

The Behavior of *Solenodon paradoxus* in Captivity with Comments on the Behavior of Other Insectivora

JOHN F. EISENBERG¹

*Department of Zoology,
University of Maryland*

&

EDWIN GOULD²

*Department of Mental Hygiene,
Laboratory of Comparative Behavior,
Johns Hopkins University*

(Plates I & II)

I. INTRODUCTION

Solenodon paradoxus, confined to the island of Hispaniola, and *S. cubanus*, endemic to Cuba, comprise the sole living members of the family Solenodontidae. A full-grown specimen of *S. paradoxus* may weigh up to 1 kgm. and attain a head and body length of 300 mm. Although large size and primitive molar cusp pattern have led taxonomists to include this genus with the tenrecs of Madagascar, further morphological studies have led certain workers to conclude that *Solenodon* is a primitive soricoid more closely allied to the shrews than to the zalambdadont tenrecs (McDowell, 1958).

The behavior of *S. paradoxus* was reviewed by Dr. Erna Mohr (1936-38). Since her series of papers, however, much more has been learned concerning the behavior of not only the solenodon but also the insectivores of the families Tenrecidae and Soricidae. For this reason we felt it would be useful to describe in detail the major features of the solenodon's behavior patterns and to interpret them within a much broader theoretical context than was possible thirty years ago.

¹Research supported by a General Research Board Grant from the University of Maryland, together with funds from the Department of Zoology.

²Research supported by the National Science Foundation, Grant No. GB 1728, and the United States Air Force, Grant No. AFOSR 586 64.

For comparative purposes the authors utilized the extensive collection of living tenrecs maintained by Dr. Gould at Johns Hopkins University, and drew upon their previous behavioral studies of insectivores, which have already been published in part elsewhere (Eisenberg, 1964; Gould, 1964, 1965).

II. SPECIMENS AND MAINTENANCE

Four specimens of *Solenodon paradoxus* (one male, three females) were purchased from a dealer in the Dominican Republic. The male (M) and one female (J) were immature and, extrapolating from their weights (Mohr, 1936 II), were judged to be four and six months old, respectively. The juveniles were studied as a pair by Dr. Eisenberg. In addition, all four animals were employed in two-animal encounters and were recorded during studies of vocal communication.

For observational purposes they were kept as pairs in 4 × 4 ft. cages having solid plywood walls and no top. The cages were provided with logs and pieces of sod but the floor was covered with newspapers as a sanitary precaution, since the animals were prone to scatter their food on the cage floor before commencing to eat. Cardboard boxes served as shelters and, again in the interests of sanitation, these boxes were replaced weekly.

At first the animals were fed a mixture of crickets, ground meat, egg yolk, canned milk,

pabulum, banana and a vitamin supplement (ABDEC). This mixture was readily taken by all four but after two months J began to refuse the preparation and was switched to dead white mice, which were beheaded and skinned before being offered.

The animals were found to be quite sensitive to minor skin irritations. Areas on the flanks and abdomen were potential loci where prolonged scratching could produce a local abrasion with subsequent infection. The tail and soles of the feet were also subject to minor abrasions which could become infected. All areas of irritation responded to treatment with White's A-D Ointment. It would appear that fresh, damp humus provides the best substrate for caged animals, but sanitary requirements necessitated the use of newspaper as the least abrasive substitute.

OBSERVATIONAL PROCEDURES

In order to study the solenodon's methods of foraging and its encounter behavior, a 4 × 4 ft. arena was utilized. This arena had an earth-covered floor with pieces of bark and logs scattered on the substrate. Observations were made at night with a dim white light or a ruby bulb. Encounters were staged by simultaneously placing two specimens in the arena. Interaction patterns were recorded on a portable tape recorder and later transcribed on paper. Supplementary observations and recordings were run in small rooms measuring 10 × 15 feet. The vocal repertoire of the animals was recorded by a Uher 300 tape recorder coupled to an Electrovoice unidirectional microphone, with tape speeds of 7½ ips. Recordings from the Uher were analyzed on a Kay Sonograph. Ultrasonic vocalizations were studied with a Granath microphone sensitive to sounds between 5 kc. and 150 kc. Sounds were transmitted from the microphone to a Precision Instrument tape recorder 202 that recorded at 60 ips. A Krohn-Hite band pass filter 310AB eliminated noise beyond and below the *Solenodon* sounds. The sounds were then played back and photographed on an oscilloscope, using a Grass instrument 35 mm. oscilloscope camera.

Body temperatures were measured throughout a 24-hour cycle by an electric telethermometer (Yellow Springs Instruments). The thermocouple was inserted in the anus of the solenodon to a depth of 2 to 3 centimeters.

III. GENERAL MAINTENANCE BEHAVIOR³

General Comments on Activity

Solenodon paradoxus appears to be strictly

nocturnal. It avoided bright lights and almost all exploratory activity was confined to the early evening hours. During the day, the animals would arouse from time to time and scratch or defecate but prolonged excursions out of the nest box were always curtailed in the presence of bright light.

In the laboratory *Solenodon* exhibits a slight diel variation in its body temperature but shows no tendency to slip into an annual period of torpor so characteristic of certain tenrecoids such as *Echinops* (Herter, 1962a, 1962b). An adult female *Solenodon* remained active throughout more than one year in captivity, including the summer months when twenty *Echinops* in the same room were torpid (room temperature 20-23° C.). Table 1 indicates the contrast between *Solenodon* and *Echinops* with respect to thermoregulation. The data in this table were recorded in March and April of 1965 when the laboratory colony of *Echinops* was torpid. The cloacal temperature of *Echinops* fluctuated with the ambient temperature, remaining only .6 to 1.6° C. above the environment, whereas the rectal temperature of a female *Solenodon* was maintained at an average level of 6.4° C. above the ambient.

Locomotion and Rest

On a plane surface during a slow walk the animals employ a crossed extension limb synchrony but when disturbed a quadrupedal ricochet is exhibited, with the forelimbs and hindlimbs alternately striking the ground. Solenodons can run surprisingly fast and if familiar with their living space they are quite able to move directly to the nearest shelter. They seem incapable of jumping but can climb, using a slow crossed extension pattern of coordination. When climbing, they reach up with the forelimbs while resting on the hind limbs and the stout, muscular tail.

When alone, a solenodon sleeps on its side, generally curled in a semicircle. When two animals sleep together the sleeping postures are quite variable, and generally one crawls under the other. The bottom animal usually maintains a posture on its side but the top animal often lies prone at right angles to its partner's body.

Attitudes During Exploration

The behavior patterns during the exploration of a novel environment are not markedly different from those of other mammals (Eisenberg, 1963; 1964). At first the animal moves slowly, pausing to assume an elongate posture generally with one forepaw raised off the ground. Later on an upright posture may be assumed with both forefeet off the ground while the head is rotated

³Unless otherwise defined, all behavioral terms are identical with those described in Eisenberg, 1963.

TABLE 1. COMPARISON OF THERMOREGULATION BETWEEN *Echinops* AND *Solenodon paradoxus**

Specimen	Number of Readings	Range of Ambient Temperature C°	Range of Rectal† Temperature C°	Average Difference between Rectal and Ambient Temperatures
<i>Solenodon</i>	10	24.0-26.8	30.5-33.7	6.4° C.
<i>Echinops</i>	33	21.0-27.3	21.4-28.4	.6° C.
	32	21.0-27.3	22.3-31.6	1.6° C.
	33	21.0-27.3	21.8-30.2	1.3° C.

*Data were taken at 3- to 4-hour intervals throughout at least one 24-hour period from three adult *Echinops* and one adult *Solenodon* during March and April, 1965.

†Cloacal temperatures for *Echinops*.

to the left or right or bobbed up and down. Cracks and interfaces are sniffed thoroughly and the long, flexible snout is inserted in any and all available niches. After a thorough investigation of a novel area the animal establishes paths which are then utilized in a stereotyped fashion.

Attitudes of Defense and Escape

When startled by a sudden motion or disturbance, a solenodon generally flees. If it is in a familiar area, the flight response is directed toward the nearest shelter. When seized by the tail, it makes strenuous efforts to pull away, but it will also turn and attempt to bite. The claws are extremely sharp and a struggling animal may inflict deep scratches on the handler. Nevertheless, with some dexterity a solenodon can be caught and held with impunity. A fast-moving, cat-sized predator should have no difficulty in dispatching it, and it is not surprising that on Hispaniola the introduced cat, dog and mongoose apparently have been responsible for the decline in numbers of the solenodon. Prior to the introduction of these animals, the island was apparently free from medium-sized or large predators.

Comfort Movements and Care of the Body Surface

The yawn, shake and stretch exhibited by *Solenodon* are basic patterns common to all mammals. In addition, the solenodon may rub its side against logs or grass and wipe its snout by lowering the head and drawing the nose through the soil. A stereotyped washing sequence involving the tongue and forepaws is lacking. The tongue and teeth are occasionally employed to clean the flanks but the forepaws were never employed in self-care. Instead, the hind feet are used to scratch almost the entire body and thus become the dominant "cleaning organs." The extremely

flexible hip joint permits a rather complete coverage of the body surface except for the rump and perineum. Interestingly, hair is entirely lacking on the rump, around the base of the tail and around the anus. It would appear that this is an adaptation to the reduced role of the mouth and forepaws in self-care.

Feeding and Drinking Behavior

The solenodon takes water from a dish and laps with the tongue in a typical mammalian fashion. Its demand for water is quite pronounced, with a prolonged intake after arousal and after feeding. Water intake is undoubtedly related to the amount of moisture contained in the food, and in the wild the solenodon's diet of invertebrates with a high water-content may permit it to move independently of a permanent free-water source. When drinking from a dish, the long snout is in the way and is generally bent upward in a slight bow. Even so, the nostrils are often submerged, whereupon the animal exhales explosively. After a period of lapping, the head is raised while the water apparently is still being swallowed. This head-raising was also noted when the animal was swallowing or chewing foodstuffs and may be functionally related to swallowing in that the esophagus is straightened and held at a constant descending slope. It also permits the animal to survey its surroundings immediately after being engaged in drinking or chewing. This could be of adaptive significance in permitting the detection of predators.

The mode of capturing food varies somewhat with the type of prey and the circumstances of foraging. The basic act is quite stereotyped: the animal moves about with its nose to the ground, sniffing and poking it into any crack or under any object. If a prey object (*e.g.*, a cricket) is contacted with the nose, the animal simultaneously extends its forepaws on either side of the prey while sliding its head forward. As it scrapes

back with its forepaws, the mouth opens and the undershot lower jaw is slipped under the cricket, thus completing the catch. The forepaws are also used to dig in the earth or tear open logs. Insect larvae or centipedes are captured easily since the narrow lower jaw fits into many of the natural cracks and larval tunnels of rotten logs.

While foraging, the snout is moved constantly. The prey is apparently located by tactile and perhaps by auditory or olfactory stimuli. The great mobility of the snout permits a considerable "search radius" as the animal moves slowly forward. The long claws and powerful forelimbs permit both burrowing and the tearing up of rotten logs. If the substrate is very loose, the animal will move forward with the tip of the snout about half an inch to an inch below the surface of the soil.

The prey-capturing movements are so stereotyped that they are often shown even with respect to prepared foods presented in a dish. Female J was prone to utilize the forepaw reach and/or digging movements when eating from a dish. As a result the food would be scattered all over the floor and each individual piece of meat would be "captured." Male M was less prone to exhibit these movements and often ate by a combination of lapping with the tongue and scooping with the lower jaw. The animals are somewhat at a disadvantage in eating soft food from a dish or from a plane surface. If the artificial foods are liquid enough they can be lapped, but more solid foodstuffs are often "captured" with stereotyped movements.

Large prey objects such as mice are picked up in the mouth, chewed and shaken by rapid, alternate, lateral head movements. While the animal sits on its hindlegs and holds the prey in its mouth, the forepaws are used (alternately or simultaneously) to tear the exposed body distally. The carcass is thus torn to pieces and each piece is picked up and eaten in turn. The jaw movements are vertical with no apparent side-to-side chewing motion, but at any given time only one side of the jaw is employed during the shearing action of the molars.

Although pieces of food are picked up and carried, the animals never cached food in the den nor did they bury food in any special place (see also Mohr, 1938).

Elimination and Marking

Urination and defecation are generally performed together after the animal has aroused and left the nest. During defecation the tail is bent slightly upwards while the animal rests on all fours in a slightly-hunched posture. As the animal moves away from the newly deposited

feces it may depress its anal region and drag it on the substrate. There is no kicking back movement or attempt to cover the feces. In captivity defecation and urination appeared to occur randomly in the cage, with one exception. If the animals defecated during the day they used one spot immediately adjacent to the nest entrance. The inhibiting effect of light appeared to prevent a longer excursion.

Marking is generally defined as a behavior pattern serving to deposit some chemical substance employed in olfactory communication. Feces and urine are potential substances for chemical communication but, as explained previously, they are not localized except at the entrance to the nest box. The animals have pronounced glandular areas on the ventrum, axilla and flanks (Mohr, 1937), but aside from the occasional side rub described under "Comfort Movements" there were no stereotyped marking movements. Perhaps glandular secretions are left behind in the course of the animal's foraging activity, or again the depressing and dragging of the anal region after defecation may serve to spread exudates from the anal glands, but novel marking movements were not observed in this study.

Construction of Artifacts

As reported by Mohr (1938), *Solenodon* digs tunnels and may live in small family groups within the same burrow system. It is doubtful whether nesting material is carried to the burrow; no transport of nesting material by juveniles or by non-breeding adults was observed in captivity. A parturient female may, however, build a nest and is quite capable of transporting materials in her mouth. Each day during July, a solitary female that had nursed a young eight months earlier, constructed a nest of shredded newspapers sometime after the daily cleaning of her cage. Earlier in the spring we observed no nest building; therefore, the behavior may be related to sexual activity.

IV. PATTERNS OF SOCIAL BEHAVIOR *Communication*

Classically, the forms of animal communication are as variable as the sense organs capable of receiving the potential signals. In *Solenodon* the small eyes and nocturnal habits preclude vision as a dominant communication channel and leave us with a consideration of the chemical, tactile and auditory senses. The forms of tactile communication will be discussed under encounter behavior. The chemical aspects of communication were not studied but judging from the ubiquitous gland fields on the body it is of no small importance. As for the auditory

TABLE 2. PHYSICAL DESCRIPTION OF *Solenodon* VOCALIZATIONS

1. Soft Squeak	Eleven recordings from two individuals were measured. Greatest energy: 2,100 cps. to 3,600 cps. or 1,800 cps. to 2,300 cps. Harmonics are present at 4,800 to 6,300 cps. or 3,300 to 4,100 cps. Duration of sounds ranged from .03 to .13 sec. Interval between sounds in a series ranged from .17 to .80 sec.
2. Twitter	Two series from one individual. Greatest energy: 1,700-2,200 cps. Harmonics are present at 2,800 and 3,300 cps. Duration of sound series is about .13 sec. while each component averages 25 msec. with a separating interval of 5 msec.
3. Chirp	Four recordings from one individual. Greatest energy: 2,500-3,400 cps. Harmonics blurred but energy distribution ranges from 1,400 to 12,000 cps. Duration: .1 to .2 sec.
4. Click	Energy concentrated at 9,900 to 31,000 cps. Average of 11 pulses: 16,000 cps. Duration: 0.1 to 3.6 msec. Average of 9 pulses: 0.8 msec. Delivered in bursts with numbers of sounds varying from 1 to 6 within a given burst.

aspects of communication, a list of sounds follows, with a discussion of their potential communicatory significance (Table 2 and Plates I & II). Although no experiments were done to verify the signal value of these sounds, the vocalizations show remarkable similarities to those of soricoids.

1. Chewing.—The vertical jaw movements generally produce an audible smacking or crunching sound. These chewing sounds often attract the cage mate.

2. Digging Sounds.—The usual shuffling sound of forepaw movements and kicking back often serve to attract the cage mate.

3. Sounds Accompanying Walking or Running.—The sounds accompanying rapid movement often induce movement and following in a young animal.

It appears that the animals learn to associate sounds of digging or chewing with food and these sounds promote aggregation and social cohesion. This was especially true of the J and M relationship. The young male (M) was quite prone to remain in contact with J, and again the sounds of her movements served to direct and coordinate his movements.

4. "Puff."—This sound is a sharp exhalation which seems to function in the clearing of nasal passages.

5. "Piff."—This explosive sound is a variant of "Puff."

6. Cough.—This sound accompanies sudden explosive exhalations through the throat.

Vocalizations

1. Twitter.—This is a sound of uncertain sig-

nificance. It is generally heard when a specimen is excited at feeding time, when an animal is picked up or during contact-promoting behavior. It appears to be a repetitive version of vocalization 3, below.

2. Chirp.—This is a single, forceful note given when an animal is in an upright defensive posture.

3. Soft Squeak.—This sound is repeated in bursts of two or three notes during contact between two familiar animals which have been separated.

4. Squeal.—This long, high-pitched sound accompanies a fight.

5. Click.—This is a sharp, high-pitched sound produced during exploration of a novel area or when initially encountering a strange animal. This vocalization is similar to the echolocation pulses of shrews (Gould, 1964). In common with shrew pulses, there is no frequency modulation.

Interaction During an Encounter

An encounter between two solenodons strange to each other is marked by several interesting features. One or both animals approach with head raised, mouth half-open, and nose twitching. Puffs and piffs are clearly audible but these sounds may be concomitants of clearing the nostrils and have no direct communicatory function. Ultrasonic clicks are produced and, in addition to their presumed communicatory significance, these sounds may serve to localize the partner. The slow approach with heads raised continues until the vibrissae touch. The noses may then touch, whereupon several variations can occur. (1) It is not uncommon for one

animal to seize the snout of the second in its mouth. The snout is gently held for a few seconds and then released. (2) Contact is also maintained by pushing the nose tip into the ear of the partner. (3) As a variant, the animals may stand parallel to one another while one (or both) pushes the nose into the axilla, groin or flank or presses the snout on top of the rump. These three patterns of initial contact serve to keep the position of the mouth "neutralized" and allow the glandular areas to be sniffed.

A similar pattern is present in two genera of tenrecs, *Centetes* and *Microgale*, and appears to serve the same function. However, the jaws merely enclose the snout of another tenrec and were never seen to clamp on it. This distinctive behavior pattern of *Solenodon*, *Centetes* and *Microgale* is obviously another variation of mouth-to-mouth contact which is discussed in a phylogenetic sense by Tembrock (1964).

Contact between solenodons may be reinforced by licking on the rump or back and in addition one animal may place its forepaws on the back of the partner while it presses the nose firmly against the rump or presses across the back and on the flank of the opposite side of the partner.

Agonistic behavior may develop out of an encounter and generally involves "rumping" or pushing suddenly with the hidequarters against the body of the partner. A partner may also be pushed by a sudden jab with the snout. Active aggression may be manifested by slapping with a forepaw, kicking with the hindfeet or delivering a slashing bite by moving the head from side to side while snapping the jaws. Occasionally, both animals may rise upright on their hindlegs and, while keeping their balance, push against one another with their forepaws. This stance may include grasping the partner with the forepaws, and if one animal is toppled both may roll together on the ground before separating.

A defeated animal will generally avoid the second by moving away or fleeing. An aggressively aroused animal has been observed to chase a second animal, but no sustained aggressive behavior was noted. None of the agonistic interactions is unique but all are variations on common mammalian behavior patterns (Eisenberg, 1962; 1963; 1964).

Interaction Patterns among Cage Mates

The two adult females (A and B) as well as the young pair (J and M) were kept as two separate social units. The cagemates slept together and exhibited little agonistic behavior except at feeding. At feeding time, rumping, wrestling, rushing and moving away were commonly ex-

hibited between J and M. J was dominant until M reached about six months of age, whereupon a definite dominance reversal occurred and M was allowed first position at the feeding dish. Gradually the rivalry at the food dish declined since M was not as prone to attack as J had been in the previous months.

The adult females slept in contact but generally avoided play or intimate contact when they were foraging in the cage. The two juveniles were quite active and indulged in frequent contact, which included nose to nose, nose to body (the body loci included those previously discussed), rubbing one side of the body against the partner, following and wrestling. Wrestling was a slow version of the upright and rolling fight described previously and it never ended in a chase or in bloodshed. Occasionally one animal would slide its head under the chin of the partner exhibiting a head over-head under configuration. Very infrequently one animal would lick the other on the back or rump. (See also Mohr, 1936 I).

V. ONTOGENETIC ASPECTS OF BEHAVIOR

Since M was judged to be about four months of age at the beginning of the study, we possessed a unique opportunity to study the changing behavior of M and his relation to J as he matured. M possessed a marked tendency to follow J and learned to eat at least one food item by association with J at feeding time; however, at the time of his dominance assertion (two months later) he was no longer prone to follow J in an open field-testing situation.

Although the following response was very strongly developed in M, J was also prone to follow and, on occasion, would move behind M if he initiated a sustained movement. M not only followed, but he also attempted to contact J whenever she stopped. He would rest his nose on her rump or nape and occasionally attempted to climb on her or under her (see also Mohr, 1936 I; 1937). Initially, he preferred to eat from the same dish as J and this led to a certain amount of antagonism from J; however, he persisted and was generally on hand whenever she fed.

J was adept at catching crickets from the beginning, but M did not attempt to catch or eat them. The animals were tested alone with crickets for five days and J always captured and fed while M would sniff and occasionally capture with his forepaws but did not feed. On the sixth night they were fed together. Since M always followed J and attempted to feed with her, he was exposed to the crickets and actually licked her mouth while she was chewing. This associa-

tion was sufficient to induce him to bite the next cricket and, after dropping it, to pick it up and eat it. Thereafter M caught and ate crickets which were presented to him. It is interesting to note that the young of *Echinops telfairi* have also been observed to lick the mother's mouth when she is feeding. The usual avoidance movements are not initially shown by the mother to her very young offspring and it would appear that parental food preferences can be transmitted to the young in this fashion. Of course, if this learning is to occur the young must be with the female as she forages, hence there must be a strong following tendency on the part of the juvenile and a further tendency to seek out and maintain physical contact with the mother when she feeds. It seems probable in the case of our *solenodons* that M treated J as a parental object and was exhibiting behavior patterns typical of a juvenile-adult situation.

In summary it would appear that the young mammal develops associations among the various stimuli such as parental odor, tactile input, warmth and nourishment. As the juvenile matures it seeks to follow the parent and maintain on olfactory and tactile input. The sounds of the parent as it moves and forages become synchronizing and directional signals to which the juvenile responds. Chewing sounds become associated with feeding and mouth to mouth contact helps to establish food preferences. The parent can serve to direct food preferences as well as the choice feeding loci. Specialized insectivores such as *Solenodon* may derive a special benefit from a prolonged association with the family group, since feeding loci and food selection could thus be insured in each generation. This may account for the small family groups of *Solenodon* that are frequently caught in the same tunnel (Mohr, 1937).

VI. SOME COMPARISONS OF *Solenodon* WITH OTHER INSECTIVORA

One of our objectives was to determine whether *Solenodon* shared behavioral traits with the Soricidae which might bear on its taxonomic status. Shrews of the genus *Sorex* and *Blarina* emit pulses which serve as a crude means of echolocation (Gould, 1964). The Tenrecidae also echolocate (Gould, 1965); *Echinops*, *Hemicentetes*, *Microgale* and probably *Centetes* utilize tongue clicks rather than pure tones as in shrews. Clicks of the tenrecs range between 5 kcs. and 17 kcs. Shrews produce ultrasonic pulses ranging from 25 kcs. to 60 kcs., the sounds probably originating from the larynx. The clicks of *Solenodon* resemble the echolocating pulses of *Sorex* more than they resemble pulses of ten-

recs. High frequency clicks of both *Sorex* and *Solenodon* are composed of pure tones in contrast to the clicks of tenrecs that drop in frequency at the end. Andrew (1964) has discussed the resemblance of vocalization in *Sorex* and *Tupaia* with respect to three general types of sounds. The twitter, chirp and soft squeak of *Solenodon* probably fit into Andrew's classification and a thorough analysis of tenrec vocalizations will probably fit into Andrew's general scheme.

When we turn to other behavior patterns the picture is less clear. All of the present day insectivores are quite specialized. Although the order Insectivora is primitive in some morphological features, its members have diversified to fill a variety of niches and, as a consequence, have evolved profound differences in behavior.

In many respects *Solenodon* has a simplified behavioral repertoire. Its main specializations apparently concern an adaptation to foraging in soft litter and rotten logs. We find a long, flexible snout; under-shot lower jaw; enlarged forepaws bearing long claws; powerful forelimbs; nocturnal habits; a reduced litter size with a prolonged juvenile development; a tendency for the young to follow the parent, and the formation of small family groups. *Solenodon* does not appear to cache food and it is doubtful that it aestivates. The specializations of its snout and forelimbs appear to have prevented the retention of or evolution of complex self-care patterns involving the forepaws and tongue. The hindfoot has remained the dominant cleaning organ and selection has favored the loss of hair on the rump and around the anus.

Sorex vagrans is specialized for foraging in leaf litter by being very reduced in size. Like *Solenodon*, the hindfoot is the dominant cleaning organ. Unlike *Solenodon*, it has not lost its hair around the perineum and rump, but uses its tongue in self-care and together with its subterranean activity is able to maintain its pelt free of foreign matter. *Sorex* is further specialized by having a pronounced tendency to cache food (Eisenberg, 1964).

The menotyphlan Tupaidae are very divergent morphologically, having specialized for diurnality and having evolved complex marking patterns involving a special chest gland. In *Tupaia glis* the forepaws and mouth are dominant cleaning organs (Kaufman, 1965). However, the specializations in marking and body care typified by *Tupaia* should not be thought of as necessarily advanced. Complex marking and cleaning movements are exhibited by many species of the Tenrecidae and Erinaceidae.

Erinaceus europaeus, the hedgehog, does not

exhibit cleaning movements with its forepaws but it does have a complex, stereotyped marking pattern termed "self-anointing" or *Selbstbespucken*. Essentially this pattern consists of licking a foreign substance (e.g., urine, feces, etc.) while accumulating a mass of saliva in its mouth. This saliva is then spread on the sides of the body with the tongue (see Herter, 1957; Eisentraut, 1953). No other insectivore appears to show this response except the arboreal tenrec, *Echinops telfairi*, which has evolved a similar pattern. *Echinops* will sniff and lick urine of another tenrec and then wipe a forepaw in the urine. Resting on three legs *Echinops* will reach back with its forepaw and spread the mixture of urine and saliva on its side. It does the same after rubbing its forefeet in sand or on the waxy surface of certain *Euphorbia* plants. As with the true hedgehog, the process is stereotyped and repetitive. In addition it should be noted that in contrast to *Erinaceus*, *Echinops* has a complex, stereotyped washing pattern involving the forelimbs in which it sits hunched on its hindlegs while alternately wiping its muzzle with its forepaws (see Herter, 1963a).

Outside the breeding season *Solenodon* generally does not build a nest. In this respect adult *Centetes*, *Erinaceus* and *Echinops* are similar. However, *Erinaceus* will build a leaf nest at the time of hibernation and young *Centetes* build a nest when the room temperature drops. On the other hand, several genera of shrews, including *Sorex* and the tenrec, *Hemicentetes*, habitually build nests regardless of the season and their reproductive state.

Finally it should be mentioned that *Centetes caudatus*, although lacking complex cleaning movements with the forepaws, has a specialized comfort movement at the time of defecation. The animal invariably digs a hole with its forepaws, deposits the feces in the hole, and then covers the feces by a combination of backward thrusts with the forepaws and the hindfeet.

We wish to reiterate that although the behavior patterns of *Solenodon* are simplified they do not necessarily reflect a behavioral simplicity common to morphologically primitive mammals. In our brief review we have indicated the existence of rather complicated marking and comfort movements in the primitive Erinaceidae and Tenrecidae as well as in the advanced Tupaiidae. It may well be that the lack of behavioral complexity is a primitive trait in *Solenodon* but it is equally probable that *Solenodon* represents an endpoint in specialization for a certain type of foraging efficiency and exhibits a reduction with respect to certain forms of behavioral complexity.

SUMMARY

Observations on captive solenodons were undertaken in 1962 and 1964 but during the winter and spring of 1965 two adult and two juvenile specimens of *Solenodon paradoxus* were studied intensively for three months. A series of standard tests were run in order to study their maintenance and social behavior. With the exception of mating behavior and early parental care, the behavior patterns of *Solenodon paradoxus* were described in detail. *Solenodon* exhibits a rather specialized set of foraging patterns with an overall simplification of its behavioral repertoire. Its vocalization patterns resemble those of the Soricidae and Tupaiidae. *Solenodon* produces high-pitched vocal pulses similar to the echolocating sounds employed by *Sorex*.

The simplified behavioral repertoire of *Solenodon* may well be the result of specialization rather than representative of a primitive mammalian condition.

ACKNOWLEDGMENTS

The advice and cooperation of Mr. Joseph A. Davis, Curator of Mammals at the New York Zoological Park, are deeply appreciated.

Initial studies of sound recordings of *Solenodon* were conducted when Gould worked under the direction of Dr. Alvin Novick of Yale University.

REFERENCES

- ANDREW, R. J.
1964. The displays of the primates. In: Evolutionary and genetic biology of primates (John Buettner-Janusch, Ed.). Academic Press, N. Y., 2: 227-309.
- EISENBERG, J. F.
1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *P. californicus parasiticus*. Behavior, 19: 177-207.
1963. The behavior of heteromyid rodents. Univ. Calif. Publ. Zool., 69: 1-100.
1964. Studies on the behavior of *Sorex vagrans*. Am. Midl. Nat., 72: 417-425.
- EISENTRAUT, M. C.
1953. Sichbespucken bei Igel. Zeit. f. Tierpsychol., 10: 50-55.
- GOULD, E.
1964. Evidence for echolocation in shrews. J. Exp. Zool., 156 (1): 19-38.
1965. Evidence for echolocation in the Tenrecidae of Madagascar. Proc. Amer. Phil. Soc. (In press).
- HERTER, K.
1957. Das Verhalten der Insektivoren. Handb. d. Zool. VIII, Lieferung, 9: 1-50.

- 1962a. Über die Borstenigel von Madagaskar (Tenrecinae). Sitzgsber. Ges. Naturf. Freunde Berlin, N. F. 2: 5-37.
- 1962b. Untersuchungen an lebenden Borstenigeln (Tenrecinae). I. Über Temperaturregulierung und Aktivitätsrhythmik bei dem Igel-tanrek *Echinops telfairi* Martin. Zool. Beiträge, N. F., 7: 239-292.
1963. Untersuchungen an lebenden Borstenigeln (Tenrecinae). II. Über das Verhalten und die Lebensweise des Igel-tanreks *Echinops telfairi* Martin in Gefangenschaft. Zool. Beiträge, N. F., 8: 125-165.
- KAUFMANN, J. H.
1965. Studies on the behavior of captive tree shrews (*Tupaia glis*). Folia Primat., 3: 50-74.
- MCDOWELL, S. B.
1958. The greater Antillean insectivores. Bull. Amer. Mus. Natur. Hist., 115: 115-214.
- MOHR, E.
1936-38. Biologische Beobachtungen an *Solenodon paradoxus* in Gefangenschaft (Parts I-IV). Zool. Anzeiger, 113: 177-188; 116: 65-76; 117: 233-241; 122: 132-143.
- TEMBROCK, G.
1964. Vergleichende Verhaltensforschung bei Säugetieren. Zool. Gart., N. F., 29: 241-261.

EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Sonographs of *Solenodon* vocalizations. The ordinate displays the sound frequency while the abscissa is scaled in milliseconds. **A.** A single chirp. Note the broad energy distribution at the onset and termination. **B.** A twitter. Note the harmonics. **C.** A single soft squeak. Note the single harmonic.

PLATE II

- FIGS. 2 & 3. Oscilloscope traces of sound pulses emitted by *Solenodon* as it searched an unfamiliar place. Sweep speed: 5 msec., unexpanded. The oscilloscope trace moved from left to right and bottom to top. The band pass filter was set at 5 kcps. low pass and 100 kcps. high pass.
- FIG. 2. Duration about 1.1 msec.; Frequency about 21 kcps.
- FIG. 3. Duration about 0.6 msec.; Frequency about 11 kcps.

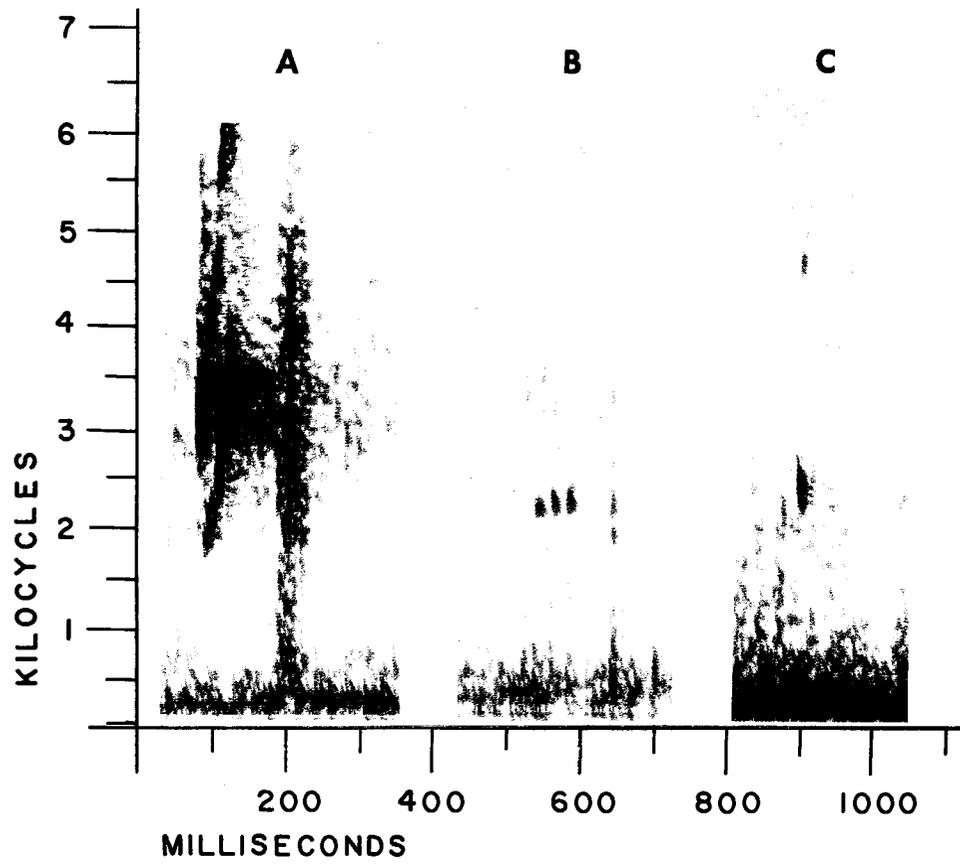


FIG. 1

THE BEHAVIOR OF SOLENODON PARADOXUS IN CAPTIVITY WITH
COMMENTS ON THE BEHAVIOR OF OTHER INSECTIVORA

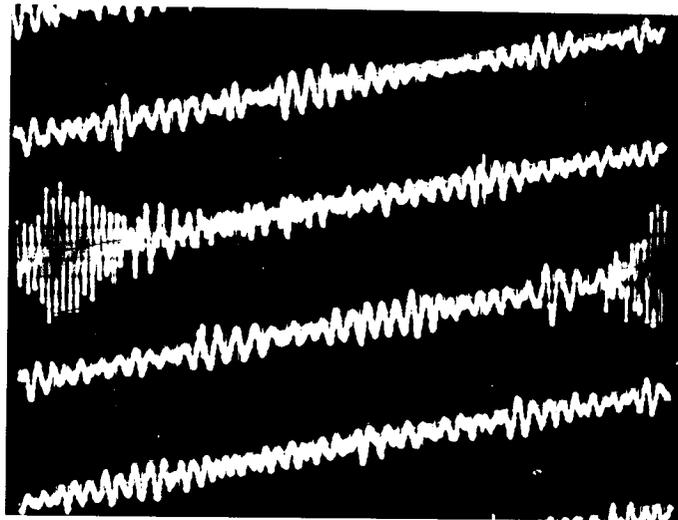


FIG. 2

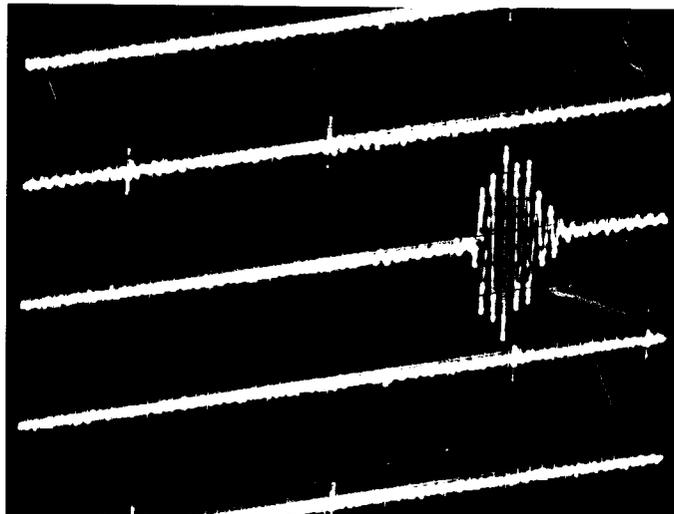


FIG. 3

THE BEHAVIOR OF SOLENODON PARADOXUS IN CAPTIVITY WITH
COMMENTS ON THE BEHAVIOR OF OTHER INSECTIVORA