.

Conclusions

There is a growing body of evidence indicating that many avian and mammalian species maintain some degree of group stability and individual recognition. These characteristics likely result in individuals forming such simple social categories as “friend” and “foe” (Schusterman et al. 2000). Behavioral interactions in the context of kinship, dominance, friendship, coalition formation, mate choice, and referential alarm calling may reveal even greater social complexity. What are the learning skills that allow an animal to organize

social and communicative information into meaningful categories? Laboratory studies suggest these skills depend on a type of relational learning that has been specifically presented here in the framework of equivalence relations.

Whereas some primatologists (Tomasello & Call 1997; Tomasello 2000) have hypothesized that relational learning is a cognitive skill restricted to primates, there is a good deal of experimental evidence showing that marine mammals such as California sea lions and bottlenose dolphins can also understand categories of object relationships (for a review see Schusterman & Kastak in press). Do these laboratory studies on physical cognition, in which sea lions, dolphins, and simians clearly show an understanding of categories of object relations, hold true for their understanding and use of categories of social relations? Based on our current understanding of social knowledge in these animals, the answer is a very definite yes for simians and probably yes for dolphins. The answer is much more problematic for sea lions and fur seals. Although species may possess comparable cognitive abilities as demonstrated in the laboratory, these physical cognitive skills may not be evident in their behavior in social settings; rather, these skills may be more obviously expressed in ecological contexts such as foraging. The extent to which individuals acquire an understanding of social relationships, and the extent to which they act on that knowledge, appears to be more strongly correlated with degree of sociality. Nevertheless, a model of equivalence relations provides a behavioral learning mechanism that is basic to the formation of flexible categories when an animal's social environment requires referential communication and dyadic or triadic relationships. These same relational skills likely extend to other contexts. No other current approaches to animal social knowledge that we know of provide an alternative process capable of explaining these behavioral phenomena.

whales and their constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology*, 29:385–389.

7. Equivalence Classification as an Approach to Social Knowledge

- Bachman, C. & Kummer, H. 1980. Male assessment of female choice in hamadryas baboons. *Behavioural Ecology and Sociobiology*, 6:315–321.
- Campaña, C., Le Boeuf, B. J. & Cappozzo, H. L. 1988. Group raids: a mating strategy of male southern sea lions. *Behaviour*, 105:224–249.
- Carr, D., Wilkinson, K. M., Blackman, D. & McIlvane, W. J. 2000. Equivalence classes in individuals with minimal verbal repertoires. *Journal of the Experimental Analysis of Behavior*, 74:101–114.
- Carter, D. E. & Werner, T. J. 1978. Complex learning and information processing by pigeons: a critical analysis. *Journal of the Experimental Analysis of Behavior*, 29:565–601.
- Chen, S. F., Swartz, K. B., & Terrace, H. S. 1997. Knowledge of the ordinal position of list items in rhesus monkeys. *Psychological Science*, 8:80–86.
- Cheney, D. L., & Seyfarth, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, 28:362–367.
- 1986. The recognition of social alliances among vervet monkeys. *Animal Behaviour*, 34:1722–1731.
- 1989. Reconciliation and redirected aggression in vervet monkeys, *Cercopithecus aethiops*. *Behaviour*, 110:258–275.
- 1990. *How Monkeys See the World: Inside the Mind of Another Species*. Chicago: University of Chicago Press.
- 1999. Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*, 58:67–75.
- Connor, R. C., Heithaus, R. M. & Barre, L. M. 1999. Superalliance of bottlenose dolphins. *Nature*, 371:571–572.
- 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance.' *Proceedings of the Royal Society of London*, ser. B, 268:263–267.
- D'Amato, M., Salman, D. P., Loukas, E. & Tomie, A. 1985. Symmetry and transitivity of conditional relations in monkeys (*Cebus apella*) and pigeons (*Columba livia*). *Journal of the Experimental Analysis of Behavior*, 44:35–47.
- de Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex among Apes*. London: Jonathan Cape.
- 1992. Coalitions as part of reciprocal relations in the Arnhem chimpanzee colony. In *Coalitions and Alliances in Humans and Other Animals*, ed. A. H. Harcourt & F. B. M. de Waal, pp. 233–257. Albany, NY: SUNY Press.
- Dube, W. V., McIlvane, W. J., Callahan, T. D. & Stoddard, L. T. 1993. The search

- for stimulus equivalence in nonverbal organisms. *Psychological Record*, 43:761–778.
- Eibl-Eibesfeldt, I. 1955. Ethologische studien am Galapagos-seelöwen, *Zalophus wollebaeki* Sivertson. *Zeitschrift für Tierpsychologie*, 12:286–303. (English translation on file at Marine Mammal Biological Laboratory, Seattle.)
- Galef, B. G., Jr. 1996. Social enhancement of food preferences in Norway rats: a brief review. In *Social Learning in Animals: The Roots of Culture*, ed. C. M. Heyes & B. G. Galef Jr., eds., pp. 49–64. New York: Academic Press.
- Gentry, R. L. 1970. Social behavior of the Steller sea lion. Ph.D. thesis, University of California, Santa Cruz.
- Gisiner, R. C. 1985. Male territoriality and reproductive behavior in the Steller sea lion, *Eumetopias jubatus*. Unpublished Ph.D. thesis, University of California, Santa Cruz.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Belknap Press of Harvard University Press.
- Hanggi, E. B. & Schusterman, R. J. 1990. Kin recognition in captive California sea lions (*Zalophus californianus*). *Journal of Comparative Psychology*, 104:368–372.
- Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, 55:1647–1658.
- Heath, C. B. 1989. The behavioral ecology of the California sea lion, *Zalophus californianus*. Unpublished Ph.D. thesis, University of California, Santa Cruz.
- Herman, L. M., Richards, D. G. & Wolz, J. P. 1984. Comprehension of sentences by bottlenosed dolphins. *Cognition*, 16:129–219.
- Herman, L. M., Hovancik, J. R., Gory, J. D. & Bradshaw, G. L. 1989. Generalization of visual matching by a bottlenose dolphin (*Tursiops truncatus*): evidence for invariance of cognitive performance with visual and auditory materials. *Journal of Experimental Psychology: Animal Behavior Processes*, 15:124–136.
- Holekamp, K. E., Boydston, E. E., Szykman, M., Graham, I., Nutt, K. J., Birch, S., Piskiel, A., Singh, M. 1999. Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour*, 58:383–395.
- Horne, P. J. & Lowe, C. F. 1996. On the origins of naming and other symbolic behavior. *Journal of the Experimental Analysis of Behavior*, 65:185–241.
- 1997. Toward a theory of verbal behavior. *Journal of the Experimental Analysis of Behavior*, 68:271–296.
- Insley, S. J. 2001. Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour*, 61:129–137.
- 2000. Long-term vocal recognition in the northern fur seal. *Nature*, 406:404–405.
- Kastak, D. & Schusterman, R. J. 1994. Transfer of visual identity matching-to-sam-

- ple in two California sea lions (*Zalophus californianus*). *Animal Learning and Behavior*, 22:427–435.
- Kawai, M. 1958. On the system of social ranks in a natural group of Japanese monkeys: basic rank and dependent rank. *Primates*, 1:111–148. (In Japanese with English summary.)
- Kummer, H. 1967. Tripartite relations in hamadryas baboons. In *Social Communication among Primates*, ed. S. A. Altmann, pp. 63–71. Chicago: University of Chicago Press.
- 1995. *In Quest of the Sacred Baboon*. Princeton, NJ: Princeton University Press.
- Oden, D. L., Thompson, R. K. R. & Premack, D. 1988. Spontaneous transfer of matching by infant chimpanzees (*Pan troglodytes*). *Animal Behavior Processes*, 14:140–145.
- Pearce, J. M. 1994. Discrimination and categorization. In *Animal Learning and Cognition*, ed. N. J. Mackintosh, pp. 109–134. San Diego, CA: Academic Press.
- Pepperberg, I. M. 1986. Acquisition of anomalous communicatory systems: implications for studies on interspecies communication. In *Dolphin Cognition and Behavior: A Comparative Approach*, ed. R. J. Schusterman, J. A. Thomas, & F. G. Wood, pp. 289–302. Hillsdale, NJ: Erlbaum.
- Peterson, R. S. 1968. Social behavior in pinnipeds. In *The Behavior and Physiology of Pinnipeds*, ed. R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, & R. J. Schusterman, pp. 3–53. New York: Appleton-Century-Crofts.
- Peterson, R. S. & Bartholomew, G. A. 1967. The natural history and behavior of the California sea lion. *American Society of Mammalogists*, Special publication no. 1.
- Porter, F. L. 1979. Social behavior in the leaf-nosed bat *Carollia perspicillata* II: Social communication. *Zeitschrift für Tierpsychologie*, 50:1–8.
- Reichmuth Kastak, C., Schusterman, R. J. & Kastak, D. 2001. Equivalence classification by California sea lions using class-specific reinforcers. *Journal of the Experimental Analysis of Behavior*, 76:131–158.
- Reidman, M. 1990. *The Pinnipeds: Seals, Sea Lions, and Walruses*. Berkeley, CA: University of California Press.
- Riess, B. F. 1940. Semantic conditioning involving the galvanic skin reflex. *Journal of Experimental Psychology*, 36:143–152.
- Sandegren, F. E. 1970. Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubata*). Unpublished M.Sc. thesis, University of Alaska, Fairbanks.
- 1976. Courtship display, agonistic behavior and social dynamics in the Steller sea lion (*Eumetopias jubatus*). *Behaviour*, 55:159–172.
- Savage-Rumbaugh, E. S., Rumbaugh, D. M., Smith, S. T. & Lawson, J. 1980. Reference: the linguistic essential. *Science*, 210:922–924.

- Schusterman, R. J. & Dawson, R. G. 1968. Barking, dominance, and territoriality in male sea lions. *Science*, 160:434–436.
- Schusterman, R. J. & Gisiner, R. C. 1997. Pinnipeds, porpoises and parsimony: animal language research viewed from a bottom-up perspective. In *Anthropomorphism, Anecdotes and Animals: The Emperor's New Clothes?*, ed. R. W. Mitchell, N. S. Thompson, & H. L. Miles, pp. 370–382. Albany, NY: SUNY Press.
- Schusterman, R. J. & Kastak, D. 1993. A California sea lion (*Zalophus californianus*) is capable of forming equivalence relations. *Psychological Record*, 43:823–839.
- 1998. Functional equivalence in a California sea lion: relevance to social and communicative interactions. *Animal Behaviour*, 55:1087–1095.
- In press. Problem solving and memory. In *Marine Mammal Biology: An Evolutionary Approach*, ed. A. R. Hoelzel. London: Blackwells.
- Schusterman, R. J., Gisiner, R. & Hanggi, E. 1992a. Imprinting and other aspects of pinniped/human interactions. In *The Inevitable Bond*, ed. H. Davis & D. Balfour, pp. 334–356. New York: Cambridge University Press.
- Schusterman, R. J., Hanggi, E. & Gisiner, R. 1992b. Acoustic signaling in mother-pup reunions, interspecies bonding, and affiliation by kinship in California sea lions (*Zalophus californianus*). In *Marine Mammal Sensory Systems*, ed. J. A. Thomas, R. A. Kastelein, & Y. A. Supin, pp. 533–551. New York: Plenum Press.
- Schusterman, R. J., Reichmuth, C. J. & Kastak, D. 2000. How animals classify friends and foes. *Current Directions in Psychological Science*, 9:1–6.
- Seyfarth, R. M. & Cheney, D. L. In press. The structure of social knowledge in monkeys. In *The Cognitive Animal*, ed. M. Bekoff, C. Allen, & G. Burghardt. Cambridge, MA: MIT Press.
- Sidman, M. 1971. Reading and auditory-visual equivalences. *Journal of Speech and Hearing Research*, 14:5–13.
- 1994. *Equivalence Relations and Behavior: A Research Story*. Boston: Author's Cooperative.
- 2000. Equivalence relations and the reinforcement contingency. *Journal of the Experimental Analysis of Behavior*, 74:127–146.
- Sidman, M. & Tailby, W. 1982. Conditional discrimination vs. matching to sample: an expansion of the testing paradigm. *Journal of the Experimental Analysis of Behavior*, 37:5–22.
- Sidman, M., Wynne, C. K., Maguire, R. W. & Barnes, T. 1989. Functional classes and equivalence relations. *Journal of the Experimental Analysis of Behavior*, 52:261–274.
- Tomasello, M. 2000. Two hypotheses about primate cognition. In *The Evolution of Cognition*, ed. C. Heyes & L. Huber, pp. 165–183. Cambridge, MA: MIT Press.

- Tomasello, M. & Call, J. 1997. *Primate Cognition*. Oxford: Oxford University Press.
- Trillmich, F. 1996. Parental investment in pinnipeds. In *Advances in the Study of Behavior*, pp. 533–577. Academic Press.
- Vaughan, W., Jr. 1988. Formation of equivalence sets in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 14:36–42.
- Wasserman, E. A., DeVolder, C. L. & Coppage, D. J. 1992. Non-similarity based conceptualization in pigeons via secondary or mediated generalization. *Psychological Science*, 3:374–379.
- Zajonc, R. B. 1972. *Animal Social Behavior*. Morristown, NJ: General Learning Press.
- Zentall, T. R. 1998. Symbolic representation in animals: emergent stimulus relations in conditional discrimination learning. *Animal Learning and Behavior*, 26:363–377.
- Zuberbühler, K. 2000a. Causal cognition in a non-human primate: field playback experiments with Diana monkeys. *Cognition*, 76:195–207.
- 2000b. Causal knowledge of predators' behavior in wild Diana monkeys. *Animal Behaviour*, 59:209–220.

8. The Structure of Social Knowledge in Monkeys

- Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.
- Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C. & Bruford, M. W. 1996. Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences USA*, 93:5797–5801.
- Aureli, F., Cozzolino, R., Cordischi, C. & Scucchi, S. 1992. Kin-oriented redirection among Japanese macaques: an expression of a revenge system? *Animal Behaviour*, 44:283–291.
- Bousfield, W. A. 1953. The occurrence of clustering in the recall of randomly arranged associates. *Journal of General Psychology*, 49:229–240.
- Brannon, E. M. & Terrace, H. S. 1998. Ordering of the numerosities 1 to 9 by monkeys. *Science*, 282:746–749.
- Bulger, J. & Hamilton, W. J. 1988. Inbreeding and reproductive success in a natural chacma baboon, *Papio cynocephalus ursinus*, population. *Animal Behaviour*, 36:574–578.
- Carpenter, M., Tomasello, M. & Savage-Rumbaugh, E. S. 1995. Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, 4:217–237.