Squirrel monkeys have been a valuable animal model in biomedical research (Abee 2000). They have been utilized in a wide variety of study areas including, but not limited to, atherosclerosis, neuroscience, pharmacology, psychiatry, toxicology, and vision research. A quick search of on-line databases MEDLINE and PSYCHINFO indicates that approximately 200 articles have been published in the last 10 yr that have used behavioral testing of squirrel monkeys. Analysis of experimental manipulations of Saimiri behavior has been an important tool. Depending on the level of analysis needed, several different behavioral testing protocols have been used successfully in biomedical research using squirrel monkeys. If a predicted effect is on the whole organism, other than studying the natural behavior of an animal, investigating its interaction with social partners and its environment has been most appropriate. If the effects of interest are more limited, more specific tests of the squirrel monkey’s motor performance, cognitive ability, or reflex actions may enable an investigator to isolate the consequence of the experimental intervention. The purpose of this article is to review how behavior has been employed using squirrel monkeys in biomedical research. We describe three general types of behavioral analysis: natural behavior, conditioned behavior, and neurobehavioral assessment profiles.

Natural behavior refers to data collected on squirrel monkeys as they move about the environment. This type of analysis includes studies of animals in seminatural and captive laboratory environments as well as field studies. Although an investigator can arrange particular situations in all three study types, a key difference between behavioral analysis and conditioned tests is usually in the investigator’s direct supply of rewards or punishments (“conditions”) in the latter.

Conditioned behavior tests (cognitive, classical, and instrumental paradigms) are used to investigate the squirrel monkey’s ability to learn or react to environmental stimuli. Classical conditioning entrains reflexive behavior to stimuli that do not normally elicit it. Cognitive and instrumental conditioning relies on animal tendencies to maximize rewards and minimize punishment in an effort to examine its ability to perform a motor skill or learn a task. In all cases, the experimenter is setting the experimental conditions and supplying the rewards and punishments that influence the animal’s actions.

Neurobehavioral assessment profiles are used to measure a subject’s reflexes, motor abilities, and emotionality in contrived situations. No rewards or punishments are given, and the animal is tested in highly structured situations. The ability of an animal to visually track a specific stimulus and the reaction of an animal to a visual cliff are examples of the types of assessments made.

In the sections below, we provide a brief review of particular terminology and methodologies associated with several behavioral paradigms. We then provide several examples of how the paradigm has been applied to the squirrel monkey. These examples are intended to inform the reader of the value of studying squirrel monkey behavior.

Natural Behavior

Naturalistic observations are made on animals without imposing experimentally contrived rewards or punishments. During behavioral observations, the subject animal is observed for the presence or absence of a particular response or set of responses. If the response is present, then the number of times it occurs (frequency or rate) or the length of time it occurs (duration) can be recorded. Ethograms may be used to operationally define a set of responses produced by the subject animals. Their use provides a consistent frame of reference both within and between study protocols, ensuring that behavioral responses are scored consistently across time. Natural behavior of an animal falls into three categories or types of responses: behavioral events, behavioral states, and behavioral stereotypes.

Many behavioral events are acts or responses that may appear to be instantaneous. Although such responses have a finite duration, they may be so brief and consistent that they may be viewed as instantaneous. Responses that may be described as “slap, grab, or hit” are distinct acts that can be reported as a frequency or rate, such as slaps per hour.

Other types of responses, such as “sitting in contact with another animal” or “huddling,” are behavioral states that last a relatively long time. A state may be briefly interrupted as individuals adjust their positions, but the duration of a bout of sitting together may be, for example, minutes or hours long. Although frequency data may be collected on...
such states, a duration measure may be more desirable. It may be expressed as minutes per hour huddled together, percentage of time in contact, or other similar measures of duration.

Sequences of responses may be difficult to analyze but may be important when examining patterns of responses such as behavioral stereotypes. One can record all items in an ethogram during data collection and then analyze for the frequencies of combinations. Such combinations are assessed as significant if they occur more often than one would predict from the individual frequencies of the two items. An alternative is to predefine the combinations or sequences of interest and then to regard and record such sequences as a single instance.

In Jeanne Altmann's (1974) review of observational techniques, four methods for collecting naturalistic data are listed: ad libitum scoring, focal animal observations, instantaneous scans of a group, and one-zero samples. The most simple method, ad libitum scoring, is to observe an animal or group for the presence or absence of a response and to record all occurrences. Animals are not observed for set periods of time so it is impossible to summarize the data in terms of frequency or hourly rate. Because no one can watch everywhere at once, Altmann criticizes ad libitum data collection, especially with a large battery of response categories applied to multiple subjects, as being inherently inaccurate. Nevertheless, an accepted use of this methodology is to develop an ethogram or categorized list of observed animal responses.

Focal animal observations comprise another observational method that enables the observer to record the onset and cessation of behavioral states and the time of occurrence of actions with small durations for a large number of behavioral categories. This technique requires that the observer collect data on only one animal at a time. Data involving other animals in the study that do not interact directly with the focal subject are disregarded. The advantage, of course, is that the observer gathers information on the frequencies, durations, and sequences for many more behavioral categories than the other techniques can provide.

Instantaneous scans of a group assess behavior states like sleeping by attending to the subjects' behavior at preselected times. The percentage of time spent in a behavioral category or response can be calculated by dividing the number of scans in which the subject is seen asleep by the total number of snapshots. Such point samples of an animal's behavioral state can be extrapolated to estimate the amount of time the subject spends in a particular behavioral category. Instantaneous scans must be performed at intervals that exceed the duration of most instances of the behavior of interest to ensure independence of sampling.

One-zero samples (Altmann 1974) comprise a form of data collection that involves recording whether a response occurs within a predetermined time frame. For example, if an animal scratches itself one or 10 times within a predetermined time block, the animal receives a score of one. If the animal does not scratch itself at all, it receives a score of zero. Altmann (1974) has criticized the one-zero scoring method, stating that it provides data that are not related to frequency or duration but are an indeterminate index of both. Although this type of dichotomous data may be useless in measuring frequency and duration, it may be used to calculate probabilities, which are comparatively useful quantitative measurements. The research investigator must choose among techniques according to the properties of the variables of interest.

Fragaszy and colleagues (1992) compared focal animal and group scan methods of data collection in the field conditions for capuchin and squirrel monkeys. They found that focal animal and group scan data provided similar population means and variances for activity profiles, foraging activities, and height above ground, all of which are behavioral states. They suggested that combining focal animal and group scans is a useful way to collect the most data in the least amount of time.

Social Behavior

Using the data collection methods summarized above, the following generalizations about squirrel monkey behavior have been made. In the wild, squirrel monkeys inhabit most types of tropical forest including both wet and dry forest, continuous and secondary forest, mangrove swamps, riparian habitat, and forest fragments (Baldwin 1985; Boinski 1987b; Hernández-Camacho and Cooper 1976; Terborgh 1983). They are highly flexible in their ability to adapt to different environments and in some geographic areas appear to prefer habitats that have been disturbed by humans (Boinski 1987b; Konstant and Mittermeier 1982). These omnivores eat insects when available but include in their diets fruit, flowers, and occasionally vertebrates such as lizards when necessary or readily available (Baldwin and Baldwin 1972a; Boinski 1988; Izawa 1975; Mitchell et al. 1991; Mittermeier and van Roosmalen 1981; Rowe 1996; Scollay and Judge 1981; Thorington 1967).

Squirrel monkeys are found in large multimale/multifemale groups numbering 50 or more animals, with reports of possibly as many as 300 (Baldwin 1985; Baldwin and Baldwin 1971; Boinski 1987; Hernández-Camacho and Cooper 1976; Mendoza et al. 1991; Rowe 1996; Thorington 1967). Group size may vary depending on habitat type (Baldwin and Baldwin 1971; Scollay and Judge 1981). Based on earlier reports, it was thought that these groups tended to disperse during the day to forage in smaller groups, rejoin for a time during the day for a rest period, and then continue foraging separately until again rejoining for the night (Thorington 1967). More recent reports reveal that these groups tend to forage as cohesive groups, indicating that earlier reports of apparent dispersal were due to the concurrent involvement of several large fruiting trees by the same troop (Mitchell 1990). Boinski (1987b) found that in Costa Rica, squirrel monkeys tended to forage more widely, rest less when food is scarce during the peak wet season, and travel least during the birth season.
In captivity, age and sex ratios differ depending on the type of social grouping maintained in the available housing. Generally, social groups are maintained in captivity with only one or two males per group because problems of aggression may develop among the males if more than two males are maintained within a social group. Groups that have access to a seminatural environment with more living space, such as the Monkey Jungle housing area in Florida, are able to house more males within the same groupings due to the increased complexity and size of the environment, the possibility of emigration to an adjacent group, and the increased provision of hiding areas. In captivity, social group size may range from a single pair to between 35 and 50 animals per group depending on available housing and the reason for maintaining the animals. Squirrel monkeys are highly social animals and in captivity should be maintained in species-typical social groupings when possible.

Vocalizations play a role in helping to maintain the social organization of squirrel monkey troops. Boinski (1991) identified four major types of vocalizations in free-ranging squirrel monkeys: smooth chucks, bent mast chucks, peeps, and twitters. She found that peep calls increased as the group spread out to forage. Twitters were associated with the beginnings of troop movement. Buben et al. (1986) found that smooth chuck calls were associated with positive, affiliative interactions among captive squirrel monkeys. Boinski and Mitchell (1997) report that chuck calls contain information about the caller identity and its current activity, suggesting that squirrel monkeys use calls to enhance group coordination and cohesion. Deaf squirrel monkeys tend to vocalize less often than their intact cagemates (Talmage-Riggs et al. 1972), and squirrel monkeys that are not in contact either visually, tactiley, or olfactorily continue to respond to specific vocalizations in appropriate social contexts (Maurus et al. 1987). These authors concluded that squirrel monkeys can differentiate individuals using vocal cues and are able to communicate within the troop even when they cannot see each other.

Social Organization

Squirrel monkey society is generally unified by the adult females because all age-sex classes except fully adult males have been shown to be more attracted to adult females than to any other age-sex class (Baldwin 1969, 1983; Scollay and Judge 1981; Strayer and Harris 1979). Sexual segregation on a seasonal basis is a unique feature of social organization in this species. Group males remain near the periphery of the group in the nonbreeding season, and the majority of social interactions between the sexes take place during the breeding season (Alvarez 1975; Baldwin 1968, 1969, 1971, 1985; Baldwin and Baldwin 1972; Boinski and Mitchell 1994; Candland et al. 1973; Coe and Rosenblum 1974, 1978; Dumond 1967, 1968; Hopf 1978; Kaplan 1977; Leger et al. 1981; Lyons et al. 1992; Mason and Epple 1969; Mendoza et al. 1978b, 1991; Scollay and Judge 1981; Strayer and Harris 1979; Strayer et al. 1975; Vaitl 1977, 1978).

There are, however, differences in the expression of this trait in the social behavior repertoire reported for populations from different geographical regions (Gonzalez et al. 1981; Mendoza et al. 1978a; Mitchell et al. 1991). *Saimiri boliviensis* (Hershkovitz 1984) demonstrate strong sexual segregation whereas *Saimiri sciureus* spp. and *Saimiri oerstedii* spp. societies are more sexually integrated (Boinski 1987b; Mendoza et al. 1978a). Some researchers have found evidence that this sexual segregation may be female initiated through active exclusion of the males (Baldwin 1968, 1969; Baldwin and Baldwin 1972; Coe and Rosenblum 1974; Dumond 1968; Fairbanks 1975; Mendoza et al. 1978b; Vaitl 1977). Reports from other studies indicate that the segregation may be due to intermale social dynamics instead of female agonism (Lyons et al. 1992; Strayer and Harris 1979).

Dominance hierarchies within squirrel monkey groups differ in form and degree depending on species. *S. boliviensis* shows a high degree of sexual segregation within their social groups, demonstrate distinct linear dominance hierarchies among males. Dominance is associated with higher testosterone levels and, generally, copulatory frequency. A separate but less distinct dominance hierarchy is seen among females of this species (Mendoza et al. 1978b). *S. sciureus* spp., which tend toward sexual integration within a social group, demonstrate a linear dominance hierarchy that includes both sexes, with all males being dominant over all females (Mendoza et al. 1978b; Mitchell et al. 1991). *S. oerstedii* spp. in the wild do not demonstrate a dominance hierarchy among either sex, and males even participate in cooperative mobbing of females for olfactory examination of estrous state during the breeding season (Boinski 1987c; Mitchell et al. 1991).

Allomaternal care (care of an infant in a maternal way by a monkey other than the birth mother) has been documented in squirrel monkeys in studies from the field (Baldwin 1969; Dumond 1968; Hunt et al. 1978; Ploog 1967) and the laboratory (Williams et al. 1988, 1994). Infant squirrel monkeys may spend as much as 30% of their time with allomaternal mothers during the first 6 mo of their lives (Baldwin 1969; Williams et al. 1988, 1994). Allomothering usually begins during the first 2 wk of life in this species (Williams et al. 1994). In the wild, allomothering is reported usually to be juvenile females (Dumond 1968). In captivity, reports have shown that the majority (53%) of the allomothering is done by young adult females aged 4 to 6 yr, and adult females aged 7 to 9 yr have provided about 20% of the allomothering (Williams et al. 1994). Females who had experienced a reproductive failure during that year (Williams et al. 1988) performed almost all of the allomothering.

Reproductive Seasonality

The yearly reproductive cycle of these monkeys includes a distinct 3-mo breeding season with a birth season approxi-
Rosenblum 1968; Rowe 1996). A unique feature of this yearly cycle is the reproductive seasonality observed in both males and females in this species (Baldwin 1969; Boiniski 1987a; Coe and Rosenblum 1978; Dumond and Hutchinson 1967; Goss et al. 1968; Michael and Zumpe 1971; Rosenblum 1968; Rowe 1996). This seasonality is termed the “fatted male” condition. Both sexes gain weight throughout the prebreeding season and attain peak weights before breeding. Weight gain in males is associated with increased spermatogenesis in preparation for breeding (Coe and Rosenblum 1978; Dumond and Hutchinson 1967; Williams et al. 1986).

The yearly cycle has been shown in some field studies to be related to annual rainfall cycles and seasonal food availability. The birth season occurs at the period of greatest food availability, thus ensuring the female adequate nutrition after parturition (Baldwin 1968; Baldwin and Baldwin 1981; Boiniski 1988; Williams et al. 1986). Changes in light cycles have also been shown to be related to the timing of the reproductive cycle (Follett and Follett 1981; Rosenblum 1968) as has humidity level (Dumond 1968). Boiniski (1987a) in her field studies in Costa Rica found a strong tendency toward birth synchrony in this species, which she suggested might be an antipredator adaptation. Estrous cycles have been estimated to be about 7 to 8 days in duration (Kaplan 1977; Rosenblum 1968; Wolf et al. 1975). This cycle length can be affected by social conditions (Hutchinson 1970; Wolf et al. 1975) and light cycles (Rosenblum 1968).

Female squirrel monkeys tend to reach maturity and begin breeding at approximately 2.5 to 3 yr of age. Frequency of female intertroop transfer varies among groups from different geographical regions. A high rate of female transfer occurs in S. oerstedii, with males remaining in their natal groups in these species; and a low rate of female transfer occurs in S. sciureus and bouliviensis spp., which demonstrate relatively high rates of male transfer (Boinski 1987c). Males reach subadult age by the time they are 2.5 to 3 yr old and generally transfer from the natal group at that time depending on species. They may then join an all-male group of juveniles and subadults for a time until they become fully adult at about age 5 yr, when they are able to work their way into the male dominance hierarchy of an established group and begin breeding.

The breeding season of squirrel monkeys shows a shift when animals are moved into the Northern hemisphere (Dumond 1968; Kaplan 1977; Lehner et al. 1967; Rosenblum 1968). Several studies have linked this breeding season shift to humidity (Baldwin and Baldwin 1971; Dumond 1968; Harrison and Dukelow 1973). It has also been linked to the photoperiod by other authors (Coe and Levine 1981; Rosenblum 1968). The breeding season of captive squirrel monkeys is probably controlled by a combination of several different factors all related to the monkey’s natural habitat (Dukelow 1985).

Conditioned Behavior Testing Protocols

In contrast to naturalistic observation, conditioned behavior testing protocols place the squirrel monkey in a situation in which it has to learn to respond to an environmental stimulus or set of stimuli. Bitterman and Schoel (1970) and Rescorla and Holland (1982) provide comparisons of the two major types of conditioning protocols: classical and instrumental. In classical conditioning, conditioned reflex actions of an animal are entrained to an environmental stimulus that would not normally elicit that reflex. In instrumental or operant conditioning, the subject is required to initiate a response that if correct, results in a reward.

Both instrumental and classical conditioning have been used with squirrel monkeys in a wide variety of contexts: aggression (Hake and Campbell 1980); cardiovascular change (Hansen and Herd 1982); drug addiction (Katz et al. 1992); motion-induced sickness (Wilpizeski et al. 1985); neuropharmacology (Auer et al. 1996; Mansbach et al. 1991); psychology of learning, memory, and cognition (Herzog et al. 1977; Irl and Markowitsch 1987; King 1971; Overman et al. 1983; Thomas 1990; Thomas and Boyd 1973); olfaction (Hubener and Laska 1998; Hudson et al. 1992; Laska and Teubner 1998; Laska et al. 1996); pharmacology (Pakarinen et al. 1996; Spealman et al. 1997; Weerts et al. 1998); and toxicology (Newland et al. 1996a,b; Weiss et al. 1979).

Classical Conditioning

Using classical conditioning, it is possible to investigate behavior that is not under conscious control of the subject. The protocol involves pairing an unconditioned stimulus (UCS) that elicits an unconditioned response in the subject with a second stimulus that does not normally elicit the response. After such pairings, this stimulus (known as the conditioned stimulus [CS]) comes to elicit the response without concurrent presentation of the unconditioned stimulus. After repeated presentations such as a ringing bell and the presentation of food (the unconditioned stimulus), which elicits salivation, the bell becomes a conditioned stimulus, which will elicit salivation (the conditioned response) without the presence of the original UCS (food). Rosenblum and Schwartz (1983) were able to manipulate the activity levels of squirrel monkeys using time of day as the UCS and a flashing light as the CS. The flashing light was initially shown only during the time of day when the squirrel monkeys were active. After conditioning, flashing the light during normally inactive times of the day caused an increase in activity. Appropriate controls include the CS alone, the UCS alone, and the conditioned and unconditioned stimuli presented in a random unpaired fashion.

Abbreviations used in this article: CS, conditioned stimulus; IBAS, Infant Behavioral Assessment Scale; UCS, unconditioned stimulus.
Weerts and colleagues (1998) employed classical conditioning procedures to elicit food calls associated with eating under conditions of no food in squirrel monkeys. Vocalizations were elicited by presentation of stimulus lights (the CS condition) that had previously been paired with either preferred foods (such as grapes, peanuts, bananas) or standard foods (such as monkey chow) when such foods were absent as well as during presentation of both food types (the UCS condition). When compared with the period before stimulus light pairings with food (a preCS condition), the rate, duration, and number of elemental units of food-related twitter vocalizations were increased during the CS conditions regardless of food type.

Instrumental/Operant Conditioning

Unlike classical conditioning, instrumental conditioning involves the use of reward and/or punishment to influence the frequency of a response from an animal. A reward or punishment may be given or denied upon the occurrence of a response designated as correct or incorrect. In discrete-trial learning, the experimenter controls the pacing of the experiment by giving the animal a set of clearly defined test trials. In other procedures, the animal is not given discrete trials but rather is free to respond at any time. These methods are called free-operant procedures.

Many readers are familiar with the operant box in which the subject is required to exhibit a particular response to receive a reward or escape a punishment. For example, the animal may be required to press a bar or lever to receive a food treat. Rather than reinforcing every response, different schedules of reinforcement can be used to increase the probability that the animal will respond. Reinforcement schedules can be manipulated by varying the number of lever presses, for example, by making the reward contingent on a specific number of responses (fixed-ratio) or by varying the number of lever presses necessary for the reward (variable-ratio). Hughes and Dykstra (1997) used squirrel monkeys on a fixed-ratio schedule of food reward to test the effects of meperidine and morphine on lever pressing. Combining meperidine and morphine with a selective opioid antagonist, they concluded that decreases in lever pressing are mediated by muopiod receptors. Similarly, Spealman and colleagues (1997) used squirrel monkeys that were trained on a fixed-ratio schedule in which lever pressing terminated a stimulus associated with electric shock to show that D1 partial agonists can act as functional cocaine antagonists and therefore may be viable candidate medications for the management of cocaine addiction. Pakarinen et al. (1996) trained squirrel monkeys on a series of fixed-ratio tasks to investigate the effects of low nonconvulsive doses of a convulsive agent. After learning a task, the subjects immediately received a dose of the agent or a control substance; then the subjects were retested the next day on the same tasks. It is also possible to make the reward contingent on when and how much the animal presses the lever, either by rewarding the animal at a fixed interval after the first lever press or by using a variable interval, rewarding the animal at varying times from the first lever press. McKearney (1990) found that serotonin agonists decreased responding under a fixed interval for both food (reward) and shock (punishment) schedules in squirrel monkeys. Newland and colleagues used variable interval testing to investigate the effects of prenatal mercury (1996a) and lead (1996b) exposure on the ability of squirrel monkeys to make a transition from one task to another.

Differences between the way squirrel monkeys respond to fixed-ratio and fixed-interval schedules were used by Katz and Witkin (1993) to study the action of addictive drugs on dopamine receptors. The fixed-interval schedule maintained relatively low rates of responding that increased until food was presented. The fixed-ratio schedule maintained relatively constant, high rates of responding. Quinpirole, a D2 receptor agonist, increased rates and disrupted the temporal pattern of responding under the fixed-interval schedule at doses that decreased rates of responding under the fixed-ratio schedule. Under the fixed-interval schedule, the D2 antagonists spiperone and haloperidol and the D1 antagonist SCH 23390 shifted the quinpirole dose-effect curve to the right. The maximal effects of quinpirole were decreased at the highest doses of the antagonists. However, only spiperone antagonized effects of quinpirole on the rates of responding under the fixed-ratio schedule. The D1 agonist SKF 38393 decreased rates of responding under both schedules. Those effects were not antagonized by any doses studied of either spiperone or SCH 23390. Rather, both antagonists enhanced the effects of SKF 38393.

Active avoidance learning, in which an animal must make an appropriate response to avoid an aversive stimulus, can be used to test memory retention and consolidation. A discrete-trial procedure can be used by allowing squirrel monkeys to avoid the aversive stimulus by responding to a signal that precedes the aversive stimulus. Sidman avoidance is a free-response paradigm in which the subject avoids the aversive stimulus by responding within a predetermined time interval. This paradigm has been used to investigate the effects of a dopamine agonist as a potential antipsychotic agent (Barnett et al. 1992; Meltzer et al. 1993, 1995; Wright et al. 1995).

Passive avoidance learning requires that the subject inhibit a learned response to avoid an aversive stimulus. The subject is first trained to perform a response reliably, and then the experimenter pairs the response with an aversive stimulus. This paradigm can be used to test memory retention and consolidation.

With discrimination learning, an animal may be presented with two or more stimuli and given the opportunity to make a choice response, with "correct" responses reinforced and "incorrect" responses not reinforced. Such discrimination learning can be used to study the animal's ability to learn antecedent-consequent relationships and demonstrate their memory of such relationships. Melia and Ehlers (1989) administered ethanol to squirrel monkeys and found significant discrimination impairment. Using the conditional object identification task, they were able to determine that the re-
duction in performance resulted from losses in ability to discriminate.

Reversal learning involves training an animal to a criterion on one discrimination task and then reversing the correct and incorrect stimuli. The ability of an animal to "learn how to learn," also known as a learning set, can be tested by presenting the subject with a series of discrimination tasks. For example, the animal may be required to learn that the color—not the shape, size, or surface texture—of the two stimuli indicates the correct response.

Another set of learning tasks involves the animals’ processing of "if-then" statements to select the correct stimulus. Such cognitive learning paradigms include matching and oddity tasks in which the subject is required to learn to choose between two objects that are either similar to or different from a reference object. Some tasks may be combined to create even more complex tasks. If, for example, trial-unique oddity problems are presented on a gray background, the task may be to choose the odd object; however, if the problem is presented on a white background, the task is to select one of the similar objects. Thomas (1996) describes examples of complex problems that have been used with squirrel monkeys as well as some of the necessary controls and cautionary interpretations.

Memory can be tested by incorporating a delay in the test. The subject can be trained to choose from a pair of objects the single object that matches one presented earlier. By varying the time interval between presentation of the initial object and the choice objects, an investigator can study such questions as memory and visual retention. Nordholm and colleagues (1995) found that linopirdine, a reported cognitive enhancer, did not influence squirrel monkey performance on a delayed matching to sample test. During the first five trials of each session, the delay was fixed at 3 sec in length. On the sixth and all subsequent trials, the length of the delay was increased, unchanged, or decreased so that accuracy was maintained at approximately 80%. After the delay, two of the three response keys were transilluminated with different color lights. A single response on the key transilluminated with the same color as the sample stimulus resulted in the presentation of food. A response on the key transilluminated with the stimulus that did not match the sample stimulus resulted in a timeout.

Hudzik and Wenger (1993) also used the delayed matching to sample paradigm to investigate the effects of commonly abused drugs on memory in the squirrel monkey. Pentobarbital and methylscopolamine decreased matching accuracy as well as mean and maximum delay values after the highest doses. Nicotine and phenylcyclidine produced small decreases in delayed matching accuracy without affecting mean and maximum delay values. Caffeine, morphine, phystostigmine, and neostigmine did not alter matching performance even after doses that markedly decreased rates of responding.

Instrumental conditioning procedures were used in the first investigations of squirrel monkey sensory abilities. For example, the kinetic sense in the form of induced motion sickness was documented using avoidance conditioning (Igarahi 1968; Roy and Brizzee 1979). Investigations of auditory discrimination in squirrel monkeys have used choice tasks. Green (1975) used earphones and active avoidance techniques to calculate auditory sensitivity and loudness curves. Interaural time-delay sensitivities and intensity levels in squirrel monkeys were measured with left-right choice tasks (Don and Starr 1972; Downey and Harrison 1972).

A series of articles demonstrated that some squirrel monkeys had forms of color blindness (dichromats) similar to those seen in humans (De Valois and Morgan 1974; Jacobs 1983; Jacobs and Blakeslee 1984; Miles 1958). Squirrel monkeys were presented with two stimuli and asked to choose the correct one in a forced-choice discrimination task. They found that all the males and approximately one third of the females demonstrated a clear red-green insensitivity.

**Neurobehavioral Assessment Scales**

Neurobehavioral assessment scales are commonly used to study the effects of different types of stressors on behavior or on the endocrinology or immunology of the study subjects. The physiological and behavioral effects of stress on squirrel monkeys have been widely documented for many types of social stressors as well as a few types of environmental stressors. This type of assessment has been used for many years in human studies to assess the development of newborns and young infants. Comparisons between human and chimpanzee responses on behavioral assessments such as the Brazelton Neonatal Behavioral Assessment Scale (Brazelton 1973) have been carried out with results demonstrating surprising similarity in behavioral response (Bard et al. 1992; Hallock et al. 1989). Although the research involving neurobehavioral assessment scales and squirrel monkeys has been developmental to date, there is no reason that it cannot be applied to other aspects of Saimiri behavior.

Infant neurobehavioral assessment in primates gained popularity in the late 1960s and early 1970s, when it was used primarily to make cross-species comparisons in development of infant nonsocial behaviors. King and King (1970) hypothesized that the amount of maternal assistance given to an infant helped to determine the strength and persistence of behaviors associated with maintaining maternal contact and nursing. As a result, species that demonstrate low levels of infant maternal assistance, such as squirrel monkeys, should show stronger, more persistent infant behaviors associated with maintaining maternal contact and nursing than species that demonstrate a higher level of infant maternal assistance, such as rhesus macaques. This hypothesis was tested in several species of monkeys (rhesus macaques: Mowbray and Cadell 1962; squirrel monkeys: Schusterman and Sjoberg 1969; King and King 1970; King et al. 1974; cotton-top tamarins: King et al. 1974) using an infant neurobehavioral assessment scale that tested two categories of nonsocial behaviors—those associated with maintaining mother contact and nursing and those not associated.
The original scale developed by Mowbray and Cadell (1962) for use with rhesus macaque infants was modified slightly for use with squirrel monkeys. The modified test battery takes about 45 min to administer once a day for the first 50 days of the infant’s life. It consists of eight different behavioral tests related to maternal contact maintenance and nursing and is intended to evaluate the following aspects of the infant’s development: presence and strength of the rooting reflex, strength and length of the clasp reflex, orientation into a head-up position within a certain time (a test in which the infant is placed head down on a cylinder inclined at an angle), and locomotor following of the surrogate for at least 20 cm. Tests related to nonsocial-, nonmaternal-related behaviors evaluated the presence of visual and auditory orienting and following, the ability to climb down from a cylinder on which the infant was placed upright approximately 12 cm from the table’s surface, and the ability to crawl and walk a given distance in a given time. All behavioral tests were scored on a scale of zero to two, with zero assigned for no response and two for a complete response.

The neurobehavioral assessment scale described above was used in slightly different forms by Schusterman and Sjoberg (1969), King and King (1970), and King et al. (1974) to test squirrel monkeys for the strength and persistence of the two categories of behaviors intended for comparison with the results found by Mowbray and Cadell (1962) in rhesus macaques. Results indicated that squirrel monkey behaviors associated with maintenance of maternal contact and nursing persisted longer and were stronger than similar behaviors seen in rhesus macaques (King and King 1970; King et al. 1974; Schusterman and Sjoberg 1969). However, measured behaviors not associated with maternal contact maintenance and nursing did not vary reliably according to species. Similar results were also found by King et al. (1974) for cotton-top tamarins, another low maternal assistance species. These results demonstrate support for the hypothesis that the amount of maternal assistance given to the infant affects the timing of the appearance, strength, and persistence of behaviors associated with maternal contact maintenance and nursing but does not have a consistent effect on the development of other nonsocial infant behaviors (King and King 1970; King et al. 1974).

The studies by Schusterman and Sjoberg (1969), King and King (1970), and King et al. (1974) were the first to use neurobehavioral assessment scales to evaluate infant development in squirrel monkeys. These studies were performed to assess the behavioral development of the typical squirrel monkey neonate. The infant assessment scale used in these studies is similar to those used today. Earlier data on squirrel monkey infant developmental behavior can be used to compare subsequent and more recent results of similar infant neurobehavioral assessments of prenatally stressed infants.

The most widely used human infant behavioral assessment scale is the Brazelton Neonatal Behavioral Assessment Scale (Als et al. 1977; Brazelton 1973), which has been modified by Schneider and Suomi (1992) and colleagues at the University of Wisconsin-Madison for use with infant primates to test for the presence of developmental delays due to effects from prenatal stress. The neurobehavioral assessment scale developed by Schneider and Suomi (1992) for use with infant nonhuman primates, the Infant Behavioral Assessment Scale (IBAS), is based on and adapted from those used to behaviorally assess human infants and is used for similar purposes in infant nonhuman primates. The IBAS is best administered at 2 wk of age, which is the critical period for specific developmental changes in infant nonhuman primates. The test has been used extensively in the University of Wisconsin Primate Center and other primate laboratories in rhesus monkeys to test for various effects of prenatal stress on infant nonhuman primate development. Results of such studies, which are similar to those seen in human infants who experienced similar types of stress prenatally, have been found to have human implications and applications for predicting effects of certain stressors on human infant development.

The IBAS test (Schneider and Suomi 1992) takes about 15 min to administer and consists of 50 different behavioral assessment scales applicable to an infant primate for assessing its developmental state at 2 wk of age. The test scores have been analyzed previously through cluster analysis by Schneider and colleagues (Schneider et al. 1991) and grouped into the following four clusters for measuring different areas of infant development: visual orienting, motor maturity, motor activity, and state control.

The visual orienting cluster consists of an average of scores measuring time spent visually orienting to a stationary object in several directions, time spent visually following a moving object in several directions, assessment of duration of looking, and assessment of percentage of time spent attending to items previously presented. The motor maturity cluster consists of the average of scores for the infant’s head posture when held in a prone position and a supine position, the infant’s ability to right its head to vertical when held at a 45° angle in several directions, assessment of the infant’s response speed, and assessment of the infant’s coordination. Motor activity consists of an average of scores measuring percentage of motor activity, assessment of coordination, degree of success at a spontaneous crawl, and percentage of inactiveness. State control is an assessment of the infant’s overall emotional state during the test and consists of an average of scores assessing the infant’s predominate emotional state, amount of struggle, ability to be consoled, and irritability or distress (Schneider et al. 1999).

Scores of the IBAS are also helpful as stand-alone indicators of the presence of prenatal stress. Postrotary nystagmus, measured after rotation on a nystagmus board, has been found to be reduced in prenatally stressed infants (Schneider and Coe 1993). Presence of strong neonatal reflexes such as the rooting reflex and the palmar and plantar grasp reflex by 2 wk of age also indicate slowed development because healthy normal infant primates are losing these reflexes as they pass through their 2-wk-old developmental transition period (Schneider et al. 1999).

Squirrel monkeys have been underutilized as a model...
species in this type of assessment due to high prenatal and infant mortality rates when exposed to stressors during pregnancy. Schneider and Coe (1993) used repeated social relationship disruption as the stressor to demonstrate the effect of prenatal stress on the infant squirrel monkey through the application of the IBAS. The experimental design used in Schneider and Coe’s study involved two experimental treatments that involved disruption of social relationships and one control treatment. Infant groups tested included the following: (1) those born into the control group, which experienced a stable social environment before and throughout the pregnancy period; (2) a midgestationally stressed group, which experienced one social group change between months 2 and 4 of pregnancy; and (3) a chronically stressed group, which experienced a social group change previous to pregnancy, one in early pregnancy between months 1 and 3, and a final group change between months 4 and 5 of pregnancy (Schneider and Coe 1993). Social group disruption has been shown to cause behavioral agitation and pituitary-adrenal response for several weeks after group formation (Coe et al. 1985; Mendoza et al. 1979). Infants from these three groups were tested at 2 wk of age using the IBAS test to determine whether developmental differences existed between and among the three different treatments.

IBAS results revealed that infants from chronically stressed pregnancies demonstrated poorer motor abilities, impaired balance, and reduced postrotary nystagmus compared with control infants. Their attention spans were shorter than those of controls, as were the lengths of their looking episodes during visual orientation testing. Midgestationally stressed infants did not show statistically different results from control infants. Schneider and Coe (1993) suggest that these results indicate deleterious effects of chronic stress during pregnancy on fetal development but that a single stressful episode occurring during midgestation will not significantly affect development of infant primates.

The IBAS is a useful neurobehavioral assessment tool for indicating the presence of prenatal stress effects on development in nonhuman primate infants. It has been successfully utilized in squirrel monkeys (Schneider and Coe 1993) to demonstrate the effects of one type of stressor, social relationship disruption, on the infant primate. It has the potential for assessing the effects of numerous other types of stressors commonly occurring in either a captive or wild squirrel monkey living environment, such as temporary crowding, social separation, and capture and handling stress in this species.

Concluding Remarks

Behavior can be a powerful tool for projects concerned with the effect of a particular treatment on the whole animal. Behavioral data can be collected in a rigorous fashion, producing consistent results both within and between studies. As with any scientific measuring device, proper standards and protocols are necessary to ensure the quality of data collected. Nevertheless, even if those protocols are followed, resulting behavioral data may miss insights into investigations that focus on single systems within the organism.

Squirrel monkeys are a commonly used experimental model in biomedical research. Their behavior and responses to different testing situations are well documented. We have reviewed the use of squirrel monkeys in three major types of behavioral testing paradigms: naturalistic observation, conditioned responses, and neurobehavioral assessment scales. Under all three protocols, squirrel monkeys have been used to provide answers to questions ranging from the effect of different socialization pressures on infant development to drug effects on an animal’s ability to learn.

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