

*J. F. EISENBERG  
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*The Tenrecs: A Study  
in Mammalian Behavior  
and Evolution*







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*J. F. Eisenberg*  
*and Edwin Gould*      **The Tenrecs: A Study  
in Mammalian Behavior  
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## ABSTRACT

Eisenberg, J. F., and Edwin Gould. The Tenrecs: A Study in Mammalian Behavior and Evolution. *Smithsonian Contributions to Zoology*, 27: 1-137. 1970.—Tenrecs are found only on the island of Madagascar. The biology of the Tenrecidae is described by field and laboratory studies that focused on comparisons of social behavior and communication in several species. Detailed observations on the behavior of *Echinops*, *Setifer*, *Tenrec*, *Hemicentetes*, and *Microgale* are related to ecological adaptations of each genus.

Experimental manipulations of *Hemicentetes* revealed that a sound-producing organ composed of dorsal quills functions to coordinate the movements of mother and infants. Evolutionary trends in structure and behavior of the tenrecs are discussed. The mammalian feeding niches of Panama and Madagascar are compared.

*J. F. Eisenberg  
and Edwin Gould*

# The Tenrecs: A Study in Mammalian Behavior and Evolution

## Introduction

The tenrecs are a diversified family of insectivorous mammals confined to the island of Madagascar. Including some 25 named forms divisible into 7 genera, these animals offer a unique opportunity for the study of behavioral evolution. They occur within a wide range of habitats and have adapted to aquatic, fossorial, and semi-arboreal ecological niches. Nowhere else have the insectivores displayed such a range of adaptation within such a limited geographical region. Although the tenrecs have exhibited a remarkable adaptive radiation on Madagascar, this has been accomplished with few major alterations in basic body plan; thus, we have in essence a mammal with many conservative physiological and morphological features including: an unstable thermoregulation, reduced visual capacity with concomitant dependence on auditory and chemical modes of communication, retention of the testes within the body cavity of the male, retention of the cloaca and retention of the conservative reproductive trait which involves the production of rather large litters of altricial young. With the tenrecs, then, we are presented with an opportunity to examine many of the current limits of adaptation developed by primitive Eutherian mammals.

On Madagascar, the insectivores reach their greatest size in the form of *Tenrec ecaudatus*. The streaked tenrec, *Hemicentetes semispinosus*, has evolved the most complex communications system and social grouping tendencies of any insectivore. Elaborate anti-predator mechanisms have been developed permitting

many tenrec species to compete successfully with viverrid carnivores and, thus, they prevail not as the dull-colored, small, cryptic mammals recognized as insectivores by naturalists in the temperate zone, but in many cases as large or conspicuously colored mammals (see Figures 1 and 2).

In 1963 Edwin Gould went to Madagascar to study the echolocating ability of tenrecoid insectivores and, as a result, became involved with the total biology of these animals. On his return, he brought many captive specimens with him and joined forces with John F. Eisenberg, who had initiated captive studies on the behavior of selected species of hedgehogs, shrews, and the hedgehog tenrec, *Setifer*.

In 1966 and 1967, Eisenberg and Gould returned to Madagascar to develop a more comprehensive field study on the behavior of the streaked tenrec, *Hemicentetes*, as well as the other genera. Preliminary results of these studies have been published in various journals (Eisenberg and Gould, 1966 and 1967; Eisenberg and Muckenhirn, 1968; Gould and Eisenberg, 1966; Gould, 1965).

### ACKNOWLEDGMENTS

Our research was supported by grants from the National Science Foundation and the United States Air Force.<sup>1</sup> Throughout the course of our captive studies,

<sup>1</sup>Research supported by National Science Foundation Grants Nos. GB7315 and GB4436 to Gould and Eisenberg; Air Force Grants Nos. 586-67, 586-66, and 586-64 to Gould; National Science Foundation Grant No. GB1728 to Gould; and National Science Foundation Grant No. GB3545 to Eisenberg. Research facilities and laboratory assistants were supported in the United States by the National Zoological Park-Smithsonian Institution.

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FIGURE 1.—*Tenrec ecaudatus*. This is one of the largest living insectivores. Spinescence is reduced in this species and the well-developed canines provide a strong biting defense against predation. Juvenile, 7 weeks old; molt to adult pelage almost complete.

facilities and support were generously extended by the National Zoological Park-Smithsonian Institution. We gratefully acknowledge the assistance rendered by Drs. C. Handley and H. Setzer who allowed us to utilize the collection of the Tenrecidae at the United States National Museum. Dr. G. Corbet kindly assisted us and permitted examination of the Madagascar collection in the British Museum.

During the three year course of our study on the Tenrecidae of Madagascar, a number of individuals at the National Zoological Park contributed their time and energy to the elucidation of some difficult problems. A. Underhill and B. Myton spent considerable time in the measurement of thermoregulation in the captive tenrec colony. M. Linnet studied the learning ability of *Microgale talazaci* in a T-maze and J. McAulay conducted a number of climbing tests in an open field arena with all three species of captive *Microgale*. Miss N. Muckenhirn aided the project

tremendously by hand-rearing both *Setifer setosus* and *Tenrec ecaudatus*. In addition, she submitted some rather excellent recordings of vocalizations from all of the Tenrecidae.

Mr. E. Maliniak, senior keeper at the National Zoological Park, was responsible for the captive maintenance of the colony. Mr. Maliniak kept excellent records concerning breeding, growth, and weight changes throughout the annual cycle. Our breeding success in captivity is in large measure due to his care and consideration. Miss G. Schuler lent her sensitive talents and was able to draw Figures 25, 29, 59, 60, 62, and 74 for this publication. Mr. A. Miller assisted in the 1966 expedition. During 1967, Mr. T. Schneider assisted in the field work in Madagascar. Drs. Charles Berlin and Richard Chase gave valuable advice and assistance on analysis and recording of tenrec sounds. Data recording and assistance during experiments was ably rendered during the 1966 field work by Mrs. E.



FIGURE 2.—*Hemicentetes semispinosus*. One of the most specialized species of the family Tenrecidae. The bold yellow and black color pattern serves as a warning coloration to predators. The barbed detachable spines on the body and crown may be actively driven into a potential predator.

Eisenberg. Mrs. W. Holden was responsible for the final preparation of the manuscript for publication. Both authors are indebted to Mrs. E. Eisenberg for her efforts in reading every word of the manuscript and offering criticism concerning our style and clarity of expression. To all of these people we are extremely indebted.

Throughout our various sojourns on Madagascar, we received excellent cooperation from both the Institut Pasteur de Madagascar and the Institut Recherches Scientifique de Madagascar. In particular, we extend our thanks respectively to the two directors, Dr. E. R. Brygoo and Monsieur Roederer. Dr. Brygoo kindly examined tenrecs for parasites and made the information available to us. The Institut Pasteur was our primary laboratory headquarters in Tananarive. We are also indebted to Dr. Dodin, Assistant Director of the Institut Pasteur for his help.

Without the excellent cooperation and hospitality from the Department of Eaux et Forêts the entire project would have been impossible. We are particularly indebted to them for use of a headquarters building at the forestry camp in Perinet. To M. Jean Jacques Natai, Ministre de l'Agriculture; M. Georges Ramanantsoavina, Directeur des Eaux et Forêts et de la Conservation des Sols; M. Henri Andriantsiferana, Directeur-Adjoint des Eaux et Forêts et de la Conservation des Sols; M. Guy Ramanantsoa, Ingénieur Principal des Eaux et Forêts, Chef de la Division des Réserves Naturelles, des Parcs Nationaux; and M. Ferreol Rakoto, Agent Technique des Eaux et Forêts; we extend our deepest appreciation.

The following report is a summary of two years field work in Madagascar coupled with the data collected at the National Zoological Park with our rather extensive captive colony.



6 to 100 foot observation with both rechargeable battery operated light sources as well as 12 volt storage battery operated seal beam lights. Since the tenrecs were so cryptic, it became necessary to supplement field observational techniques with captive, seminatural conditions by employing large outdoor enclosures. The most elaborate observation cage constructed was located at Perinet. An area of second growth natural vegetation, approximately 85 feet by 66 feet, was completely fenced in. By means of overhead platforms, animals which were placed in this seminatural habitat could be observed very effectively with infrared illumination (see Figures 4 and 5). As a result of the field techniques and seminatural observa-

tion procedures, we obtained reasonable data concerning activity periods, food preferences, location of feeding and denning sites, and grouping tendencies.

To aid in our understanding of the ecology of the Tenrecidae, it was necessary to consider predation. By an examination of owl pellets and various "sign" in the environment, we formulated certain hypotheses concerning predation by boas, owls, and viverrid carnivores. To supplement these observations, boas and civets were kept in captivity and utilized in predator tests. These tests were conducted in a room measuring approximately 10 feet by 20 feet where the predator could be allowed to run at semiliberty before various tenrecs were introduced to it.

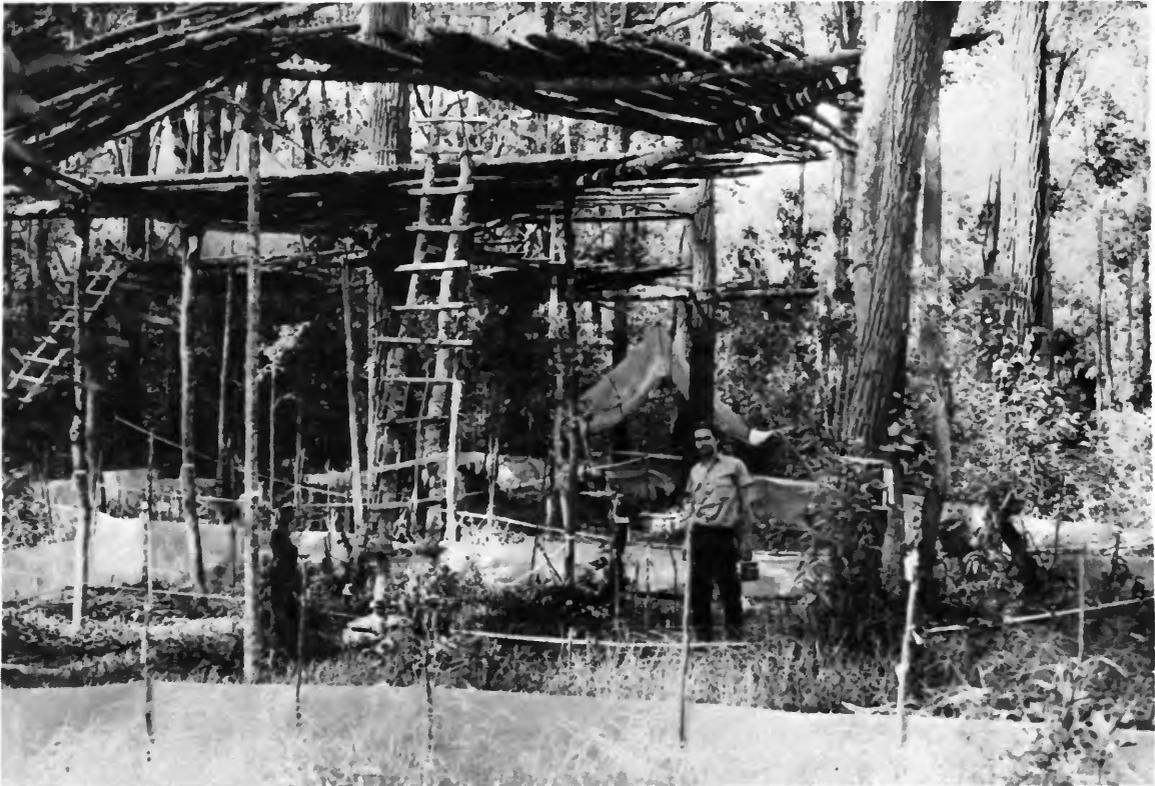


FIGURE 4.—Large enclosure with overhead platforms constructed at Perinet. Families of *Tenrec ecaudatus* or *Hemicentetes semispinosus* could be maintained in this enclosure and readily observed by means of infrared viewing scopes from the overhead platform. Ladders permitted us to quietly descend within inches of the female *Hemicentetes* as she left the nest box; in this way, glue was placed on the stridulating organ. White tapes were marked with letters and numbers as a simple mapping system. In addition, each tree and stump was lettered and numbered to facilitate recording of animal movements.



FIGURE 5.—View of small box with sliding door. This catching box was utilized in trapping female *Hemicentetes semispinosus* and displacing them with respect to their feeding young. In this way the attractiveness of the mother to the young could be studied by noting the subsequent movements of the young upon the displacement of the mother.

### CAPTIVE STUDIES

In captivity, the colony was routinely weighed and measured, giving some indication of growth potential. Rather accurate records were maintained at one period to determine food consumption for the various age and sex classes. Staged encounters between the various age and sex classes for any given species of tenrec were run according to a methodology developed by Eisenberg (1963, 1964 a, b). Such encounters permitted a description of the fundamental behavior patterns employed in social situations, including courtship and agonistic behavior. Captive breeding in Madagascar was successfully carried out with most of the tenrec species belonging to the subfamily Tenrecinae. These data enabled us to calculate such basic information as gestation period and, in addition, allowed us to supplement our behavioral studies with observations on parental care, ontogenesis of behavior, and the break-up of the family group.

At the National Zoological Park, additional records were kept on the captive colony enabling us to study such long term phenomena as growth and seasonal torpor with all concomitant weight changes and alterations of activity pattern. In addition, a breeding program was carried out at the National Zoological Park which netted us valuable data on gestation, maturation

rates, and growth. During the summer of 1966, the thermoregulatory ability of the tenrecs was also studied in some detail.

The bulk of our experimental work in Madagascar involved the analysis of communication by means of the stridulating organ found in the juvenile *Tenrec ecaudatus* and in the juvenile and adult of both species of *Hemicentetes*. By direct observation of the animals under seminatural conditions, it was possible to define those circumstances under which stridulation took place. To refine our observations, we attempted to correlate the type of stridulation with a given motivational state displayed by the animal in question. For this reason, tenrecs of the genus *Hemicentetes* were subjected to varying alterations in the ambient environment by conditioning them to either a constant amount of light or a constant sound volume and then suddenly changing the intensity of the stimulus input. By this means, the animals were induced to adopt varying degrees of spinal erection and concomitant arousal. In conjunction with these observations, we were able to monitor the stridulating response of the animals and formulate an hypothesis concerning the form of stridulation as a function of arousal. Once we could correlate stridulation type with overt be-

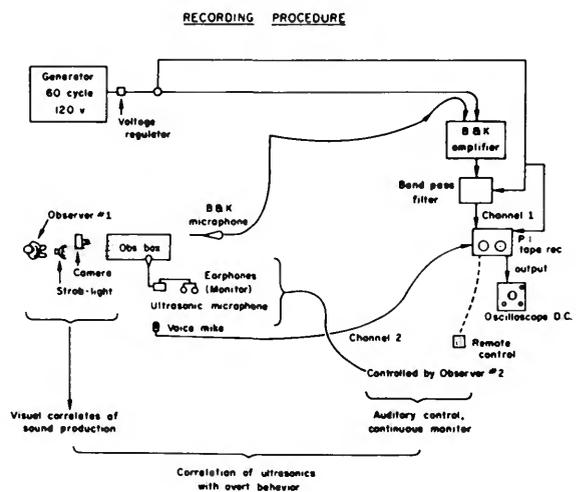


FIGURE 6.—Diagram of standard recording and playback techniques. The above figure portrays the typical hookups during recording sessions utilizing the B and K microphone, amplifier, and Precision Instrument tape recorder. Monitoring could be accomplished utilizing earphones with the ultrasonic microphone (see McCue and Bertolini, 1964; Bertolini, 1960; and Kuhl, Schodder, and Schroder, 1954) and/or with the oscilloscope. Other details are given in Appendix H.

havior, it was possible to classify the sound types and assign the varying sound types with a given motivational state. With such basic information, it was possible to design experiments which would elucidate the communicatory significance of stridulation to other members of a *Hemicentetes* group.

The sound produced by the stridulating organ has

the greatest energy concentration from 20,000 to 30,000 cycles per second. For this reason, rather elaborate recording equipment had to be employed. Figure 6 illustrates the recording and playback hook-up utilized in our experiments. Further details of procedure and results will be given in the sections to follow.

## The Island of Madagascar and its Mammalian Fauna

### MADAGASCAR: HISTORICAL REVIEW AND CURRENT STATUS OF HABITATS

The island of Madagascar is located in the western portion of the Indian Ocean roughly 250 miles from the coast of East Africa. It is the fourth largest island in the world, being 995 miles in length and having a maximum width of approximately 350 miles. It includes an area of 227,760 square miles, lying in the southern hemisphere between 11°57' and 25°38' south latitude. The island is dominated by a central plateau rising between 2500 and 4500 feet above sea level. On the east coast the plateau drops off abruptly. The eastern region is subjected to rather heavy rainfalls and supported in former times areas of true tropical evergreen forest. To the west the plateau drops off gradually, supporting a sclerophyl forest, but in the extreme southwest an almost continuously arid condition occurs. The vegetation of the southwest is characterized by scrub and spiny succulents.

Although the central plateau was forested before the arrival of man, it has undergone extensive degradation within the last 2000 years. Widespread burning and overgrazing by the cattle herds maintained in this region has resulted in a loss of humus and extensive exposure of the underlying red lateritic clay. Deforestation of the central plateau was concomitant with the extermination of the giant lemurs (*Megadapidae*), the giant bird, *Aepyornis*, and the giant land tortoises. An extensive review of the former vegetation patterns and current status of the flora is included in the publications by Paulian (1961) and Perrier de la Bathie (1936).

An inspection of Figure 3 will indicate the major vegetation zones defined by Humbert as portrayed in Paulian (1961). The eastern zone extends from the Indian Ocean to an altitude of approximately 2400 feet; thus, the eastern escarpment of the central plateau defines the limits of this vegetational zonation. The climate of the eastern zone is characterized by abundant rainfall and high winds during the austral

winter. Immediately adjacent to the coast is an area of sedimentary deposits and dunes. The vegetation here is low and herbaceous with scattered trees. As one proceeds inland toward the eastern escarpment, the character of the vegetation changes markedly. Second growth areas contain many raffia palms, the traveler palm, *Ravenalla*, and several species of bamboo. Gradually, one encounters areas of continuous forest rich in tree ferns and tropical evergreen trees up to 80 and 100 feet in height. Depending on the latitude, such tropical evergreen forest extends well up the face of the eastern escarpment. Toward the equatorial north the eastern extent of the tropical evergreen forests lies inland to some distance, but as one proceeds southward the forested belt becomes extremely attenuated in the vicinity of Fort Dauphin.

The central area, being at an elevation averaging some 2000 feet, is characterized by a variable temperature varying markedly with the season. In undisturbed areas, the vegetation is sparse and the trees do not attain the height found in the extreme eastern area. At higher elevations on the plateau, the forest gives way to low brush. The part of the plateau immediately adjacent to the escarpment often experiences rather heavy rainfall and thus supports a dense vegetation. The type of vegetation varies greatly depending on the latitude and, again, the more northerly latitudes have the potential to support a more luxuriant flora. As one moves west across the plateau, the vegetation becomes more and more spaced approximating in the extreme western edge a savannah-like condition. As one descends from the plateau to the west and enters the vegetational zone of the west, precipitation decreases markedly and the overall climate may be considered to be dry-tropical. The vegetation is characterized by spaced xerophytes. The extreme southwestern part of the island is characterized by a lack of rainfall with a highly endemic flora, including species of *Euphorbia*, *Alloe*, *Adansonia*, and numerous species of *Didiereaceae*.

Today, the central plateau has been greatly denuded.

In the river valleys to the east, rice is extensively cultivated. Eucalyptus and pine have been introduced in reforestation attempts and, as a result, much of the endemic fauna is isolated in small pockets or absent completely from the central plateau. The best areas of the eastern type of tropical forest are still to be found along the edge of the escarpment extending towards the coast only in the extreme northeastern part of the island. Pockets of forest still representative of the western zone may be found in isolated areas 50 to 100 miles inland from the west coast. In general an investigator must be very selective in order to establish a suitable study area (see Figures 7-11).

In spite of the extensive deforestation and agricultural and pastoral activity by the residents of Madagascar, some members of the native mammalian fauna have been able to adapt and perhaps have even bene-

fited from agricultural pursuits. The invasion of agriculturists on the island brought with them such introduced mammals as the house shrew, *Suncus murinus*, and the ubiquitous rodents, *Rattus rattus*, *Rattus norvegicus*, and *Mus musculus*. Such commensals of man have had an adverse effect on some endemic species especially the native rodents and smaller insectivores; however, such specialized tenrecs as *Hemicentetes semispinosus*, *Hemicentetes nigriceps*, *Setifer setosus*, and *Tenrec ecaudatus* have not suffered from man's activities. Indeed, the rice paddies supply an excellent foraging area for *Hemicentetes*, whose diet in the main consists of earthworms. In addition, the refuse heaps near villages and towns provide a foraging area for *Setifer* and *Tenrec ecaudatus*. Recent cultivation has perhaps opened new areas for colonization by some of the tenrecids.



FIGURE 7.—Typical multi-stratal tropical evergreen forest characterizing much of the eastern escarpment of Madagascar. Such forest is still present in areas which have not been utilized for primary agriculture. (View from train between Fianarantsoa and Manakara.)



FIGURE 8.—View of typical transition rainforest on the eastern plateau. Lower annual temperatures and a slight decrease in annual rainfall results in a tropical evergreen forest which does not exhibit the diversity of species or luxuriance of plant growth illustrated in Figure 7.

### THE MAMMALIAN FAUNA OF MADAGASCAR

Six orders of mammals have been represented on Madagascar in recent times.<sup>3</sup> In addition, species from four orders of mammals have been introduced within the last 2000 years by man and now have established feral populations. Today, one finds on Madagascar 11 genera of insectivores, 12 genera of bats, 10 genera of primates, 10 genera of rodents, 7 genera of carnivores, and one genus of Artiodactyla. If one includes in the fauna list those genera which have become extinct within recent times, one would need to add

<sup>3</sup> General faunal references include: DeCary, 1950. More specific treatments of mammals include: Grandidier and Petit, 1932; and Rand, 1935. Battistine and Verin (1967) discuss pleistocene extinctions. Domestic forms are not included in the present discussion.

one genus of Insectivora, 7 genera of primates, and one genus of Artiodactyla.

With the exception of the commensals of man, the mammalian fauna is now restricted for the most part to the primary and secondary growth forests along the eastern escarpment, the xeric uninhabited areas of the far west, or in the northwest lowland areas still retaining forests. The Insectivora are represented by one endemic family, the Tenrecidae, and the introduced family, Soricidae. The Soricidae include *Suncus madagascarensis* and *Suncus murinus*. The Tenrecidae are divided into two subfamilies, the Tenrecinae and the Oryzorictinae. In general, the Oryzorictinae are small and shrew-like (*Microgale*, *Geogale*) or shrew-mole-like (*Oryzorictes*). They are cryptic and seldom seen. The Tenrecinae are all larger. *Tenrec* is the largest living insectivore. The genera *Echinops* and *Setifer* are strongly convergent toward



FIGURE 9.—View of badly eroded and denuded area on the central eastern plateau of Madagascar including an isolated pocket of forest about 10 miles south of Ambatondrazaka in the Lake Aloatra basin. Soil erosion and loss of vegetation is common over much of the grazing land utilized by the pastoralists on the central plateau.

the European hedgehogs and are unique within the family Tenrecidae in possessing the ability to roll into a spiny impregnable ball. *Hemicentetes* exhibits a warning coloration, black and white in *H. nigriceps* and yellow and black in *H. semispinosus*. These species possess barbed, detachable quills and are able to defend themselves by an active offensive pattern of behavior (Herter, 1962a; Gould and Eisenberg, 1966).

The bats of the Order Chiroptera include six families, only one of which is endemic to the island. Twelve genera are encountered including: (a) Pteropidae: *Pteropus*, *Eidolon*, and *Rousettus*; (b) Vespertilionidae: *Vesperugo*, *Vespertilio*, *Scotophilus*, and *Miniopterus*; (c) Rhinolophidae: *Triaenops*, *Hipposiderus*; (d) Emballonuridae: *Emballonura*; (e) Myzopodidae: *Myzopoda*; and (f) Molossididae: *Tadarida*.

The Carnivora includes one family, the Viverridae, divided into four subfamilies, three of which are endemic. With the exception of the fossa, *Cryptoprocta ferox*, all are small in size. *Fossa fossa* is a nocturnal digitigrade carnivore resembling in its habits the grey fox. *Galidia* is diurnal, living in pairs, or as a solitary individual. In its habits it resembles the American marten. *Hemigalidia* (= *Solonoia*) is similar to *Galidia* but lacks the striped tail. *Galidictis* is an eastern rainforest inhabitant possessing a bold black and white longitudinal striped body pattern. *Mungotictis* is an inhabitant of the southwestern area and resembles in its ecology the eastern forest-adapted *Galidia*. *Mungotictis* possesses faint longitudinal brown stripes on a light buff background. *Eupleres* is apparently very rare. Its dentition is reduced and it feeds on insect larvae and worms. Natives report that it is semi-arboreal and it is known to store fat in its tail thus



FIGURE 10.—Xerophytic plant growth of the southwestern dry zone of Madagascar, east of Tuléar. In this area the annual rainfall averages less than 700 mm per year. Probably early settlers burned great forests that once grew in this region.

indicating a possible seasonal torpidity. *Viverricula* is an introduction from Indonesia which appears to do very well in and near human habitations.

The Primates are represented by ten living genera divided into three families. All forms are endemic to Madagascar. The family Lemuridae is divided into two subfamilies, the Cheirogalinae and Lemurinae. The former contains the genera *Microcebus*, *Cheirogaleus*, and *Phaner*. The Lemurinae includes the familiar *Lemur*, *Haplemur*, and *Lepilemur*. The family Indridae contains the genera *Propithecus*, *Indri*, and *Avahi*. The last family is the most specialized and least studied, the Daubentoniidae, containing the single genus *Daubentonia*. The lemurs of Madagascar have been the subject of recent monographic studies and the reader is referred to Petter (1962) and Jolly (1967).

The native rodents comprise eight endemic genera

lumped artificially into one subfamily, the Nesomyinae. In addition, the genera *Rattus* and *Mus* are well represented in settled areas. The native rodents have radiated to form several well-defined morphological types. *Brachyuromys* is vole-like while *Eliurus* is reminiscent of the European dormouse, *Eliomys*. There are several forest-adapted rats including the more common *Nesomys* and *Brachytarsomys* as well as the rare *Gymnuromys* and *Hallomys*. In the arid southwest, one rodent genus is tending toward bipedality with elongated hind feet and an elongated, tufted tail. This is the rare *Macrotrarsomys*. In the humid west near Morondava, a unique rodent genus is found, *Hypogeomys*. This form resembles a rabbit-bandicoot or, if you prefer, a rabbit with a stout tail. Little is known concerning the ecology of the native rodents.

The Artiodactyla were represented before man's in-

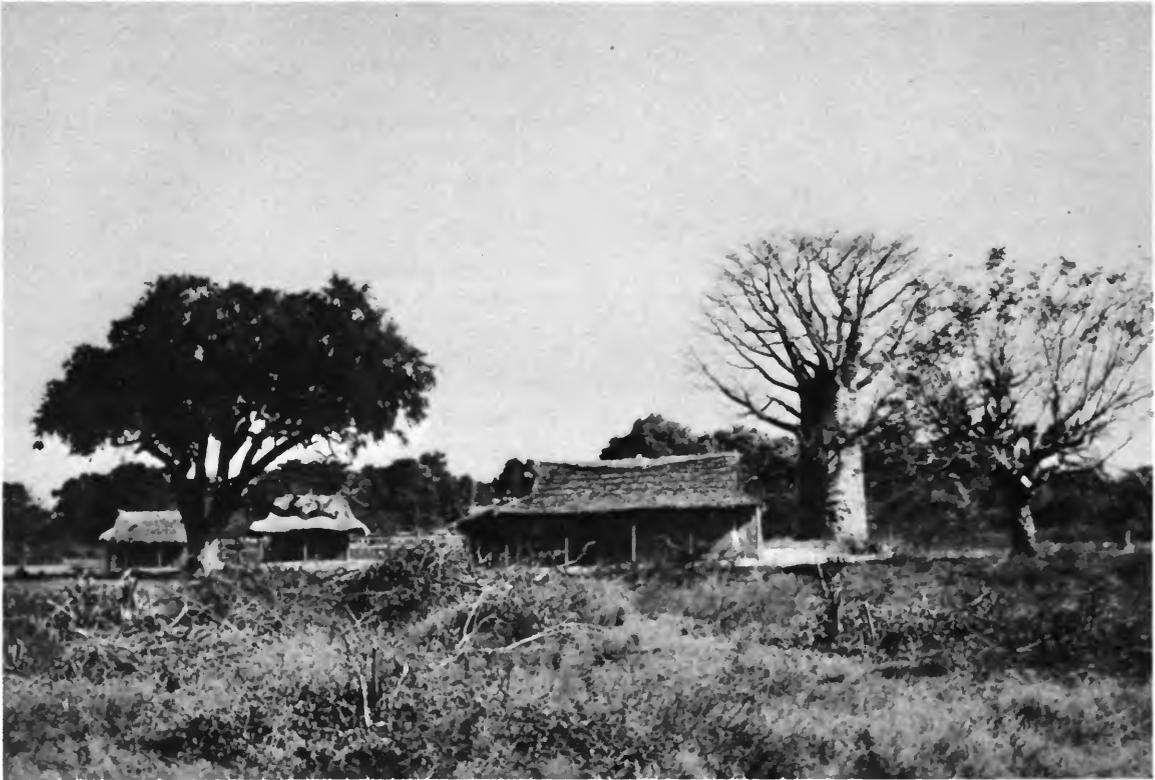


FIGURE 11.—Baobab and brush habitat in July near Morondava, west coast.

vasion by one endemic species, the hippopotamus, *Hippopotamus lemelii*. Today, Artiodactylans are represented by the introduced river hog, *Potamochoerus*.

Table 1 compares the number of genera of recent land mammals for Madagascar with the land mammals known for Panama. Such a comparison is instructive since, as in Madagascar, Panama exhibits a diversity in ecology from a seasonally arid western zone with scattered vegetation of a deciduous type to an eastern tropical evergreen forest habitat. In addition, Panama is a landbridge between north temperate and neotropical mammalian faunas, thus the opportunity for faunal diversity is maximized in Panama. Madagascar as an island represents the extreme in fauna isolation; hence, one would anticipate lack of such extensive diversity on Madagascar.

The Canal Zone area of Panama includes six genera of Marsupials. It is not surprising to find that marsupials are unrepresented on Madagascar since in the

main the mammalia of Madagascar are derived from Africa and marsupials underwent their greatest radiation in South America and Australia.

The next Order to consider, the Insectivora, is more instructive; no genera of insectivores have been recorded in the Canal Zone of Panama while twelve genera of recent insectivores have been noted on Madagascar. Although the insectivores are abundantly represented in temperate North America, only one genus, *Cryptotis*, has penetrated to South America and it is only sparsely represented in parts of Central America.

The bat fauna of the Canal Zone is represented by 40 genera whereas Madagascar has a depauperate population of only 12 genera.

The primates of Panama are represented by 5 genera whereas Madagascar exhibits 10 surviving genera and, in recent times, as many as 17 genera were to be found on the island.

The Order Edentata is represented by seven genera

TABLE 1.—Number of genera of Recent land mammals for Panama<sup>1</sup> (Canal Zone Surveys) and Madagascar

	Marsupialia	Insectivora	Chiroptera	Primates	Edentata	Lagomorpha	Rodentia	Carnivora	Perissodactyla	Artiodactyla
Panama Canal Zone										
Extant genera	6	0	40	5	7	1	19	11	1	3
Madagascar										
Extant genera	0	11*	12	10	0	0	10*	7*	0	1*
Recent fossils	0	1	-	7	0	0	-	-	-	1
Madagascar Σ	0	12	12	17	0	0	10	7	0	2

<sup>1</sup>Table adapted in part from Handley, 1966.

\*Genera recently introduced include: *Suncus*, *Rattus*, *Mus*, *Viverricula*, and *Potomocoerus*.

in Panama and nonexistent on Madagascar. Again, this is an accident of zoogeography since the Edentata evolved and radiated only in the neotropics.

The Lagomorpha are represented in Panama by one genus and are absent from Madagascar. There are 19 genera of rodents in Panama and 10 genera, including the recent introductions, to be found on Madagascar. There are 11 genera of carnivores in Panama and 7

genera on Madagascar. Panama claims four genera of ungulates; Madagascar claims two with one being a recent introduction and the other becoming extinct in recent times.

Table 2 compares the major feeding niches in Panama and in Madagascar with respect to the major genera occupying each niche within the respective geographical boundaries. An inspection of this table indicates that the ant-eating niche, well occupied by both arboreal and terrestrial forms in Panama, is incompletely occupied in Madagascar. The feeding niche defined by an insectivorous and secondarily frugivorous type is well represented both on Madagascar and in Panama. The primary carnivore niche is equally well represented. The carnivore and secondary frugivore niche is sparsely represented on Madagascar compared with Panama. The seed and fruit-eating niche appears to be equally well represented in both areas and the foliage feeding and secondary fruit-utilizing niche likewise seems to be equally filled.

Thus, with the exception of the ant-eating niche, we see that for these two tropical areas adaptive radiation has allowed occupancy of most of the major feeding niches available. It is instructive to note that primary insectivore-secondary frugivore niches are occupied in the main by lemurs and true insectivores on Madagascar whereas in Panama such a niche is occupied

TABLE 2.—Major niches and their occupants\* of Madagascar and Panama

	Ant Eaters		Primary Insectivore and Secondary Frugivore		Carnivore	
	Arboreal	Terrestrial	Arboreal	Terrestrial	Arboreal	Terrestrial
PANAMA (Major genera only)	<i>Cyclops</i> <i>Tamandua</i>	<i>Myrmecophaga</i>	<i>Marmosa</i> <i>Saguinus</i> <i>Aotus</i>	<i>Cabassous</i> <i>Dasybus</i>	<i>Eira</i>	<i>Mustela</i> <i>Urocyon</i> <i>Galictis</i>  <i>Felis</i>
MADAGASCAR			<i>Eupleres</i> <i>Echinops</i> ( <i>Microgale</i> ) <i>Microcebus</i> <i>Cheirogaleus</i> <i>Daubentonia</i>	<i>Centetes</i> <i>Hemicentetes</i> <i>Oryzorictes</i> ( <i>Microgale</i> ) <i>Geogale</i>		<i>Cryptoprocta</i> <i>Galidia</i>  <i>Fossa</i> <i>Viverricula</i>

\*Exclusive of the Chiroptera.

by marsupials and edentates, as well as primates. The carnivore-secondary frugivore niche is occupied by marsupials and carnivores in Panama whereas in Madagascar it is occupied by an insectivore and two carnivores. The foliage- and fruit-eating niche is occupied by primates, edentates, rodents, and ungulates in Panama whereas on Madagascar it is, in the main, occupied by the primates and two species of rodent. Thus, complementarity (Darlington, 1957) is exemplified, since similar niches are occupied but by differing higher taxa when one compares a continental area with Madagascar. The noticeable absence of ungulates on Madagascar has resulted in partial niche occupancy by rodents and, in recent times, by the now extinct terrestrial lemurs of the family Magadapidae.

**THE RAINFOREST AND PLATEAU**

Our study areas were chosen in order to compare and contrast the high plateau with the eastern rainforest. Alakamisy Ambohimaha, Manandroy, and Fianarantsoa typify the high plateau and, in undisturbed areas, still maintain a vegetation which is transitional between the eastern rainforest and the western transitional savannah. Ambitolah and Ranomafana are well within the typical eastern tropical evergreen forest zone. Perinet is right on the edge between the central

area and the eastern rainforest. It is still at reasonably high elevation, approximately 940 meters, and although subjected to seasonal aridity does maintain an intermediate tropical evergreen forest. This is due in part to the fact that Perinet is some 300-odd kilometers north of the Fianarantsoa study area.

In the Fianarantsoa study area of the eastern high plateau, the endemic mammals include *Hemicentetes nigriceps*, *Setifer setosus*, *Tenrec ecaudatus*, *Microgale (Nesogale) dobsoni*, and *Microcebus murinus*. Descent from the plateau to the vicinity of Ambitolah and Ranomafana results in a drastic change in faunal composition. *Tenrec ecaudatus* is still present but *Hemicentetes semispinosus* replaces *H. nigriceps* and *M. talazaci* replaces *M. dobsoni*. The carnivores, *Galidia elegans* and *Fossa fossa*, are now to be found together with the primates, *Lemur fulvus*, *Lemur rubriventer*, and *Hapalemur griseus*. The introduced viverrid, *Viverricula indica* (= *schlegeli*) is to be found in both the high plateau and lower rainforest areas.

In the vicinity of Perinet, the Insectivora include *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Microgale (Nesogale) talazaci*, *Microgale cowani*, and *Setifer setosus*. Carnivora include *Viverricula indica* and *Galidia elegans*. Primates include *Cheirogaleus medius*, *Microcebus murinus*, *Lemur fulvus*, *Hapale-*

TABLE 2.—Major niches and their occupants for land mammals\* of Madagascar and Panama—Continued

	Carnivore (or Insects) and Secondary Frugivore		Seed/Fruit (some Insects)		Primary Foliage/Fruit	
	Arboreal	Terrestrial	Arboreal	Terrestrial	Arboreal	Terrestrial
PANAMA (Major genera only)	<i>Caluromys</i>		<i>Sciurus</i>	<i>Oryzomys</i>	<i>Allouata</i>	<i>Sigmodon</i>
		<i>Philander</i>	<i>Microsciurus</i>	<i>Liomys</i>	<i>Bradypus</i>	<i>Mazama</i>
		<i>Didelphis</i>	<i>Cebus</i>	<i>Heteromys</i>	<i>Choloepus</i>	<i>Sylvilagus</i>
		<i>Procyon</i>	<i>Ateles</i>	<i>Proechimys</i>	<i>Coendou</i>	<i>Tapirus</i>
		<i>Nasua</i>		<i>Dasyprocta</i>		<i>Odocoileus</i>
	<i>Potos</i>		<i>Cuniculus</i>			
	<i>Bassaricyon</i>		<i>Tayassu</i>			
MADAGASCAR		<i>Setifer</i>	<i>Eliurus</i>	<i>Nesomys</i>	<i>Lepilemur</i>	<i>Brachytar-</i>
		<i>Galidictis</i>	<i>Hapalemur</i>	<i>Macrotarsomys</i>	<i>Propithecus</i>	<i>somys</i>
		<i>Mungotictis</i>	<i>Lemur</i>		<i>Avahi</i>	<i>Hypogeomys</i>
					<i>Indri</i>	

*mur griseus*, *Propithecus diadema*, and *Indri indri*. And finally, the native rodents include *Nesomys rufous* and *Eliurus*. Thus we see in the warmer northern regions, *Hemicentetes semispinosus* is occurring at higher elevations; *Hemicentetes nigriceps* has disappeared completely; *Setifer setosus* is extending its range into the rainforest area and the diversity of Lemuroids is increased by the addition of *Indri*.

In both areas near the dwellings of man, *Rattus rattus* and *Suncus murinus* may be found in abundance.

Appendix A includes a list of specimens collected or sighted for the three major study areas.

### THE MADAGASCAR FAUNA IN PERSPECTIVE

The mammalian fauna of Madagascar has been derived from a series of invasions beginning in the Paleocene and ending in the Pliocene. The evidence for such invasions is well discussed in Simpson (1940, 1965), and Darlington (1957). In addition to the mammalian fauna, the entire question of faunal origin for Madagascar is dealt with extensively in the publication by Paulian (1961).

The insectivores were one of the earliest invaders evidently rafting across the Mozambique channel and have undergone the longest adaptive radiation. Their invasion was shortly followed by the migration of Lemuroids to the island followed thereafter by Carnivora and rodents. The more volant Chiroptera made successive invasions at later dates. The only Artiodactylan to reach the island without the aid of man was the hippopotamus. The long history of invasions has given Madagascar a representation of some six mammalian Orders. Noticeable absences include the Perisodactyla, the terrestrial Artiodactyla, and the Lagomorpha.

The Orders with the longest continuous history on the island (Insectivora and Primates) have exhibited the most extensive adaptive radiation and have evolved

forms to fill most of the ecological niches open to them in this tropical island. All of the adaptive radiations have been accomplished from a stem form which was rather primitive in its morphology. Thus, the tenrecs are a highly radiated primitive insectivore group; the Lemuroids are a highly radiated group but based on a primitive primate plan; and, finally, the Carnivora represent a minor radiation derived from a conservative carnivore body plan, e.g., the Viverridae.

Browsing niches were filled by primates (the giant lemurs) rather than ungulates. Aquatic otter-like niches were occupied by an insectivore (*Limnogale*) rather than by otters. Terrestrial omnivore niches were occupied by insectivores and some carnivores rather than by carnivores, marsupials, and primitive ungulates. Thus, Madagascar represents a refugium for primitive mammals and, at the same time, presents us with examples of mammals which have perhaps reached the ultimate in adaptive radiation within a conservative morphological framework.

In spite of the fact that Madagascar lies almost entirely in the geographically defined tropics, many endemic mammals show seasonal periods of torpor and a marked reproductive season (Kaudern, 1914; Petter and Petter-Rousseaux, 1963; Jolly, 1967). Seasonal torpor and reproduction appear to be adaptations to seasonal aridity. The long history of seasonal aridity on parts of Madagascar is evinced by the existence of the numerous endemic xerophytic plant species and such highly adapted desert rodents as *Macrotarsomys*. Thus, it is not surprising to find fat storage and the potential for seasonal torpor in the primates *Microcebus* and *Cheirogaleus*, the carnivore *Eupleres*, and virtually all of the Tenrecine insectivores.

Before the fauna of Madagascar disappears entirely through the continued land use by man, intensive investigations of the other mammalian orders should be mounted in order to accumulate such information as we may concerning the limits of adaptive radiation within a defined morphological framework.

## Some Negative Influences on the Numbers and Distribution of the Tenrecidae

### PREDATORS AND COMPETITORS OF THE TENRECIDAE

#### Competitors

The introduction of rodents of the genera *Mus* and *Rattus* onto the island of Madagascar has probably had an important influence on the distribution and abundance of the native Nesomyine rodents. *Rattus rattus* is a serious agricultural pest utilizing both growing and stored rice as its primary food resource. Indeed, there is good evidence to indicate that the population of *Rattus* on the island of Madagascar exhibits not only short-range annual cycles in numbers but exhibits a thirty-year plague cycle which has a devastating influence on the rice crops (Rakotomanana, 1967). In its impact on agriculture, *Rattus* has very little influence upon the native Tenrecidae but, when *Rattus* exploits refuse heaps, it occupies a niche which is potentially open to *Setifer* and *Tenrec ecaudatus*. It has been noted by Petter and Petter-Rousseaux (1963) that in the vicinity of villages and towns *Setifer setosus* adapts itself to feeding on carrion and one may assume that, when rat densities are high, this potential food resource is strongly competed for by *Rattus rattus* and *Rattus norvegicus*.

The role of *Suncus murinus* as a competitor has not been evaluated. Suffice to say that it probably does not compete with any members of the subfamily Tenrecinae but surely *Suncus* must have some influence on the distribution and abundance of certain species of the genus *Microgale*. *Suncus murinus* is trapped only in the vicinity of human settlements. In these areas its food is by no means limited to arthropods and other invertebrates but rather includes all manner of human refuse in an omnivorous fashion. In the vicinity of large villages the density of *Microgale* appears to be drastically reduced. This does not seem to be a result of modification of the habitat by humans since some species of the genus *Microgale*, e.g., *M. cowani*, are

well adapted to the interfaces between brush and grassland which are used as pasture. In addition *Oryzomys* has been able to hold its own in the vicinity of Lake Aloatra in spite of extensive rice farming. Hence, one must conclude that agricultural pursuits alone are not sufficient to account for the reduced abundance of species of *Microgale* but rather that when densities of *Suncus* occur the probability of trapping *Microgale* is reduced. This indirect evidence does suggest some subtle competitive mechanisms which work to the disadvantage of certain *Microgale* species.

#### Predators

##### SNAKES

The island of Madagascar is endowed with a rich reptilian fauna including a variety of snakes, none of which are venomous. It is certain that snakes prey to an extent on the tenrecs and to this end we instituted a special investigation on the feeding habits of the Madagascan boa, *Acrantophis dumerilli*. This species is more or less confined to the eastern vegetational zone in the vicinity of streams. It particularly favors rock outcroppings for dens. To the north and in the lowland areas of the eastern vegetational zone, the species *A. dumerilli* is replaced by *Acrantophis madagascariensis* which are rather large, thick-bodied serpents, nocturnal in their habits, and sluggish in their movements.

In order to test the efficiency of predation by boas on tenrecs, a captive *A. dumerilli* was presented with an adult *Hemicentetes semispinosus* and the incident was filmed with a 16 mm. Bolex Cin camera. Before sensing the tenrec, the boa was coiled in a striking position and, as the tenrec passed its snout, it struck, grasping the prey by the rump and simultaneously throwing one coil around its head. The tenrec was constricted to death within 3 minutes. Upon releasing

the tenrec from its coils, the boa attempted to swallow it beginning first with the tenrec's rump. Apparently being impeded by the quills, it stopped, dropped the prey, grasped it by the head end, and proceeded to swallow it completely. Although the boa received some 30-odd quills in the process of constricting the *Hemidentetes*, this seemed to have no adverse effect on the feeding process and, indeed, the boa was quite able to deal with the spinescent carcass after having made the mistake of attempting to swallow it from the posterior end.

#### RAPTORIAL BIRDS

It is assumed that hawks and owls prey upon the Tenrecidae but we were unable to confirm this by actual observation or from an examination of owl pellets. Even though owl pellets decompose rapidly in the rainforest, we were able to collect five near the villages and in every case these contained the remains of *Rattus* or frogs. Rand (1936) noted that *Buteo brachypterus* and *Gymnogenys radiatus* stomachs contained in part the remains of carrion which was identified as *Tenrec ecaudatus*. One stomach of *Circus aeryginosus* contained the remains of an unidentified insectivore.

#### NATIVE CARNIVORES

The native carnivores of the family Viverridae certainly are capable of preying on all of the tenrecid

species. To facilitate discussion of predation by the Viverridae, we will consider the behavior of three species in some detail: *Galidia elegans*, *Fossa fossa*, and *Viverricula indica*.

*Galidia elegans*.—This viverrid is approximately the size of a marten and is brown in color with the tail possessing a series of black rings for almost its entire length. The ear tips are white and it is indeed a rather elegant mammal (Figure 12). *Galidia* forages on the ground as well as in the trees. It is found throughout the eastern forest zone well into the north and passing around to the northwest. Its distribution terminates somewhere in the Antsingy region. In the extreme west *Galidia* is replaced by the closely related *Mungotictis*. *Galidia* has been observed to forage quite near the dwellings of man and appears to be a versatile carnivore.

Several observations were made on its predation habits while held in captive state. Three subjects were used and, in order to facilitate prey-catching behaviors, the animals were allowed liberty in a large room. The room was decorated with certain artifacts including vegetation, rocks and earth. When presented with a *Setifer*, the *Galidia* would approach in an elongate posture. Upon scenting the *Galidia*, the *Setifer* would immediately emit an explosive hiss and curl into an impregnable spiny ball. This would cause the *Galidia* to withdraw rapidly and, after several attempts to



FIGURE 12.—*Galidia elegans*, diurnal predator of the rainforest; also sighted at Antsingy.

touch and sniff at the *Setifer*, the *Galidia* would give up its attempts to kill it.

The situation with *Hemicentetes semispinosus* was somewhat different. Two of the *Galidia* ignored *Hemicentetes* after a preliminary investigation but the third *Galidia* was able to kill *Hemicentetes*. At first it would attempt to seize *Hemicentetes* by the head for a killing bite but it was always very careful to avoid the spines. In spite of its care, the *Galidia* was struck with spines twice in the foot; these spines were removed very carefully by the animal's teeth. From the moment of scenting the *Galidia*, the *Hemicentetes* engaged in an almost continual defensive reaction. The *Galidia* continued to tease and harass the *Hemicentetes* for approximately 28 minutes. During the first 15 minutes of the interaction, the *Hemicentetes* actively moved toward the *Galidia*, bucking its head all the while and attempting to drive the nuchal crest spines into the *Galidia's* nose.

The *Galidia* employed several techniques in toying with the *Hemicentetes*: (1) She would touch it with the forepaw in the middle of the back, attempting to pin it; (2) she would place one forepaw in the middle of the back and with her muzzle attempt to turn the animal over; or (3) holding the animal on its back with both forepaws, she would attempt to bite it in the head. (4) At times she would attempt to seize the animal between both of her forelimbs and bite it on the head; or (5) she would continue to touch the animal with one forepaw, "teasing" it. Eventually, as the *Hemicentetes* became weakened with fatigue, the *Galidia* became more bold in attempting to hold the body down with her forepaws and, finally, by carefully placing one paw in the middle of its back and another paw on its head, she was able to hold the tenrec firmly to the substrate while administering a bite at the base of its skull. It would appear that an experienced *Galidia* employs a variety of techniques, including attempts to turn over and attempts to pin before actually killing a tenrec.

The *Hemicentetes* was then consumed entirely except for the rib cage and its skin. Feeding was initiated by turning the animal onto its back and chewing the nonspinescent ventral surface.

In order to estimate the attractiveness of *Hemicentetes* to the *Galidia* which would kill them, we played back certain sounds that *Hemicentetes* makes to it utilizing a loudspeaker coupled to a precision instrument tape recorder. It was found that the stridulation of *Hemicentetes* would induce approach to the loud-

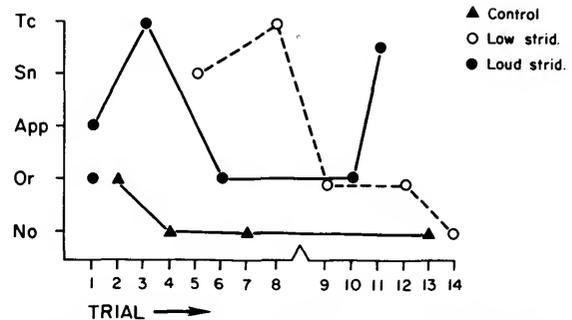


FIGURE 13.—Response of *Galidia elegans* to the sounds of *Hemicentetes semispinosus*. Subsequent playbacks indicate a decline in responsiveness on the part of *Galidia* to the same sounds of *Hemicentetes*. After Trial 8, the amplitude was increased and responsiveness was restored to the sound of loud stridulation. Responses to control stimulation were well below those of the experimental stimuli. Tc=Touch speaker; Sn=Sniff speaker; App=Approach speaker; Or=Orientate to speaker; No=No response.

speaker well above that of the control for some five repeated trials before habituation set in (see Figure 13).

That the killing of *Hemicentetes* by *Galidia* was not an artifact of captivity is certainly confirmed by the following observations: On 3 February 1966 at approximately 1500 hours, we were exploring a region of the forest near Ambitolah when we discovered one *Hemicentetes* burrow at the base of a stump which had been broken into in the vicinity of the nest chamber. The skin and forepaw of one *Hemicentetes* was deposited some 6 feet away from the actual burrow entrance and bits of skin surrounded the burrow. From the tracks we discerned that a *Galidia* had dug into the nest and killed one or two animals. Live traps had been set in the vicinity of this burrow site and, at approximately 1700 hours, one *Galidia* was trapped some 200 feet away.

*Fossa Fossa*.—The Fanaloka is approximately the size of the North American gray fox. It has a light gray body with longitudinal rows of black spots on the sides blending into short longitudinal black stripes on the neck. This animal is very fox-like in its behavior and is highly digitigrade, nocturnal, and terrestrial in its foraging habits. It appears to be confined to the mature rainforest in the eastern vegetational zone, and is not often found in the vicinity of human habitation (Figure 14).



FIGURE 14.—*Fossa fossa*, nocturnal predator of the rainforest.

Observations on captive individuals indicate that they respond mainly to scent and sounds from their prey. The ears are moved independently and apparently function in localization of small prey mammals moving in the substrate. A predation test with a captive female yielded the following results: Upon being presented with a *Hemicentetes*, the *Fossa* sniffed at it twice on the rump. Both times the *Hemicentetes nigriceps* bucked but the animal did not show a sustained bucking response coupled with offensive attack as did the *Hemicentetes* which were presented to *Galidia*.

The *Fossa* proceeded to follow the *H. nigriceps* around until it was able to position itself directly above the animal. It then bit the *H. nigriceps* in the head while the animal had its crest depressed. This was a killing bite and, immediately upon biting the tenrec, it was tossed to one side. The *Fossa* collected several quills in her lips and paused to rub them out with her forepaw. She then proceeded to eat the head and body down to and including the contents of the rib cage. The carcass was opened from the ventrum and quills were avoided.



FIGURE 15.—*Cryptoprocta ferox*, the largest Madagascar viverrid.

*Viverricula indica*.—Several attempts were made to induce captive *Viverricula indica* to kill *Hemicentetes*. This was never accomplished even when the *Hemicentetes* was permitted to remain in the open room testing area with a *Viverricula* overnight. Since we had at the time only one specimen of *Viverricula* and, further, since the habit of killing *Hemicentetes* appears to be idiosyncratic (e.g., note that two of the three *Galidia* did not kill *Hemicentetes*), we cannot conclude that *Viverricula* does not readily prey on the spinescent tenrecs, such as *Hemicentetes*. No predator

tests were run utilizing the more vulnerable *Microgale*.

*Other viverrids*.—Without running predator tests, it seems a reasonable assumption that *Cryptoprocta* (Figure 15) can and does kill *Tenrec ecaudatus*. It would appear equally possible that juvenile *T. ecaudatus* are killed and eaten by the other smaller Viverridae. All of the *Microgale* appear to be vulnerable to predation by the viverrids, although as previously stated tests were not run. The hedgehog tenrecs of the genera *Echinops* and *Setifer* may be less vulnerable

than *Hemicentetes*. *Hemicentetes* is surely less vulnerable than *Tenrec ecaudatus* if the predator is large enough to overcome the latter.

The specialized feeding habits of *Eupleres* probably rule it out as a significant predator on any of the Tenrecidae with the exception of the smaller species of *Microgale*. The feeding habits of *Galidictis* are unknown and, until further information concerning its biology is revealed, we must leave open the question of its predator capacity.

In the far west *Mungotictis* obviously occupies an ecological niche quite similar to *Galidia* and it seems safe to assume that this animal could be a significant predator on such western tenrecids as *T. ecaudatus* and *Geogale*. In the region northeast of Morondava *Mungotictis* was seen eating a dead land snail as well as lizard eggs (*Hoplurus*) that it had unearthed.

#### DOMESTIC DOGS AND CATS

The villagers were questioned concerning predation by dogs and cats on tenrecs and the reports showed remarkable uniformity. The hedgehog tenrec, *Setifer*, was seldom if ever taken whereas juveniles of *Tenrec ecaudatus* were generally attacked by dogs. *Hemicentetes* seemed invulnerable to dogs and cats; however, a missionary in Fianarantsoa reported a dog which had learned the trick of teasing a *Hemicentetes* until it became exhausted and then turning it on its back to deliver a bite to its vulnerable underside.

#### SUMMARY OF PREDATION STUDIES

Although the stomach analyses published by Rand (1935) indicate that *Galidia* and *Fossa* prey on birds, reptiles, and insects, it would appear from our studies that the native and introduced carnivores do prey from time to time on the tenrecs. Of the Tenrecinae, juveniles of *T. ecaudatus* would appear to be particularly vulnerable, *Hemicentetes* less vulnerable, and the hedgehog tenrecs the least vulnerable of all. The Oryzoricinae are probably more subject to predation than the more specialized genera of the Tenrecinae. It is interesting to compare the predator tests run with *Galidia* and *Fossa fossa*. That *Fossa fossa* was able to dispatch its *Hemicentetes* with less delay may be related to the fact that *Fossa fossa* has longer canines. A killing bite through the skull could be delivered by *Fossa fossa* with less possibility of receiving a spine from the *Hemicentetes*. Upper canines of a skull of *Fossa fossa* (USNM 318107) gave an overall length of 12.6

millimeters. A canine measurement of a mature male *Galidia elegans* (USNM 318105) gave a length of 7.25 millimeters.

#### PARASITES AND DISEASES OF THE TENRECIDAE

Ectoparasites were noted for all genera of the Tenrecidae which we captured; however, *Tenrec ecaudatus* and *Hemicentetes semispinosus*, as well as *H. nigriceps*, appear to be the most heavily infested species. Ixodid ticks were collected from *Setifer*, *Hemicentetes*, and *Tenrec*. Mites of the family Gamasidae heavily infested *H. semispinosus* and *H. nigriceps*. Fleas (Siphonaptera) were occasionally collected from *Tenrec ecaudatus* and *H. semispinosus*. The *Microgales* occasionally exhibited gamasid mites but, in general, appeared relatively free of ectoparasites. In captivity several individuals exhibited alopecia resulting from a fungus infection. This disease was readily treated with griseo fulvin.<sup>4</sup> The infestation of *Hemicentetes* with mites may in part account for the frequent change in denning sites which we noted in our mark, trap, and release studies (see p. 91).

In general, tenrecs of the genus *Microgale* were relatively free from endoparasites in the gut; however, at least one specimen of *M. (Nesogale) dobsoni* was found upon autopsy to be infected with Nematodes subcutaneously in the subserosal area of the abdomen. *Tenrec ecaudatus* may be lightly parasitized with Ascaroidea, Trichinelloidea, and Strongyloidea of the family Ancylostomidae. *Hemicentetes semispinosus* has been noted to be lightly infested with Ascaroidea. *Setifer setosus* on one occasion exhibited an unidentified genus of Taenioidea and one specimen of *M. (Nesogale) talazaci* was noted to be parasitized by Trichinelloidea (*Trichuris*).

Eighteen tenrecs examined by Dr. E. R. Brygoo, Director of the Institut Pasteur, had the following endoparasites: ten *Hemicentetes semispinosus* all negative, one *Setifer setosus* negative, five *Microgale talazaci*—four with Nematodes in the intestine, one with acanthocephala and with cestode cysts, all from the region of Perinet. One of two *Microgale dobsoni* from Manohilahy contained two Nematodes in the stomach. The material is deposited at the Institut Pasteur in Tananarive.

<sup>4</sup> Gray, C. W. "Report of the Veterinarian." 1967 Annual Report, National Zoological Park, Smithsonian Institution.

### Disease Problems in the Captive Colony

Survival in captivity has been, on the whole, rather good. At the time of writing, the following longevities have been established in the captive colony: One specimen of *Microgale cowani* is over 365 days of age. Two specimens of *M. (Nesogale) talazaci* have lived in excess of 670 days and two specimens of *M. (N.) dobsoni* have survived an equal length of time. Five specimens of *Setifer setosus* are entering their third year of life and three specimens of *Echinops telfairi* are in excess of four years of age. Three specimens of *Tenrec ecaudatus* have lived in excess of 670 days in captivity. One specimen of *Hemicentetes nigriceps* has achieved the same record, while one specimen of *Hemicentetes semispinosus* has lived over two and a half years in captivity.

Most of the disease syndromes associated with death in our captive colony have been associated with extreme obesity. It is rather difficult to regulate food intake with an appropriate amount of exercise for

the captive tenrecs of the subfamily Tenrecinae. Four cases of death in *Tenrec ecaudatus* resulted from pulmonary congestion, obesity, fatty liver degeneration, and marked degeneration of the kidney tubules. Deaths in captive *Hemicentetes* have resulted from internal hemorrhage and ulceration of the gut; hemorrhages in and around the urinary bladder; and obstructive jaundice resulting from an impacted gall bladder with associated enteritis. Death in *Microgale talazaci* has resulted from enlarged and congested spleen with associated fatty liver syndrome. One *Microgale dobsoni* died in part from ulceration in the gastric mucosa.

Most of the causes of death in the captive colony can be reduced by routine parasite checks in order to keep the level of gut nematodes within tolerable levels. In addition, the maintenance of the animals at appropriate temperatures and constant attention to quantity of food intake greatly reduces obesity and accompanying degenerative states. For further discussion of captive maintenance, see Eisenberg and Gould (1967) and Eisenberg and Muckenhirn (1968).

## A Survey of the Oryzorientinae

The Oryzorientinae or rice tenrecs are characterized by a dental formula of  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$  ( $\frac{2}{3} \frac{1}{1} \frac{3}{3} \frac{4}{3}$  by some authors). These tenrecs have long tails, reduced eyes, and are covered with a dense pelage exhibiting no spinescence. The animals have a true cloaca and the testes of the male do not descend into a scrotum at maturity but remain located in the region of the pelvic girdle. In body structure they bear a strong resemblance to the family Potomogalidae of Africa, especially the oryziorientine genus *Limnogale*. The genus *Geogale* has been found as a fossil on the mainland of Africa (see Butler and Hopwood, 1957).

Certain species of the genus *Microgale* exhibit the least morphological specialization to be found within the entire family; probably these forms most nearly resemble the ancestral species which gave rise to the whole adaptive radiation of tenrecid insectivores on the island of Madagascar. In the course of their adaptive radiation, the Oryzorientinae have given rise to fossorial, surface foraging, climbing, and aquatic forms. Although the authors studied only the genus *Microgale* and to some extent *Geogale*, the remaining two genera of Oryzorientinae will be included in the general discussion.

### The Aquatic Syndrome—*Limnogale Major*, 1896

*Limnogale mergulus* is a rather large tenrec with a total length ranging from 250 to 325 mm. Head and body length ranges from 122 to 170 mm; tail length ranges from 119 to 161 mm. The external ear and eye are reduced; the muzzle is somewhat blunt and adorned with rather stout mystacial vibrissae. There are five digits on both the hind and forefeet. The digits of the hind feet are interconnected by a pronounced skin web and this characteristic serves immediately to identify it. The animals are dark brown to almost black on the dorsum with a gray ventrum. The tail is also faintly bicolored (Figure 16). Apparently the sense of touch, via the mystacial vibrissae, is highly developed. Remarks concerning the nature of the animal's habitat,

defecation points, and probable diet were included in the article by Gould and Eisenberg (1966). These assumptions were amply confirmed in the publication of Malzy (1965).

### SEX CRITERIA

The female possesses six nipples, two pectoral, two ventral, and two inguinal. From a sample of 13 animals, Malzy reported 7 females and 6 males indicating an approximately equivalent sex ratio.

### DISTRIBUTION AND ABUNDANCE

*Limnogale* is found in fast-flowing freshwater streams at elevations ranging from 600 to 2,000 meters. At the higher elevations the animal experiences rather cool temperatures but is apparently able to maintain a reasonably high body temperature (32° C., Malzy, 1965) by feeding voraciously. The animals have been collected in only a few restricted localities, c.f., Malzy, (1965); see Figure 17).

### HABITAT AND HOME

The animals forage in streams and build a burrow on the bank at the stream's edge. For further comments

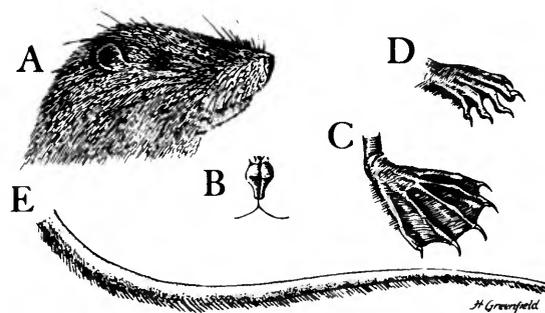


FIGURE 16.—*Limnogale mergulus*, from a preserved juvenile specimen collected by Malzy: A, head; B, nose (note leathery nasal pad); C, hind foot; D, forefoot; E, tail, slight lateral flattening (note ventral hairs).



FIGURE 17.—*Limnogale* habitat is frequently associated with the aquatic lace plant, *Aponogeton jensestralis*; note the flowers protruding above the surface of the water. Kiener (1963, pl. 98) indicates a broad distribution of several varieties of this plant extending from the northern region of Cap Masoala Maromandia to the southern area of Fort Dauphin and to the western region of Antsingy. Possibly *Limnogale* survives in these disjunct associations. The bases of these plants are the site of abundant aquatic invertebrates. Photographed in April on a small tributary of the Vohitra River about 10 kilometers north of Rogez.

concerning the nature of the habitat, see Gould and Eisenberg (1966).

#### FOODS

These animals are apparently completely carnivorous and their diet includes small frogs, freshwater shrimp, crayfish, and aquatic insect larvae.

#### REPRODUCTION

The breeding season of *Limnogale* is estimated to be from December to January (Malzy, 1965). These observations are based on rather scanty evidence however, since in Malzy's collection only one lactating female was captured in December and a nest containing two nearly grown young was discovered in January. As for information concerning the litter size, we can only

guess that it must be in the neighborhood of three young. Two young were found in the nest by Malzy. Since the female possesses six mammae, it is certainly possible that she may have up to six young but it is more probable that three is the average number.

#### NOTES CONCERNING BEHAVIOR

The only information we have concerning the behavior of *Limnogale* comes from the reports by Malzy based on several specimens which he was able to keep for a short time in captivity. It would appear that the grooming pattern is similar to that of *Microgale* and that the animals exhibit a great deal of activity throughout the day. Food intake would appear to be high and, as a consequence, the body temperature remains relatively constant for a tenrec.



FIGURE 18.—*Oryzorictes*, collected as a juvenile, 2 kilometers west of Perinet and photographed by Stephen Parcher, August–September, 1968. Rooting and digging behavior indicate that this oryzorictine may obtain most of its food beneath the forest litter. It did not burrow when placed on soft soil. Cooling induced torpor during cool nights. Note long nose, small eyes, small ears, long toes of the forefoot (Figure 19), and short tail (Figure 20); these characters suggest adaptations similar to *Neurotrichus* or the short-tail shrew, *Blarina brevicauda*, of North America.

### The Fossorial Syndrome—*Oryzorictes*

#### A. Grandidier, 1870

The genus *Oryzorictes* contains three species which exhibit varying degrees of specialization for fossorial life. The eye and external ear are reduced. The claws of the forepaws are longer than those of the hind paws and the tail is reduced in length in proportion to its total

body length (Figures 18–20). The dental formula remains  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$ . The species *Oryzorictes talpoides* has especially well developed claws on the forepaws. *Oryzorictes (Nesorictes) tetradactylus* is characterized by having only four digits on the forepaws; three have well-developed claws. All of the species exhibit a soft velvety pelage which ranges from almost black to gray-brown in color. The tail is sparsely covered with short



FIGURE 19.—Close view of long toes of the forefoot of *Oryzorictes*.



FIGURE 20.—Close view showing short tail of *Oryzorictes*.



FIGURE 21.—*Geogale aurita*. This oryzoricine is adapted to the semi-arid areas of western Madagascar. Note the rather short hind foot and large pinna. This animal apparently exhibits a seasonal torpor.

hair. *O. hova* has a head and body length of 115 mm with a tail 35 mm long. Webb collected *O. talpoides* (BM 48.84, 48.5) near Antongil Bay (49°7'E x 15°7' S) at an elevation of 500 feet as well as the region around Maroansetra (BM 48.70) and Ivohibe.

#### DISTRIBUTION

*Oryzoricetes talpoides* is found on the northeast coast extending over to the northwest in the vicinity of Majunga. *O. hova* is found on the north central plateau as is *O. tetradactylus*.

#### HABITAT

These animals apparently burrow in the humus layer found near streams and lakes. The cultivation of rice has apparently opened up a new suitable habitat for them and it is reported that these animals may be taken in the vicinity of paddy fields. Information concerning the food and reproduction of these animals is limited. The stomach of one specimen of *O. talpoides* examined by Webb in 1939 included insects and vegetable matter; a second contained earthworms and a third contained grasshoppers (BM 48.50, 48.70). In the absence of any other data, we can only conclude from an interpretation of morphology that they live in a manner similar to our North American shrew moles of the genus *Neurotrichus*.

#### The Genus *Geogale*

*Geogale aurita* (Milne-Edwards and Grandidier, 1872) may be immediately distinguished from the genus *Microgale* on the basis of dentition. In contradistinction to the *Microgales*, *Geogale* has a reduced tooth number in the pattern  $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3}$  giving a total of 34. This is a small tenrec with a head and body length of 74 mm and a tail 33 mm in length. The ear is rather large, being approximately 13 mm long, whereas the hind foot is rather short, being some 10 mm in length. The animal is light brown dorsally with a white ventrum. The animal enjoys a broad distribution being found on the west coast at Tulear and Morondava and paradoxically enough on the east coast in the vicinity of Fenerive. Grandidier has remarked on this curious distribution especially with respect to microhabitat differences. He has termed the typical western race as *Geogale aurita* and the specimen from Fenerive has been named *G. a. orientalis* (Grandidier and Petit). General notes concerning one living specimen in Gould's possession are included in the publication by Gould and Eisenberg (1966). Suffice to say that the animal appears to live in burrows in sandy soils and has the ability to exhibit a seasonal torpor. The torpor shown by the

captive *Geogale aurita* was much more profound than that noted for *Microgale dobsoni* (Figure 21).

### The Genus *Microgale* Thomas, 1883

The genus *Microgale* includes 21 named forms which were listed, in part, in the publication by Morrison-Scott (1948). The *Microgales* are shrew-like in their body form and range in size from a head and body length of 43 mm (*M. parvula*) to a head and body length of 130 mm (*M. (Nesogale) talazaci*). The tail, depending on the species, may be as short as 33 mm (*M. brevicaudata*) or as long as 158 mm (*M. longicaudata*). Most species of *Microgale* are confined to the eastern rainforest region or the moist plateau. With the exception of the forested area near Majunga which climatically is very similar to the eastern rainforest, the western portion of the island is depauperate in species of *Microgale*. Only the closely related genus *Geogale* and *M. (Paramicrogale) occidentalis* are to be found in the deciduous forest regions of the west coast.

The genus *Microgale* is divided into four subgenera: The subgenus *Microgale* proper; the subgenus *Paramicrogale*, which shows some affinities with the subfamily Tenrecinae; the subgenus *Leptogale*, which shows some affinities with the genus *Oryzorictes*; and the subgenus *Nesogale* which is characterized by a robust skull and a high lambdoidal crest. (The subgenus *Nesogale* has been raised to generic status in Morrison-Scott's review of 1948.)

In spite of the subgeneric differences, the dental formula is uniform throughout the genus, being  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$ . As pointed out by Morrison-Scott, with continued study many of the supposed species will be revealed as mere varieties of a more broadly defined species. Indeed, Morrison-Scott suggests a possible reduction of nine forms to two species in his introductory paragraphs which are in accordance with a similar conviction expressed by G. Grandidier (1934).

It is convenient to consider the *Microgales* in terms of four behavioral classes based on gross morphology. We have attempted to classify the species of *Microgale* according to functional types based, in part, on the ratio of tail length to head-and-body length, which is a fairly good indicator of arboreal ability. That is to say, the shorter the tail with respect to the head and body, the more likely it is that the animal is semifossorial or fossorial in its habits. An extraordinarily

long tail (i.e., around twice the head and body length) may mean either that the animal is a saltator and/or perhaps a climber with the tail being used for balancing and prehension. An intermediate sized tail (as long as or slightly longer than the head and body) generally indicates an all purpose animal which is both a good surface forager and a good climber. (See also the rodent studies by Horner, 1954.)

In addition, a consideration of the hind foot length within the genus *Microgale* immediately suggests that certain species may be quite able saltators. As indicated in the classical paper by Howell (1932), when the length of the hind foot is expressed as a ratio of hind foot length to head-and-body length, an animal which has a hind foot length exceeding .30 of the head-and-body length is capable of bipedal saltation. Hind foot lengths from .20 to .30 of the head-and-body length indicate a high ability to exhibit quadrupedal saltation, escape leaps, or leaps in capturing insects. In proposing our behavioral classification for the species of *Microgale*, we have taken the ratio of hind foot to body length into consideration together with the ratio of the tail to head-and-body length. We propose the following four major categories and subcategories for the genus *Microgale*:

(1) Semifossorial habits with little ability to spring, ratio of tail to head-and-body length less than .50, ratio of hind foot to head-and-body length less than .20. Example, *Microgale brevicaudata*. *M. brevicaudata* (G. Grandidier, 1899) is of moderate size, having a head-and-body length between 60 and 70 mm. In habits it probably resembles the North American least shrew, *Cryptotis*.

(2) Surface foraging forms, probably deliberate climbers with little to moderate ability to spring. Ratio of tail to head-and-body length greater than .60, less than 1.00.

(a) *M. (Paramicrogale) occidentalis* (Grandidier and Petit, 1932) is a western form characterized by its small size (55 mm head and body). It would appear to resemble the following species in bodily proportions.

(b) *M. cowani* (O. Thomas, 1883) ranges in head-and-body length from 61 to 75 mm. The ratio of tail to head and body varies from .67 to .84 and the hind foot ratio is equally variable ranging from .21 to .25. The dorsal pelage may show a faint middorsal black line and the overall color includes almost a complete black to an agouti-brown. *M. c. nigriscens* (Elliot, 1905) is characterized in the original description by

TABLE 3.—Morphological correlations among the terrestrial Oryzictinae  
(Ratios and lengths are based on averages when a series was available.)

	Head and Body Length in Millimeters							
	>40	≤60	>60	≤85	>90	≤115	>115	≤135
Fossorial or semifossorial								
T/HB ≤.50				<i>Geogale aurita</i>				<i>Oryzictes hova</i>
HF/HB ≤.20				<i>Microgale brevicaudata</i>				<i>O. talpoides</i>
Surface foragers, moderate climbing ability								
T/HB ≥.60 ≤1.00			<i>M. (Paramicrogale) occidentalis</i>	<i>M. crassipes</i>		<i>M. (Nesogale) dobsoni</i>		
HF/HB >.13 ≤.20				<i>M. cowani nigriceps</i>		<i>M. (Leptogale) gracilis</i>		
						<i>M. thomasi</i>		
HF/HB >.20 <.24				<i>M. cowani</i>				
HF/HB >.25 <.29				<i>M. longirostris</i>				
Surface foragers and climbers								
T/HB >1.00 ≤1.60					<i>M. melanorrhachis</i>			<i>M. (N.) talazaci</i>
HF/HB >.13 ≤.20					<i>M. drouhardi</i>			
HF/HB >.20 <.24			<i>M. pusilla</i>					
HF/HB ≥.24 ≤.27			<i>M. parvula</i>					
Climbers and springers								
T/HB >1.60 <2.6			<i>M. proluxicaudata</i>	<i>M. majori</i>				
HF/HB >.265 <.30			<i>M. longicaudata</i>	<i>M. sorella</i>				
				<i>M. principula</i>				

an extremely short hind foot with a hind foot to head-and-body ratio of .12. *M. crassipes* (Milne-Edwards, 1893) is considered by G. Grandidier (1934) to be a possible synonym of *M. cowani*.

(c) *M. longirostris* (Major, 1896a) would appear to be distinct from *M. cowani* on the basis of its long hind foot which may reach 28 percent of the head-and-body length. The hind foot ratio would indicate a well-developed ability to saltate quadrupedally.

(d) The larger species *M. (Leptogale) gracilis* (Major, 1896a), *M. thomasi* (Major, 1896a), *M. (Nesogale) dobsoni* (Thomas, 1884) are all very similar in bodily proportions. The status of *M. gracilis* is unclear, but *M. thomasi* may be synonymous with *M. dobsoni*. The status of the latter species has recently been clarified by Morrison-Scott (1948).

(3) Surface foragers and climbers. Ratio of tail to head and body greater than 1.0 but less than or equal to 1.5. Probably all have an ability to spring from twig to twig when climbing.

(a) Moderate ability to spring with hind foot ratio to head and body averaging greater than .20 but less than or equal to .24. *M. melanorrhachis* (Morrison-Scott, 1948) medium size with a head-and-body length greater than 70 but less than 80 mm. This species is

characterized by a dark, well-delineated middorsal stripe. *M. (Nesogale) talazaci* (Major, 1896a) very large with a head-and-body length greater than 115 mm but less than or equal to 130 mm.

(b) Semisaltators. Hind foot ratio to head and body greater than .24 but less than or equal to .27. *M. parvula* (G. Grandidier, 1934) very small with a head-and-body length less than 50 mm. *M. pusilla* (Major, 1896b) with a head-and-body length greater than 50 mm but less than 60 mm. The preceding two species may well prove to be synonymous. *M. drouhardi* (G. Grandidier, 1934) medium sized with a head-and-body length greater than 70 but less than 80 mm. This northern form from Diego Suarez shows a black middorsal stripe which is lost in the adult.

(4) Extremely long tailed forms: Possibly climbers and ricochettors among branches. Ratio of tail to head and body greater than 1.5 but less than 2.6. Developed quadrupedal saltators with a hind foot ratio to head and body greater than .26; very small to moderate in size with a head-and-body length between 50 and 75 mm: *M. longicaudata* (Thomas, 1883), *M. principula* (Thomas, 1926), *M. sorella* (Thomas, 1926), *M. majori* (Thomas, 1918), *M.*

*prolixicaudata* (G. Grandidier, 1937). The first four species may be synonyms (G. Grandidier, 1934).

An inspection of the preceding information clearly indicates that within behavioral types (2) and (3) the surface foragers and the surface foragers and climbers, we find three size classes ranging from small to moderate size and large (less than 60 mm head-and-body length, 60 to 85 mm head-and-body length, greater than 90 mm head-and-body length). The two extreme behavioral types (1) the semi-fossorial and (4) climbers and springers do not show as much variation in size but, with the exception of *M. prolixicaudata*, they tend to be within the 60 to 75 mm range of head-and-body length. Reference should be made to Table 3 for a simplified presentation of the morphological correlations among the terrestrial Oryzoricinae.<sup>5</sup>

In the present study, two of the behavioral types were available for observation. These were *M. (N.) dobsoni* and *M. cowani* in the cryptic surface foraging class and *M. (N.) talazaci* in the surface forager and climbing group. Living specimens of the other morphological types were not available to us for study.

*M. (N.) dobsoni* and *M. (N.) talazaci* are instructive in a comparative study since they are very similar when gross morphology is considered. They do exhibit some differences in their habitats. *M. dobsoni* occurs in seasonally arid areas on the eastern edge of the central plateau whereas *M. talazaci* is adapted to the more heavily forested areas in the true eastern vegetational zone. As a result *M. dobsoni* has the ability to store considerable amounts of fat in its tail and subcutaneously on its body.

### Sympatric and Allopatric Considerations

The paucity of complete collections renders a discussion of sympatry and allopatry rather difficult. Indeed, the lack of a usable series of specimens of any one species renders it next to impossible to make decisions concerning the validity of the species' names already in current use. Nevertheless, an inspection of morphology would indicate that a variety of morphological types have evolved within the generic designation *Microgale*. We have further suggested that differences in morphology are correlated with rather profound

differences in habitat utilization. It would follow from our hypothesis that a high degree of sympatry could occur since we have proposed that the key differences in morphology are related to such major differences in habitat utilization as semifossorial, cryptic surface foragers, surface foragers and climbers, and climbers and springers. With these notions in mind, it would seem worth while to relate the diversity of collection made by the Smithsonian Madagascar Expedition of 1963. The following species of *Microgale* have been provisionally identified in the U.S. National Museum collections for the locality of Perinet: *M. (N.) talazaci*, *M. brevicaudata*, *M. pusilla*, and *M. longirostris* (USNM 341698, 341694, 328688, 328693, respectively).

The specimens identified as *M. brevicaudata* have slightly longer tails than the type-specimen but appear different from a series of *M. cowani* taken by U. S. National Museum collectors at Didy. If the description of *M. cowani* is revised in the near future, the species status of *M. brevicaudata* may be altered. Similarly the status of *M. longirostris* is tentative pending further study. With these qualifications in mind, the microhabitats for the above forms were *M. brevicaudata*, areas of herbaceous plants and grass bordering the forest; *M. longirostris*, similar to the preceding; *M. pusilla*, dense grass over 15 cm high near a stream; and *M. (N.) talazaci*, in primary rain-forest often near granite outcroppings with tangled ground cover.

In a locality to the east of Lake Aloatra, by the name of Didy, four species were taken very close to one another. These include *M. cowani*, *M. melanorrhachis*, *M. pusilla*, and *M. longirostris* (USNM 328674, 328686, 327687, 328647, respectively). Didy is on the eastern edge of the central plateau and receives an abundance of rainfall. Its high elevation is in part compensated for by its north latitude; hence, the variation in annual temperature would not be as great as that anticipated at an area of comparable elevation but at a more southerly latitude such as Fianarantsoa. The microhabitats for the above species were *M. cowani*, found in dense grass from 30 to 40 cm in height; *M. melanorrhachis*, trapped in an edge habitat of brush and grass near a sedge marsh; *M. pusilla*, trapped in dense grass cover up to 60 cm in height; and *M. longirostris*, similar habitat as described for *M. cowani*.

<sup>5</sup> *Microgale taiva* (Major, 1896b) has not been considered since the original description is based on an immature specimen.

## *Microgale dobsoni*

### Physical Description

*Microgale dobsoni* is a large, terrestrial Oryzoricine with a head-and-body length ranging from 92 to 114 mm and a tail length from 102 to 108 mm. Its hind foot averages about 21 percent of the head-and-body length. The dorsum is gray-brown in color contrasting with the gray ventrum. The tail is faintly bicolor (see Figure 22). The weight of the animal varies with the season. For example, adult weights, without fat reservoirs, range from 34 to 45 grams; however, with the onset of the austral winter, they accumulate fat reserves in the tail and body and weights may reach 84.7 grams in captivity. Captive specimens retain a tendency for seasonal fluctuations in weight, reaching a maximum in November and December and declining until May when an increase occurs again.

Sexes are not readily distinguished by conspicuous morphological features. Since the animals possess a cloaca, they must be sexed by expressing the phallus by means of slight pressure on either side of the anterior edges of the cloacal lips. Out of a sample of eight

living specimens collected for captive studies, five were males and three were females.

### Distribution and Habitat

This species has been taken over a broad range from northern Betsileo to Lake Aloatra. Two trapping localities yielded *Microgale dobsoni* during the current study. One included three stations at 4.6, 5, and 11.5 kilometers east of Manandroy; the other was near Manohilahy approximately 20 kilometers west of Lake Aloatra. The trapping site at 11.5 kilometers east of Manandroy is especially instructive since this locality is still to the west of the divide which separates the climatically distinct high plateau edge from the eastern escarpment rainforest. For example, 11.3 kilometers further to the east, one is already in a region of multi-stratal tropical evergreen forest where *Microgale tala-zaci* may be trapped. At the trapping locality for *Microgale dobsoni*, the habitat is characterized by a seasonal rainfall and probable seasonal abundance in insects.



FIGURE 22.—*Microgale dobsoni*. Note the rather large ear and long, fat tail of this completely furred tenrec. The tail of *Microgale dobsoni* serves as a fat storage organ.

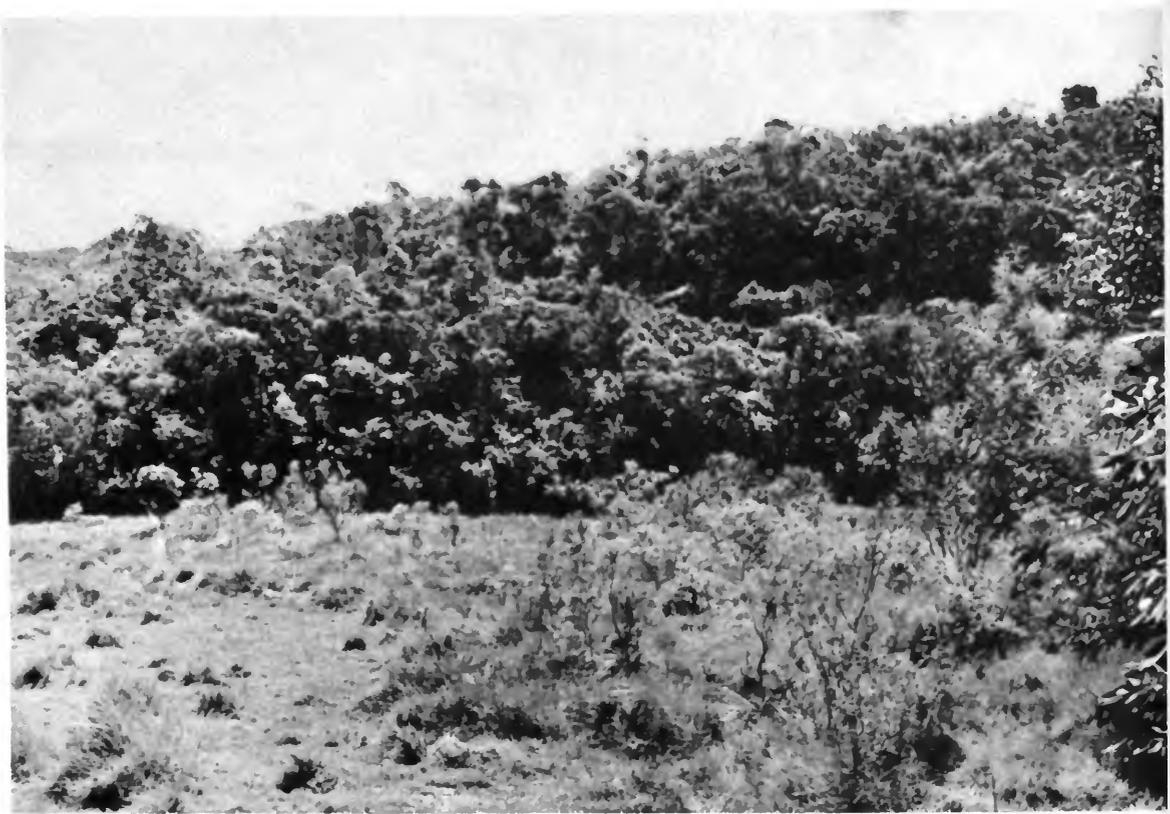


FIGURE 23.—Typical habitat for *Microgale dobsoni*. This species is confined to the high plateau edge generally in second-growth areas exposed to seasonal aridity and cool temperatures during the austral winter.

One area at 11.5 kilometers east of Manandroy is shown in Figure 23 and exemplifies a typical second-growth area probably once occupied by transitional forest between the high plateau forest and the eastern rainforest but now reduced to scrub.

The trapping area was selected to include an interface between a marsh and second-growth brush. A line of 100 traps was laid in such a way as to include high, dry ground and by gradually descending down a slight slope toward a stream running through the marshy area, the line eventually intersected with a second wooded tract. Eight *Microgale dobsoni* were taken and of the eight only one occurred in the high dry area, the rest being taken at the interface between marshy bog and the second-growth scrub. A total of nine *M.*

*dobsoni* were taken in 125 trap nights\* at the 11.5 kilometer area. Three others were taken in 45 trap nights in the areas 4.6 and 5 kilometers east of Manandroy.

*Microgale dobsoni* was abundant in the forested regions of Manohilahy (Figure 24). Seventeen specimens were trapped in 136 trap nights on 18 and 19 April. *M. dobsoni* was taken where the soil and leaf litter of steep forested slopes was moist and friable, similar to the floor of the rainforest. There were no orchids, however, and there were virtually no insect sounds in contrast to the cacophony of the rainforest region of Perinet in April. *Tenrec ecaudatus* were torpid but *Microcebus* were seen active in the dense shrub-

\* One trap set for one night equals one "trap night."



FIGURE 24.—Dense forest being cleared for a mining road near Manohilahy. *Microgale dobsoni* was abundant on the steep slopes.

bery along the road. The tails of *M. dobsoni* were not yet fat.

#### The Annual Cycle, Reproduction, and Thermoregulation

We have little data on reproduction and growth for this species. Copulation in captivity will take place during the months of December through August and captive births have occurred in February and May. However, during the trapping in the month of April near Manandroy, no lactating animals were taken and, of the eight specimens which were taken alive, none could be considered fully adult.

In captivity, special attention was directed toward weight changes and thermoregulation (see Appendix

C for an outline of thermorecording techniques). As noted before, *Microgale dobsoni* has the capacity to store considerable quantities of fat. In captivity marked fat storage will occur throughout the year if the animals are fed to excess and weight can be controlled only by limiting the diet. There is some seasonal tendency for the weights to rise and fall in captive individuals but this was masked to some extent by the relatively constant conditions under which we attempted to maintain them. *Microgale dobsoni* at no time showed any tendency to enter profound torpor, but when it becomes heavy in captivity, it will show a tendency to decline in body temperature and become inactive, eating less, and sleeping a great deal. During these periods of inactivity, there is a slight tendency for cloacal temperatures to parallel the ambient tempera-

ture when the latter is between 21° and 28.5° C. Over this range, the cloacal temperature varied between 24.5° and 32° C. Hence, it would appear that when *Microgale dobsoni* has sufficient fat reserves it will allow its body temperature to oscillate slightly within a defined range according to the fluctuation in the ambient temperature.

This fat storage phenomenon and slightly unstable body temperature probably reflect an overall adaptation to life on the high plateau edge. Although occurring in the reasonably moist area, these animals must at certain times of the year experience shortages in moisture and insects. At this time, they undoubtedly live on their fat reserves and further conserve energy by reducing metabolic rate. Our inability, however, to duplicate exactly the environmental fluctuations in the laboratory prohibited testing the hypothesis that the fat reserves may change with seasonal changes in ambient conditions.

### Feeding Habits

*Microgale dobsoni* was tested in captivity with a variety of foodstuffs and we found that it would quite readily take orthopterans, coleopteran larvae, earthworms sparingly, and raw ground meat. By observing their method of hunting orthopterans, it was quite evident that such insects provide staples in their diet. It also seems useful to repeat comments from the residents of Manandroy. One individual stated that *M. dobsoni* may supplement its diet with ant eggs. Indeed, one specimen was trapped within 2½ feet of an ant nest. Further discussion of prey-catching behavior will follow in the next section.

### Ethological Studies

#### GENERAL MAINTENANCE BEHAVIOR

*Locomotion.*—*Microgale* moves about in a stereotyped fashion. On a plane surface the basic pattern is the crossed extension mode of locomotion where the contralateral limbs are in synchrony. The tail is generally held somewhat off the substrate but its exact position depends on the degree of muscular tension in the animal's body. The tail may be quite stiffly extended as the animal explores a new area, but as it becomes more relaxed the tail may drag. The animal is able to leap a short distance if in pursuit of an insect or when climbing. In climbing a similar crossed ex-

ension pattern of limb coordination can be observed. The tail may aid the animal to maintain its balance while climbing. Most of the activity of *M. dobsoni* takes place at night.

*Exploration and utilization of the living space.*—Laboratory observations in an open field testing situation indicate that *Microgale dobsoni* climbs readily and well. A variety of tree limbs may be climbed and the animal may spring a short distance (1 inch) from one branch to another. During exploration the animal pauses frequently to sniff the substrate. The nose is somewhat mobile but the vibrissae are rather stiff. The animal will poke its nose under leaves or into the substrate, pausing to sniff in any place where prey may be hiding.

When placed in a novel environment, the animal frequently shows some period of hesitancy and exhibits a stiff or tense body posture, pausing from time to time to test the air and may even assume an upright posture while sniffing. It will then begin to progress more rapidly about the cage utilizing some of the same spots over and over again for urination and marking.

*Rest and sleep.*—Typically the animal adopts a curled posture when sleeping, with the head tucked ventrad. The animal may lie curled on its side or may rest its weight on the hind feet and the dorsal surface of its head.

*Marking.*—Chemical communication by marking with exudates from the cloacal region is very characteristic of *M. dobsoni*. Marking behavior is exhibited by both males and females during an encounter and when exploring a new area. The animal typically selects a spot near a nest box or an artifact such as twig or log and marks by depressing its perineal region upon the substrate and, while moving forward, drags the cloaca repeatedly on the same spot.

In addition we have noted that the males frequently secrete a white fluid around the eye. This secretion is sometimes apparent when the male is excited after having been placed with a female. It does not always occur during an encounter and no specific marking movement has been noted in conjunction with the secretion (see *Setifer*, pages 54 and *Echinops*, pages 62).

*Care of the body surface.*—Three basic patterns of auto-grooming may be noted. These include scratching, licking, and washing. Washing involves sitting upright, bearing the weight on the hind legs and the base of the tail, while depressing the head forward. By bring-

ing up the forepaws simultaneously on either side of the face, it will down-stroke with its forepaws on the sides of the face beginning behind the ears and brushing the fur all the way to the tip of the nose. As the

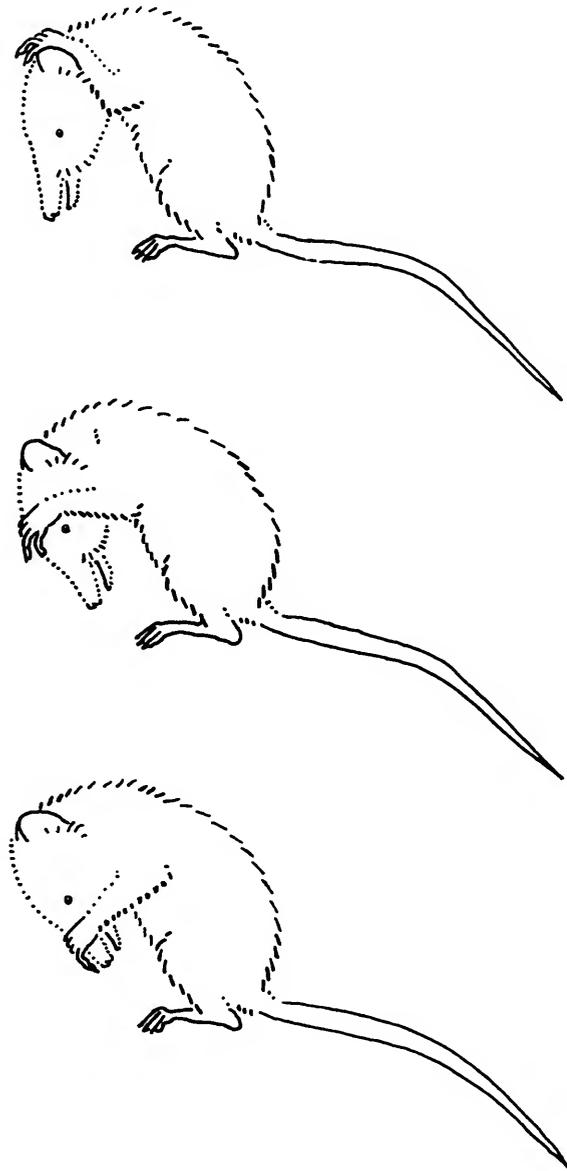


FIGURE 25.—Washing by *Microgale dobsoni*. Three parts of the face wash are indicated including the reach behind the ears and the drawing of the forearm across the facial hair to the open mouth where the forepaws are partially moistened with saliva.

paws pass the mouth, the mouth is opened slightly and the paws appear to be somewhat moistened with saliva during this terminal part of the stroke. This action may be repeated several times (see Figures 25 and 26). Such an activity probably serves a dual function. The motion of the forepaws would aid in cleaning dirt and particles away from the eyes and the nostrils and also would tend to clean the vibrissae. At the same time, impregnation of the forepaws with saliva would serve, on subsequent movements, to spread saliva over the head and face of the animal. This may be vital in chemical communication during an encounter between two individuals.

Scratching is the second major cleaning movement, being directed at the head, ears, shoulders, and ventrum—wherever the hind foot can reach.

The cloacal region may be licked and following copulation the male has been noted to lick his penis. The tongue and teeth are also employed in licking the ventrum and nibbling the toenails after an extended scratching bout.

*Nest building and burrowing.*—Detailed observations on burrowing behavior have not been carried out with *M. dobsoni*. The typical digging pattern involves alternate movements with the forepaws and kicking back the earth accumulated under its body with the hind feet. If a suitable nest box is provided, the animal will initiate nest building behavior. This consists of moving about in its living space and selecting pieces of dried vegetation such as leaves and grass stems and then carrying them back to the nest box in its mouth. Nesting material is collected in the nest box and the turning movements of the animal's body suffice to form a cup.

*Prey-catching behavior and feeding.*—When foraging the animal moves about sniffing the substrate, pausing to dig from time to time or insert its nose under leaves or fallen branches. If it hears an insect moving, such as a grasshopper, it will assume an elongate posture and rush suddenly at it attempting to seize it with its mouth. It may half spring toward an insect and pin it down with the forepaws while simultaneously biting it. The forepaws are not used to hold the food. The animal may pin down the food with the forepaws and chew, shaking its head occasionally from side to side to tear off pieces but chewing and shaking may proceed without using the forepaws. Insect prey may be carried into or near the nest box where it is devoured. No highly developed tendency to cache food has been dis-



FIGURE 26.—*Microgale dobsoni*. Terminal phase of washing as illustrated in Figure 25.

played by *M. dobsoni*. Chewing movements involve an up and down motion of the jaw with no lateral movement discernible.

*Defensive and offensive behavior.*—When tested with the odor of *Galidia elegans*, *M. dobsoni* will turn immediately and exhibit the defense reaction. During this behavior, the mouth is held widely open and the animal remains orientated toward the odor source. Typically the animal is silent and shows only the gaping response but it may emit a squeal or a prolonged squeal, termed a scream. If a finger or foreign object is poked at the animal during the gape response and the vibrissae are touched, it will bite vigorously. If the animal is moving about in a novel living space and suddenly startled, it will attempt to escape by fleeing to the nearest cover.

#### SOCIAL BEHAVIOR

*Communication.*—In this and all subsequent sections dealing with social behavior, a social context

includes that situation which involves two or more interacting conspecifics. By interacting the animals are exchanging some form of information and this leads to a second definition. When a discrete behavior pattern of one animal causes a response on the part of a second animal, we may speak of a communication system with the first animal acting as the sender and the second acting as the receiver (Eisenberg, 1967; Marler, 1961). We may consider the mode of communication in terms of the sense organs involved, such as visual, tactile, auditory, or chemical signals. Since the eyes of the *Microgale* are so reduced in size, we may rule out any discrete forms of visual communication; indeed, it would appear that almost all information exchange between or among *Microgales* involves audition, chemical cues, or tactile input. When interacting, the animals may influence one another by the sounds of their movements, such as rustling through the leaf substrate. When slightly alarmed the *Microgale* may

exhibit a general trembling and pattering with a forepaw but this appears to be unritualized.

Vocal communication involves the following categories: a soft squeak which may be repeated and termed a twitter; a louder squeal which may, under higher intensities of motivation, be emitted as a long squeaking trill; and finally, a prolonged emission which may be termed a scream or wail. These three types form a graded series. In addition, there is a sound type with low frequency components which may be termed a churr or buzz (see Table 4 and Figures 27 and 28).

Tactile communication occurs during contact configurations such as nose to nose contact, nose to ear, nose to side, nose to anal genital region, and during all forms of rubbing the sides together or crawling over and under one another.

Chemical communication has been indicated under marking and we have also inferred that chemical communication may be involved when saliva is spread on the face during washing behavior. In addition, it should be noted that under the heading tactile communication, we have discussed several postures which involved touching the nose to glandular areas such as nose to ear, nose to crown, nose to nose, and nose to cloacal area. These sites for tactile input involve corresponding glandular areas and all such areas are

potential sources for chemical cues. Contact configurations must not be underrated in any extended discussion of *Microgale* behavior; however, we are lacking the experimental evidence to confirm the exact role of such configurations in the integration of behavior.

The white secretions from the glands associated with the eye of the male may also serve in chemical communication but the functional significance is obscure.

*The encounter.*—The behavior of *Microgale dobsoni*, upon introducing a conspecific, permits us to describe a number of interactions based on a functional classification. Several types of encounters were run following a methodology described by Eisenberg (1963). (Refer to Appendix D for a discussion of encounter techniques.)

All things being equal, the following generalizations can be made concerning the behavior of encountering animals. If a stranger is introduced into a resident animal's cage, the resident will generally show defensive behavior or attack toward the alien during the initial phases of the encounter. An encounter on neutral ground generally involves only cursory contact which may later be followed by overt sexual behavior in the case of a male-female encounter or in a male-male encounter by attempts toward sexual contact by a dominant male with agonistic behavior

TABLE 4.—Physical properties and circumstances of occurrence for vocalizations of *Microgale dobsoni*

Sound Type	Sample Size	Note Structure	Temporal Patterning	Frequency Range (Hz)	Dominant Frequency Range (Hz)	Duration (seconds)	Circumstances of Occurrence	
Clear tones with harmonics	Wail	2	Almost constant frequency	May be repeated once or twice .7 sec. interval	4, 000-4, 500	4, 000-4, 500	.45-.55	Produced when forced on its back—submissive in character.
	Squeak	12	Chevron shaped note	Repeated in bursts of 3 or 4 notes .085-.1 sec. interval	100-6, 000	3, 000-6, 000	.05-.10	During agonistic encounter—defensive in character.
	Twitter	80	Ascending tone	Repeated in long bursts .08-.20 sec. intervals	3, 000-7, 000	4, 000-7, 000	.03-.05	During encounters and initial contact—defensive in character.
Noisy sounds	Buzz	2	Vibrato form	Long note not repetitive	1, 500-10, 500	3, 000-7, 500	.47-.50	During attack-chase sequences.

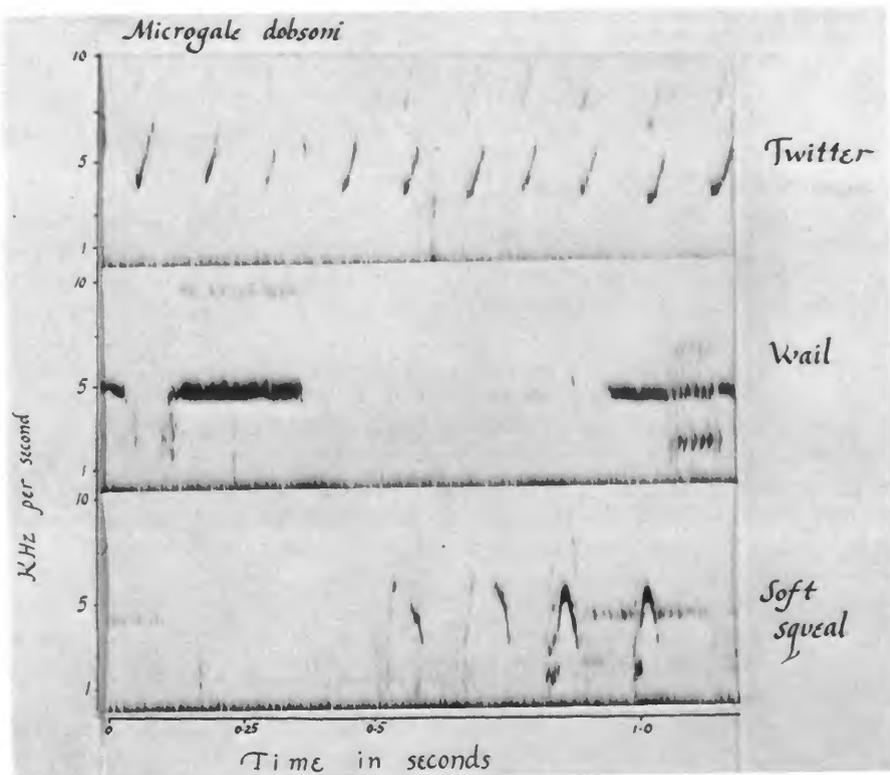


FIGURE 27.—Vocalizations of *Microgale dobsoni*. Twitter: A repetitive call exhibiting an ascending note form. Wail: Note the simple note form and relatively constant frequency. Soft squeal: Special attention should be given to the chevron-shaped note form.

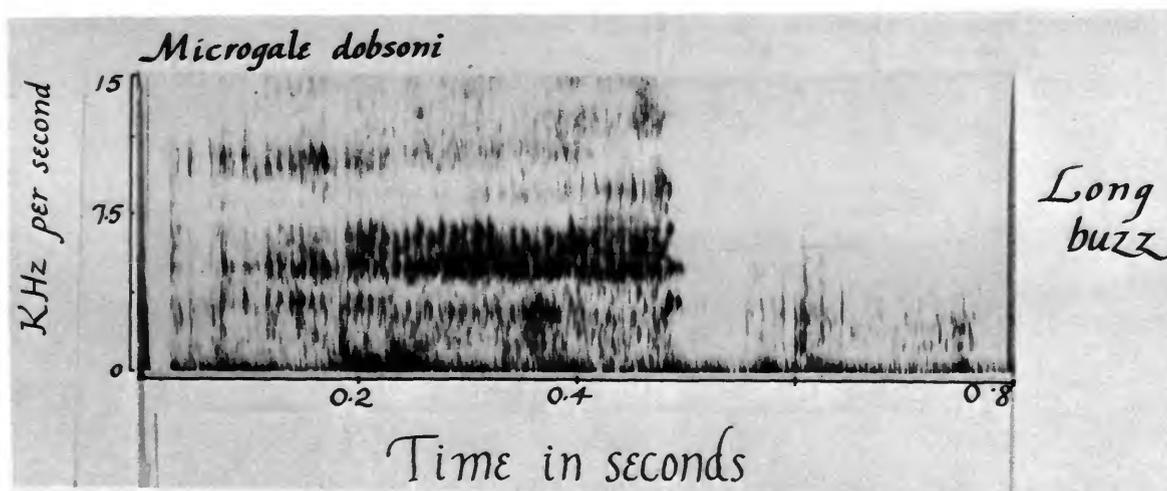


FIGURE 28.—Vocalizations of *Microgale dobsoni*. Buzz: A sound of long duration showing some harmonic characteristics with the superimposition of noise.

on the part of the subordinate. This latter behavior on the part of the subordinate may lead to a fight. Perhaps the simplest way to describe the behavior of *M. dobsoni* in a social context is to cite four actual protocols.

The first type of interaction typifies an encounter between three strangers in a neutral area, that is, an area in which none of the animals has had experience.

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Two animals actively exploring in the arena: First animal is investigating the underside of a leaf lying on the soil. Second animal approaches, contacts its tail and turns away to initiate independent exploring. Second animal approaches first animal again and contacts it nose to side. Animals stand with body axes parallel, both nuzzling each other in the inguinal region. Second animal breaks and moves away; first animal follows nose to rump, nose to base of tail, then breaks off while second animal moves away. Contact again between a third individual and the first animal; mutual nose to inguinal region; body axes parallel but oriented in opposite directions. Third animal puts head under first animal's body; first animal starts to move away; then first animal exhibits nose to nape of neck while third animal places its nose in the cloacal region of the first; crawling over by the first animal and grooming the third animal who is crawling under. Forepaws of first animal on rump of third animal as third animal moves away; break off. First animal encounters third animal, nose to side, nose to nape; third animal gapes, opening mouth widely. First animal moves away and proceeds exploring alone.

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Second example of encounter behavior. Male introduced to second male's cage: Alien male approaches resident who approaches also. Alien male utters a soft squeak; resident utters a buzz. Body axes aligned parallel with mutual nose to perineal region of partner. Alien continues to press nose into perineal region of resident male; resident male rolls onto his back. Break apart. Contact between alien male and resident, mutual gaping. Alien male squeals which grades into a prolonged trill. Open mouths are interlocked. Break off and move away.

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Example of male-female encounter with the female partially receptive: Animals contact and pass with body axes parallel to one another rubbing their sides; reencounter nose to nose, then nose to side by male, followed by nose to perineal region of female. Male begins squeaking and trilling—break apart. Repeat

procedure and then male stands while female touches nose to side of male, then she places her forepaws on the male and male rolls over onto his back. Female nibbles and bites at his hair, actually pulling some strands of hair out. (This is grooming behavior but with aggressive overtones.) After a continuation of the contact promoting behaviors with grooming the male mounts and thrusts approximately 19 times in about 10 seconds. He then dismounts and licks his phallus. During the mount and thrusts, the female gaped and squealed, pulling away, thus terminating the mount sequence. Four more series of mounts occurred, each about 10 seconds in duration, with 18, 13, 10, and 15 thrusts during the mounting periods. In each case, the break occurred when the female either pulled away from the male or rolled onto her back, squealing. After a long burst of thrusting, the male will lick his phallus.

---

Example of interaction and copulation by a male and female *M. dobsoni* with the female very receptive. Synopsis: Precopulatory behavior included nose to nose, nose to ear with the male following the female; the female paused to twitter, turned to the male; mutual gaping exhibited. At one point the male was gaping at the female and then moved his head to one side and demonstrated a nose to ear. This orientating toward each other, mutual gaping, and contact nose to nose, nose to ear, nose to nape, proceeded with interspersed driving for some 15 minutes. Finally, the male mounted, utilizing a neck grip. This was repeated for several rapid mounts terminating after a few thrusts whereupon the male dismounted. In one case the male fell to one side as he dismounted. Finally the male mounted for about 7½ minutes. During the long mount, the male thrust at the rate of about 2 per second in bursts of 5 to 7 or 10. At the conclusion of the long mount, the male initiated driving again but the female turned to him and, exhibiting a gape or partial gape, repulsed him with twitters. The male persisted in driving, interspersed with brief mounts while thrusting at a rate of approximately 5 times per second. This sequence continued for some 20 minutes with intermittent chases. The male was removed as interaction apparently became more and more aggressive with the female squealing and fleeing from the male.

#### DISCUSSION

We would now like to explore in depth our analysis of the male-female interaction patterns displayed by

*Microgale dobsoni*. During an encounter situation, initial contact would seem to be made by one animal approaching another and touching it somewhere on the body, perhaps the tail or the side, and then withdrawing or holding its position. The animal being contacted frequently turns to the contacting animal so that a nose to nose configuration occurs. This nose to nose configuration may result in a gaping reaction on the part of both animals with subsequent withdrawal only to reinitiate similar contact procedures or may be followed by contact promoting behaviors which further the familiarity of the two animals with one another. This would include naso-cloacal examination, perhaps by one animal, very often by both. If the encounter does not interrupt itself with agonistic behavior, such as the gaping reaction, then contact promoting behavior proceeds by further nasal investigation, generally nose to ear or nose to crown, nose to body, again naso-anal mutual, and finally, by grooming behavior. Grooming involves nibbling or mouthing the fur very often with the forepaws of one animal placed against

the other's body holding it down somewhat. This may be displayed by either the male or the female. Reference may be made to Figure 29 which illustrates the major initial contact and contact promoting behaviors displayed by *Microgale dobsoni*. If contact promoting behavior proceeds without interruption, it may then pass on into sexual behavior.

Two types of sexual behavior may be noted, that which proceeds with very much resistance on the part of the female which in turn gives rise to a mixture of contact promoting behavior and agonistic behavior patterns. This would include the following types of interaction: Male attempting to mount while grooming and female exhibiting a gape reaction and jump away; or, while male stands with forepaws on female attempting to seek a neck grip, female rolls over on her back thus bringing her ventrum against the male's at right angles. In this position, the animals may begin to lock their forepaws about one another's body and tumble together while biting in a ritualized fashion at their fur, or the female, upon being

### CONTACT AND MATING

MICROGALE

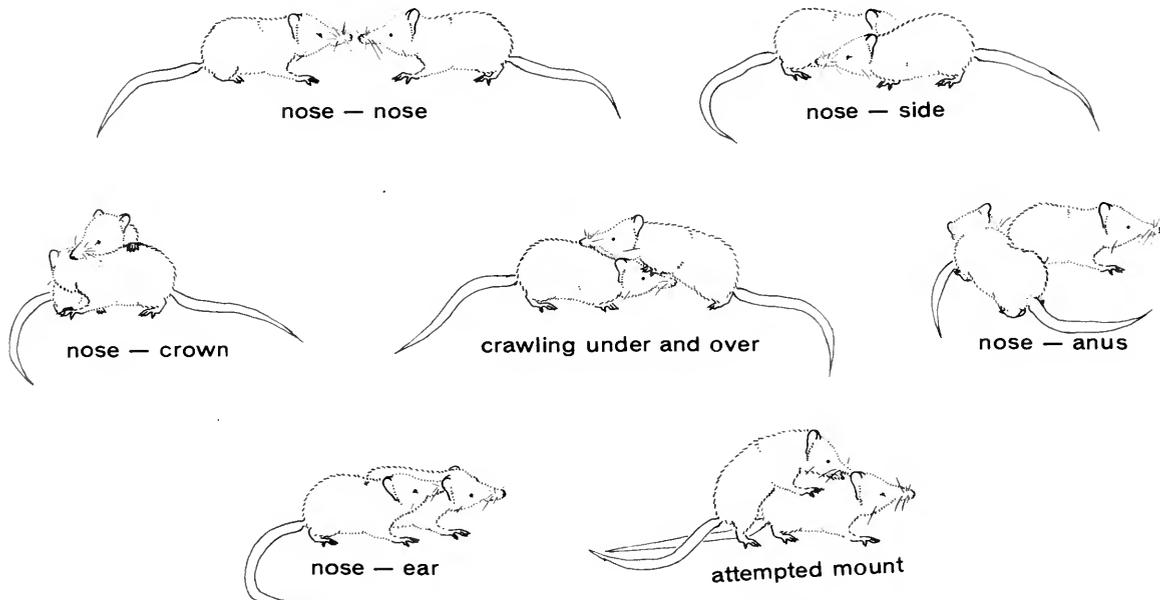


FIGURE 29.—Precopulatory and copulatory behavior by *Microgale dobsoni*. The typical configurations displayed during initial contact include nose to nose, nose to side or groin, nose to crown, crawling over and under, nose to anal genital region, nose to ear, and finally an attempted mount including the neck grip by the male. (Nose-anus is equivalent to nose to posterior portion of cloaca.)

mounted, may turn to one side and begin to groom the male. If the male rolls on his back, the grooming may continue. Grooming may have an aggressive character in that the female instead of gently mouthing the male's fur may actually pull pieces of hair out of the skin. An alternative to this would be where, upon being mounted by a male, the female may leap forward and move away. If she moves away slowly, and the male pursues, this can be termed a chase-flight reaction.

Mixed agonistic tendencies may not occur if the female permits mounting by standing and raising her tail somewhat. The male would then proceed with his neck grip and begin to achieve intromission followed by thrusting. Thrusts occur in bursts of about 7 to 10 at a rate of approximately 2 per second. A burst of thrusts may be interrupted by the female rolling to one side or attempting to pull away from the male. If the female is exceedingly receptive, the mount, with bursts of thrusting, may be as long as 7½ minutes, as in one case. This long mount with continued bursts of thrusts is characteristic not only of *Microgale dobsoni* but also of all of the genera and species of the subfamily Tenrecinae which we deal with in subsequent sections.

The foregoing discussion indicates that receptivity on the part of the female varies. It is difficult to define an exact behavioral estrous response in tenrecs. Suffice to say that the female seems to show varying degrees of receptivity in part dependent on the season. During the nonbreeding season when the animals are obese, the tendency to mate may be vastly reduced and, after a brief agonistic interaction, the members may settle down in the same cage and tolerate one another. This would appear to be a period of anestrus. During the breeding season, the female shows varying degrees of receptivity and, indeed, by means of sustained encounter with the male, may be brought to a condition of full receptivity. We rather suspect on the basis of our limited observations that the female *Microgale dobsoni* is an induced ovulator and may show varying degrees of receptivity depending on ovarian condition which in turn is related to a cyclic physiological process more geared to an annual cycle than to a discrete estrous period which is more familiar to us with rodent studies.

Male-male interactions are typically concerned with the initial contact behaviors, followed by contact promoting behaviors, as in the male-female encounter, but these patterns generally lead to agonistic behavior. This results from the fact that one male or perhaps both

will attempt to initiate sexual relations with the other male which are eventually broken off by the continued resistance from the more subordinate male. Strong resistance on the part of both animals leads to a general fighting behavior which includes locking and rolling, chasing, nipping, and fleeing.

Vocalizations seem to be of paramount importance during the encounter behavior of *Microgales*. The soft squeaking sound which has a dominant frequency from 3,000 to 6,000 cycles per second and has a chevron form is of moderately short duration and repeated. This sound often made by the male would seem to inhibit aggressive behavior on the part of the female and facilitate contact. In addition, it should be noted that the female may make this sound as well; it may serve a similar function to reduce agonistic tendencies on the part of the male. A series of louder squeaks which are typified by an inverted chevron pattern having approximately the same frequency range but being of shorter duration and repeated at a more rapid rate are characteristic of the female who is partially receptive but is exhibiting mixed agonistic tendencies towards the attention of the male. Similarly, if a male is being aggressed against by a female, his soft squeaks may grade into this squeak series which we have termed previously a twitter or trill.

In a defensive situation where the animal is facing out from the nest with the mouth partially open, a series of soft grunts may be given which have not been recorded but would seem to have lower frequencies involved rather than the high pure tones one finds in the soft squeak. A fully aroused animal defending itself against the approach of another will emit what has been termed a scream. This is a long sound being 0.3 of a second or more in length and being in general nonrepetitive. Although the dominant frequencies lie around 5,000 cycles per second, it is not as pure in tone as the soft squeaks or trill types. The aggressive buzz is similarly a nonrepetitive, noisy sound seemingly occurring at lower intensities than the defensive scream and often involved with an approach or attack motivation. Reference may be made to Table 4 for a physical analysis of the sound types produced by *Microgale dobsoni*.

Although we have discussed sounds used in encounters, we do not wish to underemphasize the role of olfaction. It should be pointed out again that during initial contact and contact promoting behaviors the nose is placed in areas of primary glandular secretion.

Furthermore, nosing and licking these areas would insure not only that the responding animal was obtaining chemical information but further that the two animals by interacting in this manner serve to spread each other's scent upon one another. This is especially true of such behavior patterns as aligning the body axes and rubbing against one another or crawling over or crawling under. Such special attention to glandular areas in the form of ritualized contact configurations is characteristic of many other mammals.

The importance of our analysis of *Microgale* interactions cannot be overemphasized. In body form and in general ecology, *Microgale* probably represents a very close analog in form and function to the ancestral tenrec. The ancestral form for all the Tenrecidae was probably a small, furry, long-tailed insectivore which by adaptive radiation gave rise to the present day forms found on Madagascar. Some insight into the behavior patterns of *Microgale* is essential for delineating the core repertoire from which all other more specialized forms of tenrecids represent variations on a common theme. For this reason we should like to compare and contrast the interaction patterns of *Microgale dobsoni* with those of another insectivore somewhat conservative in body plan also, the house shrew, *Suncus murinus* (Family Soricidae).

*Courtship and copulation in Suncus murinus.*—Four pairings were staged to give us a range of variability. A given female exhibits a predictable tendency to mate after a certain amount of stimulation from the male. Several points of interest emerged during the observations, including: the female is highly defensive toward the male when he is placed in her cage. At the same time the male must explore the cage, sniff her defecation spot and mark before he settles down to attending the female. The male's attentions include orientating toward her and, during the initial phases, the female turns to him and wards him off either physically by a short rush, generally accompanied by a churring squeal, or by chirping loudly. The chirp components increase as the female becomes more and more prone to accept the male. The male, on the other hand, will turn away from the female and move off sometimes wriggling his tail and moving his rump from side to side as he moves away. This movement is reminiscent of the female's receptive movement which also includes a hip movement and tail waggle. The male will return and orient to and approach the female repeatedly and eventually the female becomes receptive and does not

turn to face the male any more but begins to walk from him wriggling her rump and tail. At this point, the male generally attempts to mount. He apparently receives some stimulation from her wriggling tail as he attempts to mount. The mating act consists of a series of attempted mounts with or without intromission by the male. The male breaks off each time to wash his genitalia.

The mount series ends with a successful terminal mount including intromission and ejaculation. Immediately after ejaculation, the female refuses to accept the attentions of the male and returns to the original defensive activity, repulsing him, although the male may make repeated attempts to mount. If a second male is placed with the female, she will go through the original phases of defensive behavior but submit to being mounted again. Thus, the female will not often accept the same male twice in succession but may be induced to accept a second male. The marking movements by the male in her cage are quite evident and consist of rubbing the cheek and face as well as the perineal region at selected points in her cage. The female marks less than the male.

Note should be made of the following points after reading the *Suncus* summary. First, although the female eventually becomes receptive to mounting, she initially shows a pronounced agonistic tendency toward the male. The female, throughout the encounter, continues to squeak loudly at the male while keeping her body axis oriented directly toward his; mouth to mouth, nose to nose, mutual gaping and squeaking characterize the early phases, and it is only when the female begins to turn away from the male that the male attempts mounting. Mating behavior in *Suncus* consists of a repeated series of mounts with thrusting, concluding with a terminal mount resulting in ejaculation. In contradistinction to *Microgale dobsoni*, there is no long mount but rather a series of very short mounts with thrusting. Note again, in *Suncus murinus* that contact promoting behavior is reduced and occurs briefly after the female begins to show initial signs of receptivity. As in *Microgale*, it would appear that the activities of the male, with respect to the female, eventually trigger the female's full sexual response and nothing comparable to immediate lordosis, as seen in some of the rodents (e.g., *Rattus norvegicus* and *Mesocricetus auratus*), is to be found in these insectivores. Rather the participation of the male is essential in bringing the female into a full receptive state.

#### PARENTAL CARE BEHAVIOR

Two litters of three *Microgale dobsoni* were born and raised in captivity. Gestation has been estimated for one pregnancy at 62 days. Data on parental care are incomplete but the female builds a rather complex nest of leaves and paper strips within her nest box. The female will actively retrieve young which have been displaced from the nest by seizing the skin or body in her mouth and dragging or carrying the infant to the nest.

#### ONTOGENY OF BEHAVIOR

At birth the young are hairless except for the major vibrissae. The eyes and auditory meatus are closed.

The tail is subequal to the head and body and measurements for the neonate are H.B.=48 mm, T=29 mm. Growth becomes asymptotic at 50 to 65 days of age. The molt to adult pelage is complete at 95 days. The young begin to leave the nest to forage actively at 22 to 23 days.

#### SOCIAL ORGANIZATION

Judging from our trapping results, *Microgale dobsoni* does not exhibit any profound grouping tendency. The animals are well spaced in their environment and would appear to dwell in a solitary fashion. No tendency to form compact cohesive groupings can be discerned in our trapping patterns.

## Other Species of *Microgale*

### MICROGALE TALAZACI

#### Physical Description

*Microgale (Nesogale) talazaci* is the largest species of *Microgale*. It has a head-and-body length exceeding 100 mm with the greatest size in our series reaching 125 mm in length. The tail is slightly longer than the head and body, with a maximum measurement of 160 mm. The hind foot is approximately 21 percent of the head-and-body length, being some 20 to 21 mm in length. The dorsum is a very dark brown to almost black with the ventrum being a washed-out gray. The tail is uniformly colored. The extremes in captive weights ranged from 39 grams to 61 grams; however, this should not be interpreted as evidence for an oscillation in weight comparable to that displayed by *Microgale dobsoni*. Actually, any given individual shows a remarkably uniform weight throughout the year. One male and one female, which we have been observing for two years, have shown less than 10 grams variation in weight throughout a given year. Average weights for a group of ten *Microgale*

*talazaci* in captivity were between 50 and 60 grams (Figure 30).

The sexes are very similar in size and no pronounced dimorphism is discernable. The animals may be sexed only by expressing the phallus of the male from the cloaca, as described for *M. dobsoni*. Sex ratios in a sample of some 14 animals were approximately equal.

#### Distribution and Habitat

*Microgale talazaci* appears to be found in a broad strip from north to south in the true eastern rainforest region. We were able to trap the animals at two localities, Ambitolah and Perinet. At the collecting locality near Ambitolah, a pair was taken in adjacent traps on a small island formed by the deflection of a stream on either side of a rock outcrop. This area was very moist and located in a multistratal tropical evergreen forest habitat. In this same habitat *Galidia elegans* and *Fossa fossa* were trapped, and *Haplemur griseus* and *Lemur fulvus* could be seen with little difficulty.

At Perinet a total of 18 *Microgale talazaci* was live-trapped in 539 trap nights. This species was taken in greatest abundance in those areas where neither *Rattus*



FIGURE 30.—*Microgale talazaci*. This is the largest species of terrestrial oryzorictine. Note the extremely long tail and absence of any fat storage function. This species is an able climber and its tail exhibits some slight prehensile ability.

*rattus* nor *Suncus murinus* were present. *M. talazaci* was taken as far as 240 feet from a stream on a hillside in rather dense multistratal tropical evergreen rain-forest. They were also taken on the banks of streams and on the banks of lagoons which were overgrown with papyrus. In general, the animals were always trapped in association with reasonably mature second growth or multistratal primary tropical evergreen forest (see Figure 31). Although the animals were trapped on the ground, their behavior in captivity would indicate that they are able climbers; Webb trapped several in trees (BM 48108).

The soil in these tropical evergreen forest regions consists of a rich humus with some scattered leaf mold in the form of a thin layer on top of a red lateritic soil. Near the base of tree roots are to be found small burrows, 2 to 2.5 cm. across, and 1 to 1.5 cm. high.



FIGURE 31.—*M. talazaci* habitat. This species is confined to the multistratal tropical evergreen forests generally in the vicinity of streams. Such a habitat exhibits little annual variation in temperature and rainfall.

By digging in the soil, we have found that a given burrow may connect with tunnels which are under the topsoil and root "mat" which overlays the red, hard soil. It is assumed that these tunnel systems are used in part by *M. talazaci*.

### The Annual Cycle, Reproduction, and Thermoregulation

Data concerning the timing of reproduction are very limited for this species. At Rogez a female with two embryos was taken in August and a lactating female was taken in February. Webb recorded two embryos each in two females on 22 October. Embryos were also noted in a 6 November collection (BM 48106, 4897, 48113). Captive births have occurred in March 1968 and July 1969. Weight changes in captivity indicate that, although *M. talazaci* is able to store some fat, there is no fat storage process comparable to that displayed by *M. dobsoni*. Furthermore, checks on thermoregulation indicate that *M. talazaci* tends to maintain a higher body temperature throughout the year than is the case with *M. dobsoni*. The lowest cloacal temperature for *M. talazaci* was 30° C. Cloacal temperatures in general ranged between 32° and 34° C. It would appear that *M. talazaci*, living as it does in a more stable environment, has not evolved semi-torpor as a means of surviving extended dry periods as has *M. dobsoni*. This supposition is strengthened by the fact that *M. talazaci* does not accumulate fat in the manner described for *M. dobsoni*.

### Feeding Habits

*M. talazaci* was tried with a variety of foodstuffs in captivity and it was found that they prey readily on a variety of insects, including coleopteran larvae and orthopterans and dragon flies. The animals may be easily converted to a raw chopped meat diet but are loath to take fruit.

### Ethological Studies

#### GENERAL MAINTENANCE BEHAVIORS

*Locomotion*.—*Microgale talazaci* employs the crossed extension coordination pattern as its predominant mode of terrestrial progression. In addition it may exhibit the quadrupedal ricochet. The tail is generally carried off the substrate with varying de-

degrees of tension in the tail reflecting different degrees of overall muscular tension in the subject. *M. talazaci* is an able climber and will spring from one branch to another. When climbing or moving about in the branches, the tail is frequently draped on a twig and the tip may be slightly coiled around a twig or projections in the bark, thus exhibiting some latent prehensibility but in no way comparable to the prehensile tail of such an arboreal mammal as the mouse opossum, *Marmosa*.

*Exploration and utilization of the living space.*—As indicated under the section on habitat, the animals appear to utilize burrows. While engaged in live trapping at Perinet, we obtained more animals than we could utilize in our captive studies. As a consequence several of the captured animals were released from the traps at their capture site. Notes were made of their behavior. In one case, upon release a subject went down one of the small burrows previously described. As noted, such a burrow may connect with an extensive tunnel system under the thin humus and root "mat." Other specimens when released crawled under a log or crept off through the leaf and grass litter on the forest floor. In one instance, a released animal ran along a well defined trail which was located along the edge of a bank approximately six feet from a path. One specimen was observed to jump from buttress roots to buttress roots, balance on a root edge, run along the length of a root, climb down, and then disappear into a burrow. When running along the surface of the ground and not under leaf cover, the animals kept the body close to the contour of the ground thus rendering themselves very inconspicuous before slipping away under leaves.

From these observations and those in our standard testing arenas (see Appendix C), we may conclude that these animals make versatile use of their habitat. They can forage on the ground very ably and remain quite inconspicuous. They are able climbers, but it would appear that a tunnel system in the soil offers some protection for them. In addition, regular pathways utilizing available cover in the habitat are employed by these animals.

*Rest and sleep.*—The postures and associated behaviors are similar to those described for *Microgale dobsoni*.

*Marking.*—As noted for *M. dobsoni*, this species marks by means of the perineal drag.

*Care of the body surface.*—The behavior is essentially the same as described for *M. dobsoni*.

*Prey catching.*—Behavior is essentially the same as that described for *M. dobsoni*.

*Defensive and offensive behavior patterns.*—As noted for *M. dobsoni*, *M. talazaci* will, upon being startled, flee or, if in the nest, will exhibit the open mouth threat (gape reaction). Occasionally when defending the nest it will produce a soft grunting sound with the mouth half open. Generally, during the gape reaction, it is silent or expels its breath in a soft hiss. Although unquantified it is apparent that *M. talazaci* is more aggressive than *M. dobsoni* and will vigorously defend its nest against any intruder.

#### SOCIAL BEHAVIOR

The patterns of social interaction displayed by *Microgale talazaci* are very similar to those described for *M. dobsoni*. One characteristic of *M. talazaci*, however, may be noted: males and females upon initial contact appear to establish a stable relationship with one another earlier than is the case with *M. dobsoni*. This may be evidence for a continued pair association on the part of *M. talazaci* throughout the annual cycle. By this, we do not mean to imply that the male in any way participates in parental care, but only that a given male and female may come to be familiar with one another and, indeed, utilize the same tunnel and burrow systems over a prolonged period of time. Our oldest pair of *M. talazaci* generally lost weight when separated from one another and reached a weight equilibrium when placed together again. A high degree of tolerance is shown between a pair of *M. talazaci* whereas male-male interactions and female-female interactions are characterized by avoidance or mixed agonistic tendencies.

*Spacing and social organization.*—*Microgale talazaci* cannot be said to exist in great density and do not form colonies. One pair of animals was trapped on consecutive nights at the same locus. Another pair of animals was trapped in adjacent traps. Two other pairs were taken 30 feet from one another and another pair at approximately 60 feet apart. Twelve specimens of the 18 collected at Perinet were taken at distances exceeding 1,000 feet from each other.

*Development of young.*—Two litters of one and two animals were born to two females at the National Zoological Park. Gestation is estimated at 63 days. In growth and development this species parallels *M.*

*dobsoni*. Measurements at birth for one specimen were: H.B.=43 mm; T.=27 mm; weight=3.6 gm.

## MICROGALE COWANI

### Physical description

*Microgale cowani* is a small tenrec with a head-and-body length of approximately 61 to 75 mm and a tail length of approximately 47 to 68 mm. The hind foot is about 15 mm in length. Thus, the tail is markedly shorter than the head and body and the hind foot approximately 21 to 23 percent of the head-and-body length. This would lead us to classify it as a surface foraging form. The weight ranges from 10.9 to 12.1 grams (see Figures 32 and 33).

The dorsal pelage ranges from agouti brown to black. One captive individual noticeably darkened at the conclusion of its first annual molt. Within a given

series of specimens one can discern a variable tendency for the expression of a black middorsal stripe, but this pattern is not as pronounced as one finds in *M. melanorrhachis*. The ventrum in *M. cowani* is generally brighter in color than the dorsum and tends to be a gray-brown. The tail is correspondingly faintly bicolored.

### Distribution and Habitat

This species has been widely collected in the eastern forest regions of Madagascar. Our particular specimen was captured in a grazing area approximately 3 kilometers west of Amparafara. The animal was trapped in an area of badly grazed-over land near second growth scrub. The discrete trap locus was in a tussock of grass. Other mammals in association with *Microgale cowani* were the insectivore *Suncus murinus* which



FIGURE 32.—*Microgale cowani*. This species is one of the smallest of the Oryzoricinae and shows some modifications for a semi-fossorial way of life. Note the reduced pinna and short tail. This inhabitant of second-growth areas is quite cryptic and resembles in its behavior the temperate zone shrews.



FIGURE 33.—Specimen in Figure 32 was trapped at the base of the second clump of grass from the left.

was trapped about 50 yards from the locus of *M. cowani*.

#### General Remarks on Behavior

Our single living specimen of *Microgale cowani* exhibited the following noteworthy behavior patterns. It is extremely cryptic. Upon being placed in an open field testing situation, it shows no tendency to climb and makes use of all available cover, moving in a very cryptic fashion under leaves with the body pressed closely to the substrate.

The animal exhibits a typical face washing pattern as described for *M. dobsoni* and *M. talazaci*, i.e., sitting

on its hind legs and stroking simultaneously with its forepaws on both sides of its head beginning behind the ears and carrying the stroke down to the tip of the nose. The mouth is held open during the terminal phase of the down stroke. The animal feeds on earthworms and was readily induced to accept a chopped meat mix diet. The animal will nest-build by carrying leaves into a nest box. Defensive behavior includes open mouth threat and biting. The chief characteristic of this species, when compared with *Microgale talazaci*, would be its tendency to remain cryptic making use of all available cover in an open field testing situation and its extremely reduced tendency to climb.

## *Setifer setosus*

### AN INTRODUCTION TO THE TENRECINAE

The subfamily Tenrecinae includes four well-described genera and a fifth genus *Dasogale* which is based on one specimen. We shall confine our present discussion to the four genera, *Tenrec* [= *Centetes*], *Hemicentetes*, *Setifer*, and *Echinops*. All members of this subfamily have a cloaca and the males possess testes which are located near the kidneys and undergo no descent during maturation. All species exhibit some spinescence but barbed detachable spines have evolved only in the genus *Hemicentetes* and only the genera *Setifer* (Figure 34) and *Echinops* (Figure 35) have completely spinescent dorsums plus the ability to roll into a ball. All species show a loss or reduction in tail length and one can note a decrease in tooth number for three of the four genera when compared with the genus *Micro-*



FIGURE 34.—*Setifer setosus*. This is the larger of the two species of hedgehog tenrec. The animal's dorsum is covered with stout nondetachable spines. It can roll into a ball presenting an almost impregnable defense to small predators.

*gale*. The discovery of the subfossil *Cryptogale australis* (Grandidier, 1928) has provided a link between the Oryzoricinae and the Tenrecinae. This species exhibits, in its skull morphology, a marked resemblance to the Tenrecinae yet retains a size and tooth structure reminiscent of the Oryzoricinae.

### **SETIFER [= ERICULUS] SETOSUS** (FRORIEP, 1806)

#### **Physical Description**

*Setifer* has a dental formula of  $\frac{3}{3} \frac{1}{1} \frac{2}{2} \frac{3}{3}$  ( $\frac{2}{2} \frac{1}{1} \frac{3}{3} \frac{3}{3}$  Herter, 1964) giving a total number of 36. The tail is reduced and stout and ranges from 15 to 16 mm in length. Length of the head and body for adult animals ranges from 150 to 220 mm. The hind foot is around 30–31 mm in length. Weights of the animals taken in the field range from 180 to 270 grams. In captivity the animals have a tendency to become rather obese and much greater weights can be achieved. The dorsum is covered with densely packed spines which are not barbed and do not readily detach. The ventrum, face, and limbs are covered with sparse hair. The vibrissae are very prominent and organized into the basic clusters: genal, mystacial, mental, and superorbitals.

The color of the spines varies somewhat depending on the geographical locality, and three subspecies have been proposed on the basis of presumed local color variation (see Grandidier and Petit, 1932). As a general rule, those specimens from the eastern rain-forest area exhibit a more pronounced deposition of melanin in the distal portions of the spines giving an overall darker effect than the high plateau denizens from drier areas. The sexes are not noticeably different in size and the possession of a cloaca necessitates that sex determination be conducted by manual expression of the phallus. The nipples are quite prominent in the lactating female and she possesses five pairs.



FIGURE 35.—*Echinops telfairi*, the lesser hedgehog tenrec. The climbing ability of this species is quite pronounced. Offensive and defensive behaviors are patterned in an identical fashion to those displayed by *Setifer*.

#### Distribution and Habitat

*Setifer* is found in the northwest of Madagascar in the region of Majunga and its distribution extends down the eastern coast. It appears to be absent from the arid southwest and its ecological niche is occupied there by the genus *Echinops*. *Setifer* is rather abundant in the eastern portions of the high plateau and does not seem to be unduly disturbed by agricultural pursuits. It is much less abundant in rainforest areas. We found it to be rather sparse in the vicinity of Perinet and no specimens at all were collected in the area of Ambitolah and Ranamafana.

#### Burrows

Four burrows of *Setifer setosus* were examined; two in the vicinity of Manandroy and two slightly to the south

of Alakamisy Ambohimaha. In three cases the burrows were occupied by single individuals and, in one case at Manandroy, two adult males were present in the same nest chamber. One of the burrows appeared to have been little modified by its occupant and indeed was in part formed from crevices in association with the root system of the tree which grew near the entrance to the tunnel. Some attempt had been made by the occupant to enlarge the entrance as well as certain points of constriction in the "tunnel" system, but there was no leaf nest. It may be assumed that a burrow of this type is occupied for a short time.

Another well-formed burrow was located 102 feet away. The tunnel itself was approximately 60 mm in diameter; the nest cup was about 75 mm in diameter and lined with leaves. Both of the previously mentioned burrows were on a north-facing slope above a rice field in association with a sparse undergrowth of

ferns and grasses. Feces were placed near the entrance of both burrows. The two burrows which we opened at Manandroy were very similar having short tunnels approximately 2 feet long leading to a nest cup lined with leaves. Again feces were deposited near the entrance. Both of the preceding burrows were near the edge of cultivated fields but placed well into an area of undergrowth.

### The Annual Cycle and Reproduction

In the vicinity of Manandroy and Alakamisy Ambohimaha, collections were made during January and April. During a previous expedition to Madagascar, Gould had sampled the same area near Manandroy in July. From these two separate studies, we are able to conclude that in this area of the high plateau the relative abundance and activity of *Setifer* is sharply curtailed during the austral winter. The total population of *Setifer* is not necessarily in hibernation during the austral winter but apparently many individuals are semi-torpid for varying intervals of time. Our studies would indicate that depending on local climatic conditions and the relative abundance of food, *Setifer*, as a population, may be active throughout the year but individuals do have the capacity to become torpid for varying periods of time and may spend the better part of the austral winter with a restricted foraging radius, passing much time in a semitorpid state. For example, although pregnant females have been collected in this area during the month of February, our population sample in January and in early February of 1966 clearly indicates that reproduction is synchronized to begin in mid-October.

From Alakamisy Ambohimaha, 24 individuals were collected over a period from 31 January to 3 February. These individuals were weighed and measured and subsequently released. Ten adult individuals were between 160 and 200 mm in total length with a modal value in the range of 180 to 190 mm. The remaining group of 14 individuals ranged in size from 110 to 150 mm in total length. Based on captive growth curves, we estimate this size to represent a subadult age class of 2 to 8 weeks.

With this in mind, it can be said that for the local area of Alakamisy Ambohimaha and Manandroy, the *Setifer* population initiates synchronized breeding activity in mid-October. Since it has a gestation period of some 63 days, this would mean that the size class of

young from 110 to 150 mm were the "young of the year" born as a result of the first mating period beginning in late September and extending to mid-October of 1965.

A subsequent sampling in the same area in April yielded 24 individuals. Of the 24, only two were of the size between 130 and 140 mm total length. All other individuals ranged in size from 150 to 220 mm in total length. This clearly indicates that births were sharply curtailed during the lapse interval between our first sampling and the final sample. The population was characterized by a preponderance of adults in April. This conforms to our hypothesis that, although some breeding may be carried on throughout the austral summer, the majority of breeding activity at this particular latitude and elevation occurs in the austral spring, probably from late September on through to mid-October resulting in an almost synchronized production of young which, in all probability, winter over to reproduce in the following spring.

### Activity and Thermoregulation

Herter's studies (1964) indicate a pronounced nocturnal activity rhythm and our field observations agree. Seven sightings of foraging individuals in the field were made at night. No *Setifer* were ever spotted during our daytime activities in the field. Herter's data indicate a bi-modal activity peak with the first maximum occurring at approximately 1900 hours and the second maximum occurring at approximately 0200 hours. The increase in activity is paralleled by a pronounced increase in body temperature and an increase in breathing frequency. In Herter's study body temperature showed a maximum at approximately 0200 hours only to sink to a minimum at approximately 1200 hours.

We know from Herter's study and our own observations that the activity of *Setifer setosus* is depressed at lower environmental temperatures. For example, a tremendous reduction in the activity of *Setifer* could be induced by lowering the ambient temperature to 14° C (Herter, 1964). At Fianarantsoa during the month of February, temperatures within the animals' holding cages ranged between 21° and 24° C. At this temperature the animals were active at night and fed well. During a temperature drop over a four day period at Fianarantsoa to a range of 16.8° to 20° C.

with an average high of 19° C., the animals exhibited less activity and a decreased feeding tendency.

Our measurements of cloacal temperature in the field indicated, for the month of February, an average of 29.6° C. and a range of 28.5° to 30.5° C. (N=9). These temperature readings were made during the theoretical increase in body temperature as determined by Herter between the hours of 1500 and 1800. Ambient temperature at this time ranged between 21.3° and 24.3° C. A series of temperature readings made with our *Setifer* during the same period but between 0900 and 1000 hours during the theoretical low in body temperature gave a range for *Setifer* between 27° and 32° C. with an average of 28.7° C. (N=5), over an ambient range of 23° to 24° C. Some two weeks later during a period of low ambient temperature described previously, a sample of seven indicated a range of body temperature from 19.1° to 32.3° C. with an average of 26° C.

Further temperature studies were conducted at the laboratories at the National Zoological Park during the month of July 1966. During this time a number of individuals were found to have body temperatures approximately equal to the ambient. An equal number of individuals were found, however, to have body temperatures rising some 6° to 7° above the ambient. All of this tends to confirm our original hypothesis that given a reasonable range of ambient temperatures from approximately 20° to 27° C., *Setifer* will not necessarily enter a torpid state during the austral winter, but may continue to be periodically active and feed. Not all members of a given colony or a given field sample are in synchrony with respect to torpor.

Because of the tendency for *Setifer* to continue activity even during the austral winter, we were forced to restrict the food intake of our captive animals. During the second year of maintenance, we deliberately withheld food from the animals over an 8–10 week period. In the previous year of captive maintenance, our *Setifer* colony members had achieved rather high weights. By subjecting our animals to an 8–10 week fast during the austral winter, we were able to bring weights down within the normal field range. Upon introducing the animals to food, we were able to induce a successful recovery in weight and, in two cases, successful breeding.

It seems, on the basis of our field and captive experience, that *Setifer setosus* is capable of maintaining a body temperature higher than that of the

ambient throughout its annual cycle. Depending on local conditions, it can become semitorpid to torpid and subsist without food for a period exceeding two months. Subject to local conditions, populations of *Setifer* may enter semitorpor and reproduction may be synchronized by the seasonal return of higher temperatures and the increased abundance of food.

### Feeding Habits

*Setifer setosus* was tested with a variety of foodstuffs and found to be quite omnivorous. It will feed upon earthworms, grasshoppers, raw ground meat, and carcasses of mice, but it seems to be incapable of killing prey larger than insects, worms, and baby mice. Petter reports that *Setifer* will take carrion, and we observed *Setifer* foraging around garbage dumps in the vicinity of human dwellings.

### Ethological Studies

#### GENERAL MAINTENANCE BEHAVIORS

*Locomotion.*—*Setifer setosus* employs a crossed extension coordination pattern during locomotion and has not been seen to employ quadrupedal saltation. When running it does rise up on its toes, keeping the heel off the ground. *Setifer* climbs very well but slowly and continues to employ the diagonal coordination pattern. The short, muscular tail may be used as a source of support during its climbing activities.

*Exploration and utilization of the living space.*—As stated previously *Setifer* is nocturnal. Observations in an open field testing arena or observations in the field indicate that *Setifer* moves about pausing from time to time in an elongate posture sniffing and testing the air while slightly bobbing its head up and down. It may also assume an upright posture bearing its weight on its hind feet and tail but this is seldom shown. When placed in a novel environment, the animal may exhibit some initial hesitancy before beginning to locomote and sniff the substrate, inserting its nose under leaves, and occasionally digging in the earth with its forepaws.

One free ranging specimen which lived very near to our laboratory at Fianarantsoa would come in the evening to visit our garbage area. Upon being disturbed, this animal twice showed an escape reaction employing the same route. This was to climb the vines over an outbuilding and proceed to the roof, where-

upon it would run along the gutter and descend by means of a wall to the opposite side of the building. This familiarity with the environment would indicate that *Setifer* shows trail stereotypy and also indicates its remarkable ability to climb.

*Rest and sleep.*—*Setifer* typically sleeps in a curled posture with the head tucked under the body. At very high temperatures *Setifer* may recline with the body axis aligned horizontally and the ventrum spread on the substrate or may even lie on its side.

*Marking.*—Marking movements while exploring a novel area include rubbing the chin or cheeks on twigs and exhibiting the typical perineal drag as described for *Microgale*. In addition to marking with glandular areas, *Setifer* will deposit its feces near the entrance to its burrow. This may have some significance in chemical communication. *Setifer setosus* will generally urinate outside of the burrow but, in captivity, we have noticed from time to time a tendency for urination very near the burrow or in the burrow tunnel. This may serve to demarcate an inhabited area with an individual's scent.

*Care of the body surface and comfort movements.*—As with *Microgale*, three patterns may be noted. Scratching is the predominant grooming pattern, and the animal reaches most anterior areas of its body with its very flexible hind limb. The second grooming movement includes the face-wash which involves sitting upright and bringing up both forepaws simultaneously to wipe on either side of the face. The movement is repeated several times and includes a stroke from the ear to the tip of the nose. As with *Microgale*, in the terminal phase of this movement, the mouth is partially open and apparently saliva may be applied to the forepaws and thus spread on the face. Licking is generally confined to the cloacal region. Other comfort movements include the typical mammalian patterns of yawning and stretching.

*Urination and defecation.*—Defecation involves a pause in forward locomotion. The animal partially extends its hind legs and raises its tail while expelling the fecal mass. Urination also involves a brief pause with tail raising.

*Nest building and burrowing.*—*Setifer* has rather strong claws and is quite able to dig into an earth substrate. Burrowing sites are generally chosen in the vicinity of a log or tree root and, as indicated in a previous section, natural crevices may be utilized. Nesting material, generally leaves or grass, is transported

by picking it up with the mouth and carrying it into the tunnel to be deposited in the terminal chamber.

*Prey-catching behavior.*—The mouth is employed almost exclusively in the capture of prey. *Setifer* will approach and sniff at a prey object such as an orthopteran and then suddenly seize it with its mouth and commence chewing. The forepaws may be used to pin down food while it is torn to pieces but no special forepaw involvement is shown during prey capture.

*Offensive and defensive behavior.*—*Setifer* displays a variety of reactions to disturbing stimuli. Upon being approached in the field by a human observer, *Setifer* initially will often flee. By conducting speed tests (see Appendix E), we established that, over a distance of 15 feet, *Setifer* can attain a speed of 3 feet per second. If a *Setifer* is pursued and cornered by a human or a dog, it will exhibit varying degrees of offensive and defensive behavior.

Arousal is always accompanied by spinal erection. Spinal erection coupled with rolling the brow forward to cover the eyes thus presenting a crown of spines directed forward is termed "brow rolling." In this position the animal will generally buck with its head and often produce the "crunch" sound which may be a result of clicking the teeth. The head may be bucked and switched rapidly from side to side with the mouth held half open. If an object is extended toward a *Setifer* at this time, it will be bitten. At high intensities, the animal may partially roll into a ball while exhibiting a gaping mouth. As an alternative to crunching, the animal may hiss and puff by rapid inhalation and exhalation. These vocalizations range in duration from .05 to .18 seconds. The energy is concentrated at approximately 1,000 to 3,000 cps but is broadly distributed and there is little harmonic structure.

Complete defensive behavior is produced when the animal rolls into a ball, tucking the head toward the ventrum. Spinal erection is maximal at this time. While rolled in a ball, if the animal is disturbed, it produces the putt-putt sound. This sound has little harmonic structure with the energy broadly distributed up to 12,000 cps. It is very brief, being uttered in bursts of eight to ten with a pulse duration of .025 seconds. When tested with the odor of *Galidia* or when presented with a living *Galidia*, *Setifer setosus* responds by hissing, rolling the brow forward, exhibiting maximal spinal erection, and then proceeding to buck and produce the crunching sound. Continued stimulation

causes the animal to roll into a ball. Even when rolled in a ball, *Setifer* may not remain completely defensive and, if prodded, it may unroll and buck while suddenly emitting an explosive puff or hiss (see Figure 34 and Appendix G).

#### SOCIAL BEHAVIOR

*Communication.*—As outlined under *Microgale dobsoni*, communication patterns include all those activities which are found in a context involving two or more interacting conspecifics.

Vocal communication involves a series of grunts, squeaks, and chirps during the contact-promoting process. A grunt occurs occasionally when the animal is apparently not highly motivated but disinclined for contact. A squeak may occur in response to mildly disturbing stimulations. The chirp is specific to the mating context. Chirps are most frequently produced by a female during the initial phases of mounting by a male. The chirp is a harmonic tone which may range from 1,000 to 3,000 cps having an average duration of .05 seconds. The sound form is chevron-like rising from a minimum to a maximum pitch and falling rapidly over an interval of .05 seconds. The range in frequencies in a typical pulse is approximately 1,000

cps. During agonistic encounters with conspecifics, the crunch, putt-putt, and hiss and puff sounds may be produced in contexts as defined under offensive and defensive behavior (Table 5 and Figures 36 and 37).

Tactile communication occurs during the typical contact postures which will be described in detail in the subsequent section. These include naso-anal, naso-nasal, nose to ear, nose to body, attempted mount, and in the agonistic context, butting with the head.

Chemical communication has been described under the section titled "Marking" (p. 53). In addition, we should like to point out that *Setifer setosus* males secrete a white substance around the eye. This may be involved in chemical communication (see also *Echinops telfairi*, p. 59).

*The encounter.*—Two-animal encounters were run in a neutral arena and the following adult sex combinations were studied: Male to male, male to female, and female to female. Male-male and female-female encounters in a neutral arena were characterized by a small amount of interaction including nose to body followed by moving away. This latter sequence was frequently shown in the male-male encounters. In female-female encounters, nose to nose or nose to body followed by slight following and moving away were typical. In general one can conclude that an avoid-

TABLE 5.—Physical properties and circumstances of occurrence for some vocalizations of *Setifer setosus*

Sound Type	Sample Size	Note Structure	Temporal Patterning	Frequency Range (Hz)	Dominant Frequency Range (Hz)	Duration (seconds)	Circumstances of Occurrence
Clear tones Chirp	5	Modified chevron	Repeated .16 sec. interval	1,000–3,000	2,000–2,500	.03–.05	Made by female during mounting by male.
Noisy sounds Putt putt	9	Wide energy distribution	Repeated ~.05 sec. interval	~50–9,000 Faint overtones to 20,000	50–4,000	.03–.07	Mild disturbance when either rolled or uncurled in nest.
Hiss-puff	12	Wide energy distribution	Repeated <.05 sec. interval, but organized into a short long alternating series; probably corresponding to inhalation and exhalation.	50–5,000	1,500–2,500 3,000–5,000	.08–.23	During head butting and offensive—defensive behaviors.

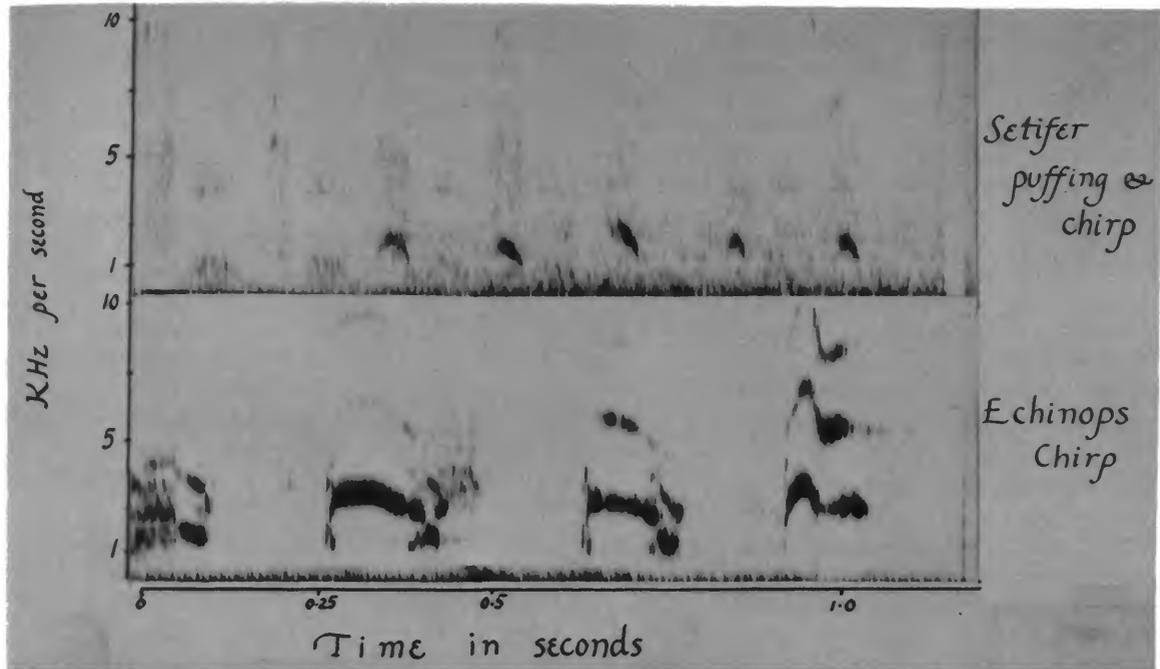


FIGURE 36.—Vocalization of *Setifer setosus* and *Echinops telfairi*. Chirp series: The similarity in tonal structure is quite evident but note the modified chevron form of the syllable for *S. setosus*.

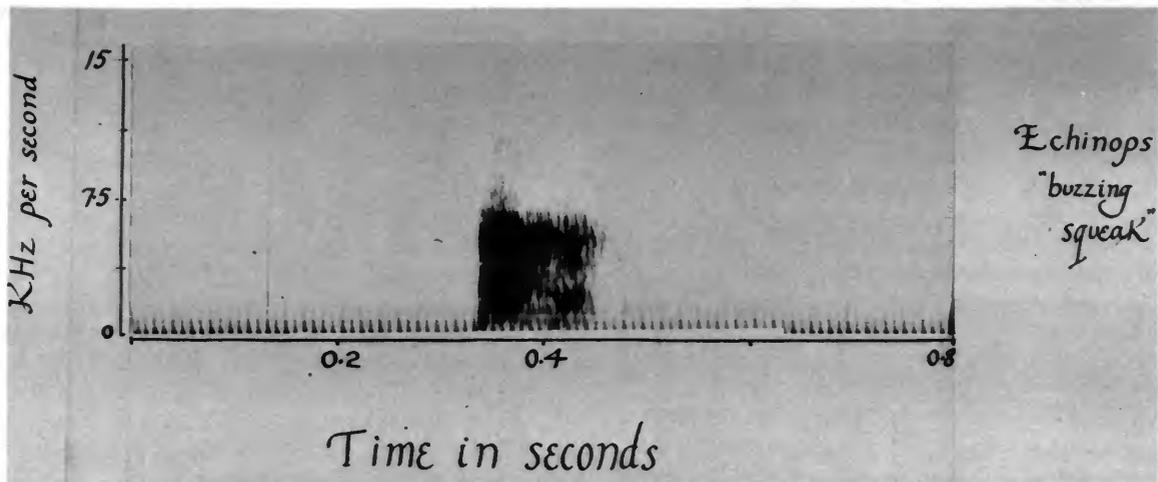


FIGURE 37.—Vocalization of *Echinops telfairi*. Buzzing squeak: Compare with the buzz produced by *Microgale* in Figure 28.

ance response is shown during an encounter in a neutral arena between members of the same sex. On the other hand, male-female encounters were characterized by much more contact-promoting behavior including nose to nose, nose to cloaca, nose to ear, and nose to body by the male and reciprocal naso-anal, naso-nasal touching, and nose to face touching by females. Males alone showed attempted mounts. Females, if unreceptive, would exhibit bucking behavior or would move away. In male-female encounters males showed up to 5 times as many occurrences of following than did females.

The functional organization of encounter behavior may be considered by turning to the two protocols.

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Example of male-female encounter with the female partially receptive, 23 August 1966, 1520 hours: Animals placed in arena occupied by female. Male started moving about the cage immediately sniffing the substrate. He paused at the female's nest box and rubbed the side of his head rhythmically on her box while walking around it. Male then went over to the water crock which had been used by the female and rubbed his head about the rim of the crock. 1527 hours: Male walking about the cage and approaches the log (containing the female). He scents the female's location in the log through an opening. The female moves backwards. He then climbs the log and enters the cavity occupied by the female and subsequently climbs over her. Female immediately comes out in the open; male follows. Male is exhibiting discharge from the vicinity of the eye. 1535 hours: Male attempts mount. No sounds heard from either animal. Female proceeds back into the log and male follows. 1537 hours: Male mounts female and copulation proceeds. 1555 hours: Copulation still in process. 2005 hours: Chirping call by female heard.

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Comments: Duration of first mount exceeded 28 minutes. Male marks female's nest box and subsequently exhibits white secretion around his eye.

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Example of male-female encounter with the female very receptive, 16 September 1966, 1500 hours: Male number 2 placed with female number 4. Female had just completed her molt. (Shedding of quills generally follows a period of prolonged torpor, and receptivity in females appears to follow the completion of molt.)

Upon introduction, the male approaches the female. There was a naso-anal investigation while the female urinated, holding her tail up. The male paused to lick the female's urine and then defecated. Then as the female moved away, there was naso-cloacal investigation; a nose to side by the male, and the male proceeded to follow the female. The female showed tail-up position while urinating and during the original naso-anal investigation continued to show this tail-up posture as the male followed her. He attempted to mount. The female showed very little resistance, holding the tail-up posture. The male then made several attempts to mount while gripping her with the forelegs and standing, bearing his weight on one hind leg. He then used the other hind leg to scratch at her external genitalia, gently. This apparent stimulating movement was repeated on at least four occasions, alternating from the left hind foot to the right hind foot in no set pattern. Then the male mounted the female and attempted intromission. Intromission was successful and no chirping sounds were produced by the female.

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To summarize, during a male-female encounter, it appears that initial contact may be established by a nose to body or ear and nose to cloacal region. The male may initially mark in a female's territory by rubbing the face and chin on objects. Urination on the part of the female seems to be a chemical indicator to the male. The white discharge around the male's eye is not specific to the mating situation but adult males do show it and apparently it is in some way correlated with sexual readiness on the part of the male.

Mating generally takes place within the nest box or in artifacts such as a log placed in the encounter arena. The mount with intromissions is prolonged as was the case in *Microgale dobsoni*. Initial unreceptivity on the part of the female is displayed by moving away, spinal erection, and chirping during the mount. What was not mentioned in the protocols is that the male frequently uses a neck grip holding the female's spines in his mouth while positioning himself. In addition, the reader will note the use of the hind leg in the male to stimulate the cloacal orifice of the female prior to intromission. This same behavior will be noted in *Echinops telfairi*.

#### PARENTAL CARE BEHAVIOR

*Setifer setosus* was successfully bred in captivity twice. The period of gestation is approximately 65 days. Dur-

ing the week preceding parturition, the female shows increasing nest building behavior. Parturition has not been observed. After the birth has been completed, the maternal behavior consists of licking the young, huddling over them while they nurse, and an increased defensive behavior if the nest is disturbed.

Nursing appears to persist well into the third week when the female begins to show a decline in interest toward the young. When the young are approximately 14 days old, they will begin to accompany the female outside the nest during her trips to the food dish.

#### ONTOGENY OF BEHAVIOR

At birth, the eyes and the auditory meatus are closed. The spines are slightly visible on the dorsum. Sparse hairs may already be present on the ventrum. The young animal can turn over if placed on its back. It can back up or crawl slightly forward. At this time it exhibits very poor hind limb coordination. The eye

opening period takes place from the 9th to the 14th day. Response to sounds is first indicated at 10 days of age. The young animal may begin to sample solid food at 14 days of age and, by this time, its locomotor patterns are reasonably well coordinated. A growth curve is represented for two litters in Figure 38.

#### SOCIAL ORGANIZATION

Based on our observations of individuals foraging in the field, these animals are generally solitary as adults. Of the four nests that were opened, one was occupied by two males; the other three by single individuals. Considering the spacing and distribution of the nests, we can conclude that this animal is generally solitary as an adult but may form a male-male consortium during the nonbreeding period or during the breeding season a temporary male-female consortium. The only other social grouping would appear to be the female-young unit during the rearing phase which may occupy

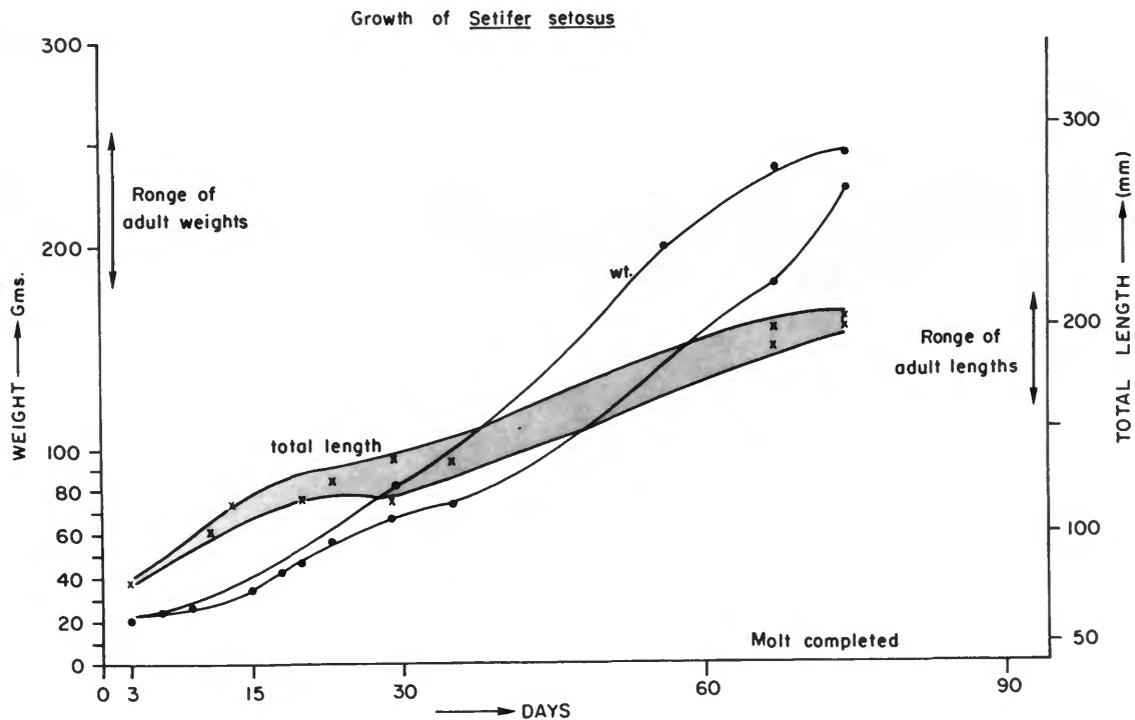


FIGURE 38.—Growth curve for *Setifer*. Total length shows a steady increase and is the most reliable indicator of age up to approximately 70 days. The molt takes place over a period of approximately 30 days being completed at about 2 months. The range of adult weights and lengths are included.

some three weeks. Undoubtedly the young do accompany the mother during the initial foraging period and learn the route back to the nest, but this period perhaps lasts for only three days. Inferences are difficult

to make without exact field data and this interpretation is based, in part, on our experience with the other Tenrecidae and observations in the National Zoological Park.

## *Echinops telfairi* (Martin, 1838)

### Physical Description

Although superficially similar to *Setifer setosus*, the dental formula of *Echinops* is unique and exhibits the most profound reduction in tooth number within the family Tenrecidae. The dental formula is  $\frac{3}{3} \frac{1}{1} \frac{2}{2} \frac{2}{2}$  with a total of 32 teeth. In total length, *Echinops* is slightly smaller than *Setifer* ranging from 140 to 180 mm. Weights in captivity range from 110 to 250 grams depending on whether the animal is in full condition or if it has recently emerged from torpor. There are no profound external differences between the sexes. Since the animals possess a cloaca, sex determination is accomplished by manually expressing the phallus. The males, however, do appear to have a broader head with a slightly greater distance between the eyes when viewed frontally. Color variation has been noted in *Echinops* and several subspecies have been proposed (Grandidier and Petit, 1932); however, it is to be noted that within a given population one may find individuals exhibiting extreme variations in color from a pale, almost white condition to a very dark body color resulting from more intense melanin deposition in the annular bands of the quills. The laboratory population captured by Gould showed such variation and we are led to conclude that within a given population a condition of genetic polymorphism occurs and the ratio of pale individuals might indicate that a simple Mendelian recessive is responsible for the difference in color (see Figure 35).

### Distribution and Habitat

*Echinops* is confined to the more arid southwestern portion of Madagascar and has been collected at Morandava and Tulear. The animals appear to den in tree cavities and may be taken on the ground under logs, at the base of trees, or off the ground in hollow tree cavities of limbs and trunks (see Gould and Eisenberg, 1966). The distribution of their nests implies that they have considerable arboreal ability and this is indeed

the case. Observations in captivity would indicate that the animals can forage for insects in trees as well as on the ground.

### Activity and Thermoregulation

The extensive studies of Herter (1962b) indicate an endogenous diel rhythmicity in metabolic rate. This is reflected by a decline in internal temperature with cloacal temperatures reaching a minimum slightly before noon and beginning to increase coupled with an increase in breathing frequency until the maximum cloacal temperature is reached at approximately midnight.

The degree of oscillation in body temperature is in part a function of the ambient temperature. Since *Echinops* comes from an area of Madagascar which is subject to extremes in seasonal temperature, we might conclude that a given population could exhibit synchronized torpor on an annual basis. This is probably quite adaptive since the abundance of insect prey may be influenced by temperature and seasonal aridity. Since both of these factors are manifest in an extreme condition in their native habitat, it seems safe to conclude that an annual season of torpor is shown. For example, in the laboratories at the National Zoological Park during the beginning of the annual decline in activity over an ambient temperature range of 23° to 26.8° C., our laboratory population exhibited a morning cloacal temperature range from 24° to 28° C. and a late afternoon range from 27.5° to 30.7° C. Laboratory population synchrony was much more pronounced in *Echinops* than was the case in *Setifer*.

### The Annual Cycle and Reproduction

If the propensity to assume torpor is indeed seasonal in the wild, we may conclude that the season of reproduction is likewise synchronized. In the laboratory, the animals continued to show from 1963 to 1966 an annual tendency to decline in weight to a minimum of

approximately 110 grams and then commence feeding and rise to maximum weight again. During 1963, 1964, and 1965, minimum weights were achieved in September with maxima approximated in May and June. Under this rhythm, births took place in the months of November, December, and January. In 1966 and 1967 we attempted to monitor this rhythm by depriving the animals of food during the months of July, August, and September. In this way, maximum weights were maintained in April, May, and June, and minimums were achieved in January and February. This allowed us to control reproduction and litters were produced in April and May of 1966 and in June of 1967. It would appear, then, that feeding and activity do operate in part on an endogenous rhythm but can be modulated by environmental conditions. One environmental condition is to lower the ambient temperature which induces prolonged torpor; the other is to deprive the animals of food.

Gestation is approximately 66 days. This means that if animals emerge from torpor in the wild in September, one would anticipate that, after an initial feeding phase, breeding would take place in early October and litters would tend to be produced in December or January.

### Feeding Habits

The animals will take a variety of animal food including insects, baby mice, and chopped horse meat. A detailed preference analysis was published by Herter (1963a).

### Ethological Studies

Previous data concerning the behavior of *Echinops* has been published by Herter (1962b, 1963a), Honegger and Noth (1966), and Gould and Eisenberg (1966). Because of the existing data, we will use this section as a summary rather than a detailed redescription.

#### GENERAL MAINTENANCE BEHAVIOR

*Locomotion.*—The animal moves with a typical crossed extension pattern. During rapid locomotion it can rise on its toes and the heel does not contact the substrate. The animal moves ably in the trees or on a plane surface (see photographs in Honegger and Noth, 1966) and the tail serves as a brace. Observa-

tions on its swimming behavior are included in Herter (1964).

*Exploration and utilization of living space.*—The animals are strongly nocturnal. At approximately 1900 hours the animals commence activity and begin leaving their dens to forage for food. As noted before, they climb spontaneously and well. During climbing the animals are able to grip rough bark while continuously sniffing and nosing the substrate. Upon approaching junctures of limbs, the animals will pause to test the air and may lick their lips. This produces a slight clicking sound which apparently is involved in their echolocating ability (see Gould, 1965).

*Rest and sleep.*—The animal typically sleeps in a curled posture with its head tucked ventrad. At high temperatures the animal may recline with the body axis fully extended.

*Marking.*—In captivity the feces and urine may be deposited at specific points in the cage. Feces and urine are implicated in chemical communication (see p. 62). When exploring in a new area, the animals have been observed to depress the cloacal region and drag it on the substrate; as noted for the other forms, this has been described as the "perineal drag."

*Echinops* exhibits a very special self-marking movement that has been described by Eibl-Eibesfeldt (1965) and Gould and Eisenberg (1966). In the latter publication this movement is compared and contrasted with an analogous behavior pattern in the true hedgehog, *Erinaceus*. This scent marking pattern involves approaching a foreign chemical substance, sniffing or licking it, lifting the head, and salivating slightly. Then one forepaw is rubbed rhythmically in the chemical substance, and while rising partially on its hind legs the tenrec then turns to one side to spread the chemical substance with its forepaw on its side quills. As has been noted before, this spreading of foreign odors on the quills is also exhibited by the hedgehog, *Erinaceus europaeus*, but in the latter case it does not involve the use of the forepaw but rather the foreign chemical and saliva are spread with the hedgehog's tongue (Gould and Eisenberg, 1966).

*Care of the body surface.*—As noted with *Setifer*, the animal grooms its spines primarily by scratching. It will lick its cloacal region and ventrum. *Echinops* will exhibit the face wash by sitting upright and employing the forepaws to stroke simultaneously on either side of the head (see also *Setifer*, p. 53, and *Microgale*, p. 34). The washing movements occur

TABLE 6.—Physical properties and circumstances of occurrence for some vocalizations of *Echinops telfairi*

Sound Type	Sample Size	Note Structure	Temporal Patterning	Frequency Range (Hz)	Dominant Frequency Range (Hz)	Duration (seconds)	Circumstances of Occurrence
Clear Tones Chirp	20	Modified chevron many harmonics	Repetitive series .17-.63 sec. interval	1,000-5,000	2,500-4,000 or 1,000-1,500	.08-.20	Produced by female while male is mounted.
Noisy sounds Buzzing squeak	3	Vibrato form and noise	Not often repeated but often combined within a chirp series	50-5,000	1,500-6,000	.08-.15	Produced by unresponsive female during encounter with male.
Hiss	3	No structure	Repetitive	50-4,500	50-3,000	.20-.30	Defensive behavior with brow folded forward.

alone or in conjunction with the self-marking movement described in the previous section.

*Nest building.*—This behavior is highly developed. Leaves and dry grasses will be transported in the mouth to the burrow and placed therein to form a cup.

*Prey-catching and feeding.*—Prey-catching behavior involves orientation to the prey object, such as an insect, sniffing and seizing it with the mouth. There is little involvement of the forepaws in the capture of prey, but the forepaws may be used to brush food and align it if, for example, an insect is seized crosswise in the mouth.

*Defensive and offensive behavior.*—As noted with *Setifer*, *Echinops* can roll itself into an impregnable spiny ball. Various degrees of spinal erection may be displayed during arousal. The brow may be rolled forward and the animal will switch its head from side to side or buck up and down attempting to drive the spines of the head into an enemy. The tendency to exhibit the gape reaction or to bite is reduced in *Echinops* compared with *Setifer*. The crunch sound is strongly associated with the bucking response as in *Setifer*.

#### SOCIAL BEHAVIOR

*Communication.*—As noted with *Setifer* visual communication is probably negligible. Tactile, chemical, and auditory signals predominate during their interaction.

During an encounter in a neutral arena, two strange

animals will show exploratory behavior. Tongue clicks may be produced at this time and are implicated in echo-location (Gould, 1965); however, such potential signals may serve in locating a conspecific. A mildly disturbed animal may show "brow rolling" to a conspecific while producing a train of discrete "putt-putt-putt" sounds similar to those produced by *Setifer*. The bucking, defense behavior is accompanied by the "crunch" sound. The animal may hiss repeatedly when rolled in a ball or when retreating with the brow rolled forward.

In addition to these agonistic sounds, the animals produce a series of squeaks which grade in intensity and duration. Mildly disturbed young produce a high peeping sound; the adult produces sounds ranging from this infant sound to very distinct "chirps." As with *Setifer* the chirps are produced by females during the initial phases of courtship and mating (see Table 6).

It should be noted that during courtship behavior and marking, *Echinops* will frequently show a rhythmic motion of its body musculature. This movement produces a slight abrasion of the dorsolateral quills, one against another, with a very low sound being produced. The exact significance of this sound and its context are not clearly understood.

Tactile communication occurs during nose to ear, nose to body, nose to anal region, or when rubbing against one another, or crawling over and under.

Chemical communication is implied by the locus specificity of defecation and the spreading of scents on the quills (see p. 60). In addition the males often secrete a white substance around the eye as described for *Setifer*.

*The encounter and mating.*—Male-male behavior in *Echinops* usually involves avoidance or actual fights. Males can be extremely aggressive to one another and, during the process of mutually sniffing each other's sides with the body axes oriented in the opposite direction, they may begin to butt one another and attempt to bite each other's flanks. Persecution by a dominant male will eventually result in the subordinate rolling completely into a ball or fleeing.

Interaction between males and females was studied intensively. During an encounter between a male and a female, the female would often move away and defecate and/or urinate. The male would persistently follow and sniff her trail. Frequently, the animals would make contact. Contact was generally initiated by a male, approaching and sniffing the female's side and then passing by her while rubbing his body the length of her side. The male may pause to sniff her ear and, if the female were receptive, mating would take place. The following protocols are offered as examples:

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Mating test with female unreceptive; male had been introduced to female's cage, 3 January 1966, 1500 hours: Male approaches, lowers head with spines erect and butts female in the side. Female turns away. Female moves to her box; male follows. Female stops; male sniffs her around the face and ear. Female turns her side toward him with spines erect. Female enters her box; male follows and attempts to mount. Male mounts gripping with his forelegs and the female arches her back, turns the tip of her nose up and with half open mouth exposes her teeth. The female emits a loud chirp during the mount and the male releases the female. The animals break apart with male leaving.

Female leaves her nest and male approaches. They encounter nose to nose. Female exhibits a half open mouth; male moves to one side and noses the female's ear. Male attempts to mount; female chirps. Male dismounts and moves away. A repeat with the male approaching nose to nose; male nose to female's ear, then attempts to mount. Female chirps; male continues with mount and grips female's spines in the middle of her back with his mouth. Female will turn and bite at his flank. Male grips female's flanks with his hind legs

while working his cloaca ventrad. Male emits a sustained puffing while female continues to chirp. Female pulls away. Encounter discontinued.

Mating test with female receptive. Male introduced to female's cage, 31 December 1965: Female out exploring. Male begins following; female defecates; male pauses to sniff then approaches female, touches nose to side and passes along her body rubbing his side against her. Female moves away to her box, male follows, pausing to sniff the box. Then he enters the box, exhibits a nose to her ear. He attempts to mount and the female shakes her head.

One hour later, the male approaches the female who urinates and defecates. He attempts to mount, and noses her ear. The female moves away; he follows. Ten minutes later, the male mounts again, while the female raises her tail. Male slides backwards attempting intromission. The male, preceding intromission, will attempt to scratch at the cloacal area of the female with his hind foot. Male continues mount and finally relaxes grip while the female remains motionless. Copulation is terminated after a total of 18 minutes mount with thrusting. Male initiates exploration after a rest period of approximately 17 minutes while the female remains in her box.

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We offer the following comments: Note the similarity to the mating ritual in *Setifer* including the prolonged mount, genital stimulation of the female by the male employing the hind foot, the neck grip of the male in seizing the spines of the female at her nape, the initial contact involving nose to ear and face, and nose to body. Finally the chirping of the female during the initial phases of mating is almost identical to *Setifer*. We would further like to call to the reader's attention the fact that in *Setifer* and *Echinops* there is a tendency for mating to take place in the female's nest box or a suitable cavity. One feature not noted in the protocol but noted in others is the fact that the male generally licks his genitalia at the conclusion of a long mount.

#### PARENTAL CARE

Preceding the birth of the young, the female indulges in considerable nest building behavior. The retrieval of nesting material persists throughout the first week in the rearing phase. Nest defense by the female increases profoundly during lactation, and she will utter the putt-putt sound if disturbed and attempt to bite.

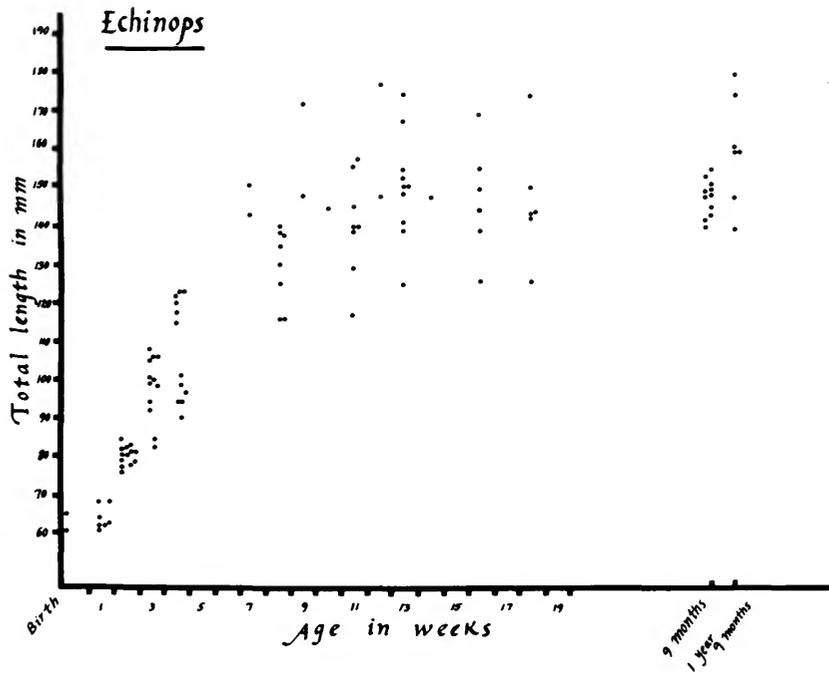


FIGURE 39.—Total length of *Echinops* is a reliable indicator of age until about 56 to 63 days.

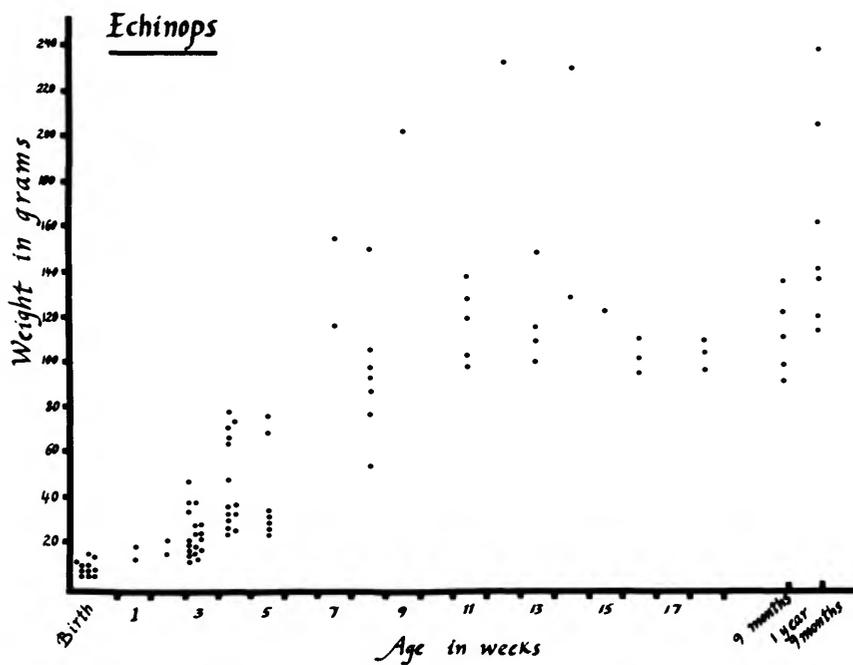


FIGURE 40.—Weight of *Echinops*. Note the great variation after six weeks.



FIGURE 41.—*Echinops hibernaculum* photographed immediately after opening hollow log (July 1963; about 20 kilometers east of Morondava). Head is to the left. Note extended body posture.

The female will retrieve the young if they are displaced from the nest, apparently in response to the peeping call that the young produce when mildly disturbed. The female will position herself over the young through lactation and, as the young mature, she may lie on one side during lactation. During the early phases of rearing, the female will lick the young especially in the area of the genitalia. Further comments on parental care are included in Gould and Eisenberg, 1966.

#### ONTOGENY OF BEHAVIOR

Complete ontogeny of behavior has been described by Gould and Eisenberg, 1966. We reiterate briefly the process. At birth the young *Echinops* are nearly naked. The auditory meatus and eyes are closed. The animals can locomote forward with poor hind limb coordina-

tion. The degree of spinescence at birth is variable but in general the tips of the spines are protruding through the skin; however, at this time the spines are very soft and hair-like. The animals can right themselves when placed on their backs. At this age the animals will roll into a ball when disturbed. Eye opening occurs between 7 and 9 days of age. At 10 days of age, the young begin to follow the female to the entrance of the nest. The auditory meatus opens at around 14 to 16 days of age. At this time they can locomote very well holding the ventrum off the substrate. The young begin to take solid food at around 2 weeks of age; weaning begins at approximately 18 days. Nursing in captivity may persist until the animals are 4 weeks old but they have been taking solid food as a supplement since approximately 3 weeks of age. Growth curves are presented in Figures 39 and 40.

## SOCIAL ORGANIZATION

Most of the generalizations in this section are based on observations in captivity. It would appear that *Echinops* forages alone except for the female-young unit. This unit persists until the youngsters are approximately 4 to 5 weeks of age. Apparently the young accompany the female on her foraging expeditions from the age of about 3 weeks on. On 28 January 1967 near Morondava, an adult female (total length

151 mm) and 2 juveniles (total length 124 mm) were collected from the same tree hollow. Some initial following tendency is exhibited by the young as early as 2 weeks of age. *Echinops* would appear to exhibit a mild degree of social tolerance and Gould and Eisenberg (1966) have noted that more than one individual may be found during the period of torpor. Three *Echinops* were found hibernating alone and two groups of two each were discovered (Figure 41).

## *Tenrec* [= *Centetes*] *ecaudatus* (Lacepède, 1799)

### Physical Description

As an adult, *Tenrec ecaudatus* is one of the largest living insectivores. It has virtually no tail and, when compared with the preceding genera of hedgehog tenrecs, its spinescence is vastly reduced. The dental formula is variable, being  $\frac{2}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}-\frac{4}{3}$  giving a total of 38 to 40 teeth. In contradistinction to all the preceding genera, this genus exhibits a profound difference in morphology when the juvenile and adult are compared. For this reason, the two age classes will be described separately.

In adult animals, the male is considerably larger than the female. His head is broad with a rather pronounced distance between the eyes which is markedly different in appearance from the female when the two are viewed frontally. The male possesses large masseter muscles which contribute to the broad appearance of his head. In addition, the canines of the male are very enlarged. The animals have a head and body length ranging from 265 to 390 mm. Captive weights range from 1600 to 2400 grams. These weights are somewhat excessive since the animals have a tendency



FIGURE 42.—Adult male *Tenrec ecaudatus*. This is the largest species of Tenrecidae. Male is displaying gape or open-mouth threat. Note the enlarged canine teeth and the extreme breadth of the male's head. Compare with photograph of female, Figure 43.

to become rather obese in captivity. Indeed, one individual reached a maximum of slightly in excess of 3000 grams. The color of the pelage varies with the geographic origin but in general is a reddish, agouti brown. The face is a light tan and the ventrum is a light yellow. The dorsum is covered with coarse hairs some of which exhibit an almost spinescent character, especially on the crown and nape where one may speak of true spines. In addition to the dorsal hair covering, the dorsum is adorned with long hairs which protrude beyond the coat and are black in color. These are apparently involved in the perception of tactile stimuli. The hairs are exceptionally long in the middorsal area. The vibrissae are well developed in the classical pattern as outlined for *Setifer* and *Echinops*. The pentadactyl paws and hind feet are adorned with stout claws (see Figure 42).

The young juvenile *Tenrec* ranges in size from 85 to 160 mm in head-and-body length. The ventrum is a light yellow brown and the dorsum is colored contrastingly with dark brown longitudinal bands separated by five longitudinal bands of white spines. In the middorsal region, the row of white spines is doubled and, by means of a specialized dermal musculature, these spines may be vibrated together in the middorsal region to produce a sound (see Gould, 1965). The contrasting pattern of dark brown and white is lost at the molt to the subadult pelage. At this time the white spines are replaced by hairs. Molt begins at approximately 36 days of age and is generally completed at an age of 2 months (Figure 1). This pelage change is accomplished within the total-length-size class of 160 to 260 mm. Some middorsal spines may persist in the subadult animal and still produce sounds but these are gradually lost without replacement as the animal matures (see Figure 43).

### Distribution and Habitat

*Tenrec ecaudatus* is widely distributed over the whole island of Madagascar. It occurs in a variety of habitats,



FIGURE 43.—*Tenrec ecaudatus* mother and infants. Note the pronounced spinescence and the infant striped pattern reminiscent of the coat color in *Hemicentetes*. The spines in the posterior dorsal midline are organized into a functional stridulating organ. This group came from Maroanetra and was photographed at the Institut Recherches Scientifique de Madagascar Parc Zoologique in Tananarive.

generally characterized by some brush or undergrowth for cover and near some source of free water. Thus, the animals may be found in the rainforests of the east and in the gallery forests bordering the river systems of the west. In the vicinity of paddy fields, the animals are to be found in abundance. The animal seems equally adapted to the plateau situation and the coastal, humid rainforests.

#### Burrows

The structure of the burrow varies depending on the season of the year and the age and sex classes inhabiting it. Rand (1935) describes two burrows excavated in the vicinity of Ivohibe during the austral winter.

These hibernating burrows were rather long and deep extending for over two meters at a depth of one meter.

During the breeding season and period of maximum activity, the females tend to construct deeper more complicated burrows, whereas the males may inhabit rather shallow systems. The description of a burrow excavated in the vicinity of Ranomafana follows: This burrow was located in natural forest at the edge of a cultivated field. The entrance lay some 7 feet above a stream. It was situated between two large stones and extended to a depth exceeding 4 feet. One of the large rocks was of sufficient size to make it impossible to reach the nest chamber although it could be touched with a stick. Another burrow system which had been excavated by the townspeople near Ranomafana was noted also to be in the vicinity of a stream.

A burrow was excavated in the vicinity of Perinet and had the following structure: It descended for a distance of about 3 feet to a blind leaf-filled chamber; however, it had more than one entrance. One entrance was situated at the base of a stump and the other which branched in a Y-pattern from the original tunnel exited on the other side of the stump near a root system. It would appear from Rand's work that the hibernating burrow of *Tenrec* often exhibits a single entrance plugged with earth; however, an active breeding burrow may have a Y-shaped entrance with two possible exit points connecting to form a tunnel ending in a blind nest chamber.

In order to study the microclimate of a burrow system, two burrows were selected in the vicinity of Perinet. One of these burrows proved to be empty. It was situated near the bank of a stream in primary rainforest. The ambient temperature over a 24-hour period ranged from 18° to 22.5° C. Over the same ambient range the temperature range in the burrow was 19.7° to 21.1° C., at a depth of 84 mm. A second set of 24-hour measurements was made with a burrow occupied by a female and four young. The ambient range of the shade temperature at this location was from 18° to 29° C.; over the same ambient range the burrow temperature was 22.5° to 25.5° C. This measurement was made at a depth of approximately 60 mm. Such measurements indicate that during the austral summer the burrow definitely serves to buffer the extremes of temperature to which a *Tenrec* may be subjected.

#### Activity Patterns

A family of *Tenrec* including a mother and four babies were allowed liberty in the large observation arena at Perinet (see Figure 4). Within this enclosure the animals constructed a burrow and we were able to monitor their activity using a photo cell device coupled to an event recorder (see Appendix F), which monitored the amount of activity at the feeding station. Such a measure, of course, does not indicate the amount of activity in other parts of the living space, but it does reflect the overall activity in the living space, since when the animals are out they make frequent stops at the feeding locus. The feeding locus was established by placing a dish of meat, to which the animals were conditioned to come, and, in addition, scattering numerous earthworms in the soil immediately adjacent

to the feeding dish. Thus, in order for the animals to forage, they spent considerable time digging in the soil immediately adjacent to the dish. During such a period of time they interrupted the photo cell device.

Activity was monitored over a 48-hour period and both 24-hour intervals were remarkably similar. A bimodal peak of activity was shown confined to the hours of darkness. Activity reached an initial maximum at 2000 hours and reached a second maximum between 0100 and 0200 hours. The first peak of activity extended from 1930 to 2130 hours; the second activity peak which was not so pronounced had a longer interval extending from 0030 to 0500 hours. Such observations are in remarkable agreement with field observations. There were ten field sightings of *Tenrec*, two which occurred in the late afternoon when there was still some daylight. The eight others occurred between 1800 and 2100 and 0100 to 0500 hours (see Figure 44).

#### The Annual Cycle, Thermoregulation, and Reproduction

During 1966 our captive colony showed a decline in feeding tendency beginning in early June and extending until the latter part of August when the animals again exhibited increased activity and feeding, reaching maximum weights in February and March, 1967. In May of 1967, we restricted their diet and induced a dramatic decline in weight persisting until late July when the animals were fed sufficient quantities to restore them to a more normal field weight.

During the first season in captivity, the decline in weight was paralleled by an absence of thermoregulation. Over an ambient range of 20° to 27.5°C., the colony exhibited cloacal temperatures varying less than half a degree from the ambient. These captive observations support the field observations that in most areas of Madagascar, especially on the high plateau, *Tenrec ecaudatus* enters a period of torpor in the austral autumn which persists on through the austral winter ending in the austral spring around August or September.

The gestation period is 56 to 64 days. Based on a rather extensive sample of specimens collected at Perinet, we found during the interval of 17 February to 3 March 1967, a size range in juveniles from 130 to 260 mm in total length. The majority of individuals had an average length of 180 to 190 mm. From this

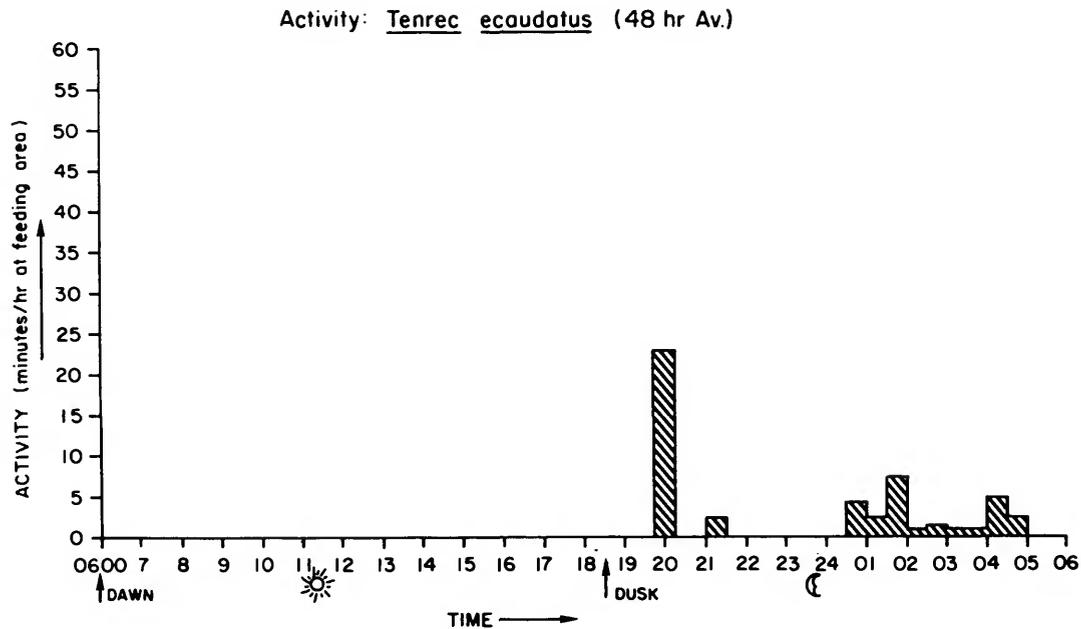


FIGURE 44.—Relative activity for *Tenrec ecaudatus*. Monitoring the activity of *T. ecaudatus* for 48 hours indicates maximum feeding shortly after dark. Activity is intermittent with a tendency toward bimodality during the dark phase.

sample of 40 juvenile animals, we can conclude that breeding at Perinet occurs from the middle of October to early November. This inference is based on our knowledge of the growth curve and the gestation period of approximately 2 months. We can infer from the distribution of our size classes in the juveniles that the oldest juveniles caught were approximately 2 months of age. This would imply conception in the female at 4 months preceding the capture date of the juveniles.

To summarize, in the vicinity of Perinet as well as in the vicinity of Manandroy, *Tenrec ecaudatus* exhibits a seasonal torpor during the austral winter with breeding commencing in the austral spring during the month of October and early November. Young are then born in December and January and complete their growth and molt to subadult pelage by March and April. It would appear that unless circumstances are extremely favorable only one litter is produced on the average; however, the presence of rather small young during March does not preclude the possibility of two litters a year especially if the first litter is lost immediately in December.

### Feeding Habits

*Tenrec ecaudatus* feeds on a variety of invertebrates, including earthworms, grubs, and orthopterans. It takes raw ground meat and mice. In general its prey-catching response strongly suggests that the animal may take other smaller vertebrates such as frogs or snakes. Its adaptability to novel foodstuffs suggests that the animal is rather omnivorous.

### Ethological Studies

#### GENERAL MAINTENANCE BEHAVIOR

*Locomotion.*—*Tenrec ecaudatus* typically moves with a diagonal limb coordination. It will climb using the diagonal pattern, but it does not habitually take to trees. We have observed them climbing rather steep rock faces and climbing on chicken-wire fences. *Tenrec* has been observed to swim in rice paddies and, when startled, will take readily to water and move from one bank of a pond to another.

*Exploration and utilization of living space.*—When

moving about in a novel environment, the animal will pause exhibiting an elongate posture and frequently lift its head and bob it slightly while inhaling and exhaling. This has been termed "testing the air." One forepaw may be raised during the tense investigation of a novel environment while the other limbs remain planted firmly. Upon settling to an investigation, the animal may move forward slowly, pausing from time to time to insert its nose into cracks, under logs, and in the soil. Upon perceiving a potential food item, it may dig in order to retrieve its prey. When foraging unspecifically, the animal will move along with its nose only a few millimeters from the substrate or actually inserted in loose earth. Upon being startled, it will again freeze and test the air.

In a novel environment the animal will frequently emit a piff sound which apparently has some communicatory significance to conspecifics. If, for example, another *Tenrec* is moving in the vicinity and the piff sound is given, it would appear to serve as an identifier and is immediately responded to by the perceiving animal. When exploring in a novel environment, the animal soon sets up stereotyped routes and such stereotypy has an obvious adaptive advantage for, if the animal is frightened, it can automatically seek a route to its nest location.

*Rest and sleep.*—In the nest chamber, the animal typically sleeps in a curled posture with the head tucked ventrad. It may rest on its side in the curled position and, at higher temperatures, the animal may lay out full length.

*Marking.*—When exploring a novel environment or during an encounter, the animal frequently exhibits movements which may serve to distribute chemical signals in the environment. A commonly observed pattern includes the "perineal drag" where the animal depresses the cloacal region while locomoting forward thus dragging the cloaca against the substrate. The animal has also been noted to rub its sides against objects in the environment using a typical extension and flexion of the body while leaning against an object such as a log. Urine and feces are deposited in a locus specific fashion (see following section).

*Care of body surface and comfort movements.*—*Tenrec ecaudatus* exhibits the typical vertebrate patterns of yawning, stretching, and shaking. During the stretch when the body axis is elongated and the epaxial muscles slightly contracted, the crest may be erected. Crest erection may also occur in association with the

yawn. The typical grooming pattern involves the hind foot and is termed scratching. Snout, ear, head, shoulders, under the armpit and the middle of the back may be reached by the flexible hind foot. The cloacal region and ventrum may be licked with the tongue and the toes may be nibbled after scratching. The forepaws are not involved in a face wash such as we have noted for *Setifer*, *Echinops*, and *Microgale*.

*Urination and defecation.*—Feces may be deposited near the entrance to the burrow but, in general, urination and defecation take place at a specific locus in the environment and involve a specific set of movements. Typically the animal moves forward sniffing the substrate until it encounters the location of fecal deposition. It then begins to dig with its forepaws excavating a small hole. It turns and backs into this hole and positioning its hind feet, tenses its body while it defecates and frequently urinates. It then pauses, dips its perineum, wiping the cloacal region, and kicks back to cover the feces and urine. This movement is employed by the individual when alone in its own environment and may also be exhibited as a group activity by the female and her young. Upon leaving the burrow, the female will go to her defecation spot near the entrance, dig, deposit feces, and then kick back. Generally, during this time, if the young are accompanying her, they will participate in the same reaction adjacent to her and the deposition of feces and urine can be almost synchronous once initiated by the mother.

*Nest building and burrowing.*—As described on p. 67, these animals do construct a rather long but simple tunnel system. The animal carries in its mouth the leaves and grass used to construct the nest. Nestbuilding behavior is shown by both sexes and, once the young have become old enough to locomote, at about the age of 3 weeks, they will also exhibit the transport of nesting materials to the burrow site.

*Prey-catching behavior and foraging.*—Foraging by *Tenrec* generally consists of probing with the nose in cracks and interstices between logs and earth. It will dig in order to excavate prey and, if it is a small prey object such as a worm or insect larvae, the prey is seized in its mouth with a slight shake of its head and immediately chewed and eaten. On the other hand, *Tenrec* may take rather large prey such as mice. Some experiments were conducted in order to analyze the mode of prey catching. Here are two examples:

An adult male in his home cage was offered a white mouse. The animal approached the mouse in an elongate posture and, after several hesitant attempts, rushed at the mouse and bit it once. The mouse was tossed to one side, whereupon it ran ahead a few paces and fell to one side twitching for perhaps some 90 seconds before dying. The mouse was examined and had two puncture wounds from the canines anterior and posterior to the shoulder. This prey-catching response demonstrates that the mouth alone may serve as a prey killing and capture organ. Furthermore, with large prey such as a mouse, there is a tendency to bite and toss or drop the prey only to return after it has ceased moving.

In contrast with this procedure, is the following protocol. A mouse was placed in a cage containing six young *Tenrecs* and their mother. As the mouse moved across the floor, one of the juveniles approached, evidently attracted by the sounds, and touched it with its nose. It immediately bit at the anterior part of the mouse, biting it through the head, and then shaking laterally back and forth with a slight upward and downward movement. It continued to hold the mouse by the head, then pinned it down with the forepaws, and bit repeatedly over the mouse's anterior end. When the mouse was still, it began to chew and eat the animal from the head end.

A second mouse was introduced into a cage containing four juveniles and their mother. In this case, the mouse was approached, touched with the nose, seized with the mouth at the midpart of its body and repeatedly bitten while moving the head laterally. Then the prey was pinned with one forepaw while the animal delivered a series of rapid bites to the head and finally began chewing the mouse at the anterior end while it dangled loosely from the mouth of the *Tenrec*.

From this description we can conclude that the mouth is the primary organ of capture and killing. If the prey is large and struggles, it may be shaken from side to side and tossed or alternatively it can be pinned with the forepaws while bites are delivered at the head end of the prey.

*Offensive and defensive behavior.*—When startled, the *Tenrec* will generally run. For its size it can develop a rapid speed over a short distance. Three individuals

tested in an arena were able to average 3.4 and 4.4 feet per second. The startle reaction generally involves pilo-erection. The crest and hairs in the middorsal line are prominent at this time.

Response to a predator odor is marked including pilo-erection, stamping of the forepaws, hissing and puffing, and, if brushed on the tactile hairs, the animal will deliver a slashing bite and even rush at the predator. If disturbed in the nest, the animal will attempt to attack, hiss, stamp its feet with erect crest, and exhibit a gape reaction with the mouth being held half to wide open. If contacted on the sensory hairs of the face or body, it will turn and deliver a slashing bite. When a female accompanied by juveniles is presented with predator odor, the whole group will orientate toward the source of stimulation exhibiting pilo-erection, stamping, hissing, and gaping. If they are persistently teased with a piece of cotton soaked in predator urine on the end of a stick, the whole group can be induced to rush and bite collectively at the offending object. This type of reaction with a group can be induced only if there is no possibility of flight (for example, in a testing arena). The first impulse of the animal when startled in a field situation is of course to freeze and then, if further perturbed, to flee rapidly.

#### SOCIAL BEHAVIOR

*Communication.*—Auditory communication involves a variety of sounds which appear to be homologous with similar sounds noted for the preceding genera. During offensive and defensive behaviors, the animal may stamp alternately with its forefeet producing a sound. With half open mouth, the animal may hiss and, if cornered and teased, the animal will exhibit a crunching sound perhaps by grinding its teeth. If seized, the animal can emit a grunting sound which at high intensity approximates a squeak or chirp. As noted before under exploration of the living space, the animal when mildly disturbed will emit a piff sound which appears to serve as an identifying signal. (See Table 7.)

Chemical communication is implicated in the locus-specific deposition of feces and urine; we have noted under marking (p. 70), the side rub and the perineal drag.

Tactile communication is employed in a variety of contact postures including nose to rump, nose to side, nose to nose, nose to cloacal and inguinal region, nose

TABLE 7.—Physical properties and circumstances of occurrence for some vocalizations of *Tenrec ecaudatus*

Sound Type	Sample Size	Note Structure	Temporal Patterning	Frequency Range (Hz)	Dominant Frequency Range (Hz)	Duration (seconds)	Circumstances of Occurrence
Clear tones Ah Ah sound	11	Descending tone, harmonics present	Repetitive .16-.20 sec. interval	300-3, 500	500-1, 000 or c. 1, 000	.06-1.7	Produced by unreceptive female when male is mounted.
Noisy sounds Grunt	2	Vibrato and noise	Interspersed with preceding sound	50-5, 000	50-1, 500	.50	Produced by unreceptive female when male is mounted.
Puffing	12	Slight harmonic tendency; much noise	Repetitive .22-.24 sec. interval	250-2, 000	250-1, 000	.10-.14	Arousal and threat toward alien stimulus.

to ear, and a grooming reaction which involves nibbling or licking the hip or nape of the partner. The possibilities for visual communication appear to be limited due to the small eye possessed by the animal and its nocturnal habits. As was noted under the description of the juvenile, young *Tenrec ecaudatus* have the ability to produce sounds by rubbing the dorsally situated spines together. The function of this stridulation will be discussed in a separate section.

*The encounter.*—Staged encounters in both a neutral arena and the home cage of a resident were run between males and females. In a neutral arena, avoidance is initially shown. After an exchange of piff signals, the animals will approach and initiate contact. In the case of a male-male encounter or a female-female encounter, contact is brief and the animals generally separate to explore alone. During the breeding season adult males will fight if placed together, and males and females will attempt to interact and show varying degrees of sexual behavior. A sexually active male will attempt to mount all females which he encounters; even pregnant females may be mounted and intromission can take place if the female is not too resistant. It is convenient to consider two phases of interaction: the contact promoting behaviors and the sexual behavior itself.

*Contact and sexual behavior.*—Contact involves nose to rump, nose to side, nose to nose which may, in a slightly aggressive context, involve what we have termed nose-fencing. This occurs when the animals

stand together with mouths half open and push each other's nose to one side alternately. At times the nose of the partner may be grasped in the mouth without biting. In addition to the preceding, a nose to cloaca posture may be shown and a nose to ear. Highly aggressive animals may gape at one another.

More advanced contact promoting behavior involves licking by the male, especially in the area of the female's hip and her nape. The licking and nibbling of the fur on the hip may be exhibited as a gentle bite on the part of the male. The male will attempt to mount a female who does not move away after the initial investigatory phase. The male mounts by gripping with his forelegs, posterior to the female's forelimbs. At this time the male continues to lick and nip at the crest of the female. If the female is unreceptive, she may utter a "nyah" sound in bursts of three or four and this appears to be homologous to the chirp of slightly unreceptive female *Echinops* and *Setifer*. If the female is receptive, she is generally quiet after an initial vocal phase when the male effects intromission. The mount of the male is extended and may last from 5 to 12 minutes. During mount with intromission and thrusting, the male continues to lick and nibble the crest of the female and may grunt while clapping his jaws. This is a very characteristic sound and is repeated throughout the better part of the mount sequence. At the conclusion of a mount, the male on dismounting will sit upright while licking his genitalia.

For purposes of comparison we offer the following descriptions.

Simultaneous introduction of male and female to new cage, 14 November 1966: Male gapes and hisses, then he smells the female; licks his lips and sniffs her crown. They separate and explore. Male attempts contact but female runs off after turning to him and gaping. In about 5 minutes the male no longer makes any attempt to mount on contacting the female. The female moves to nest box; male follows and mounts. Male makes clapping sound while licking her crest but the female is so small he is unable to obtain intromission. After about 3 minutes, the female withdraws leaving the male in the box.

Simultaneous introduction, 14 October 1966: Female exploring; encounters male; nose to nose. Male nose to crown and nose to her ear and again nose to crown. Male follows female as she moves off. Male yawns. Female and male face one another nose to nose and "nose-fence." Male turns to one side; mounts and commences thrusting. Male moves head from side to side, opening and closing mouth while grunting. Mount duration is 5 minutes 1 second. Male stops grunting, dismounts, and washes genitalia. The male initiates nose to crown of female, nose to side, nose to crown. Female moves away; male follows. Female yawns. Male mounts again near corner of the cage after about 7 minutes of following.

*Male-female interaction.*—As with the preceding genera, we may note that males will initiate sexual behavior regardless of the female's initial receptivity. The female who is initially unreceptive may respond with a series of stereotyped vocalizations. This may not in itself deter the male. The mount duration of the male is prolonged. The neck grip manifest in *Echinops*, *Setifer*, and *Microgale* is modified in *Tenrec ecaudatus* to a ritualized biting and clapping of the mouth while the head is moved from side to side. Grooming in *Tenrec ecaudatus*, which was manifest in *Microgale* but absent in *Echinops* and *Setifer*, appears to be confined to nibbling the fur in the region of the nuchal crest and the side. Such grooming may grade into nips or be displayed as a nip initially (see Petter and Petter-Rousseaux, 1963; Gould and Eisenberg, 1966).

*Agonistic behavior.*—Fighting behavior typically in-

volves pushing with the nose, and standing side by side while pivoting on the forefeet, thus causing the rump to smash into the side of the opponent. The shoulder may be used to push an opponent aside or the animals may stand side by side with body axes oriented in opposite directions and initiate a bite to the hip. This may be simultaneous with the animals circling and tumbling about while biting one another. A losing animal typically flees and is chased for a short distance. Fights most frequently occur between males.

#### PARENTAL CARE

As indicated on p. 67, the pregnant female seeks out a burrow and generally enlarges it. Nest building increases before parturition and a compact globus nest is constructed in the terminal chamber of the tunnel system. When the female has young, her tendency to defend the nest is increased and includes hissing, foot stamping with erect crest, and biting and slashing at an intruder. The female will position herself over the young while they nurse. She will lick the young especially in the area of the genitalia. Licking, in *Tenrec ecaudatus*, persists until the young are approximately 30 days of age. The female will retrieve the young when they are displaced from the nest by picking them up in her mouth and dragging them back to the central chamber. This begins to wane when the young are approximately 3 weeks old. As the young mature, the female is prone to lie on her side to permit nursing rather than attempt to huddle over them. The nursing response begins to wane when the young are approximately 4 weeks of age.

#### ONTOGENY OF BEHAVIOR

After a gestation period of some 58 to 64 days, the young are born in an altricial state but more advanced in development than most insectivores. Total length at birth ranges from 84 to 92 mm and weight from 22.8 to 27.4 grams (sample of four). The dorsal longitudinal tracts of pale hairs are visible at birth, and are approximately 5 mm long. On the ventrum, two rows of abdominal teats may be observed in the young animal. The claws are well formed. The head and ventrum are lighter in color than the dark longitudinal stripes. The eyes and auditory meatus are closed.

The animal can produce a small piff sound and squeak. It can locomote using the crossed extension pattern with some hind limb coordination. At approximately 7 days of age, the spines are quite visible in the

longitudinal white stripes of the body. Especially prominent are the spines in the middorsal stripe which will become the stridulating organ. At 11 days of age, the scratch reflex is observed. It shows greater balance during turning, and the hind limbs are better coordinated with the forelimbs during forward progression. It can now stand higher on its legs when locomoting.

Eye opening begins at 9 days and is completed at 14 days. Solid food begins to be eaten at approximately 25 days of age. The molt to the reddish brown body hair begins at approximately 36 days of age and the longitudinal bands of spines and the striping effect is not discernible at 60 days of age. A growth curve is portrayed in Figure 45.

At approximately 3 weeks of age, the young begin to accompany the mother on her nightly foraging trips. The typical pattern of movement is linear, with the youngsters forming a line behind the female, although this linear pattern may vary depending on the speed of the mother. Sometimes the young may move two or three abreast behind the female. If the female stops, the young will cluster around her. They will rest when

she rests, and when she forages they will cluster around the area of her activity. If the female is disturbed by some alien stimulus in the environment, she will orientate toward it and the young will do likewise.

To summarize, the response of the young to the mother: suckling and huddling in the nest occupy the first 2 weeks of life. Linear following and clustering when the female stops lasts from about 3 weeks to 35 days of age. During the interval from 35 days of age to 60 days, the young begin to forage as juvenile units and continuous contact with the female is reduced. The molt to the subadult pelage and the loss of the juvenile pelage is complete at approximately 60 days of age.

#### STRIDULATION AND COMMUNICATION

Gould (1965) first noted that the juveniles of *Tenrec ecaudatus* can produce a sound by rubbing together the quills of the middorsal region. The sound is pulsed having a broad energy distribution between 12 and 15 KHz.

In order to study the possible function of stridulation in *Tenrec ecaudatus*, a number of juveniles were

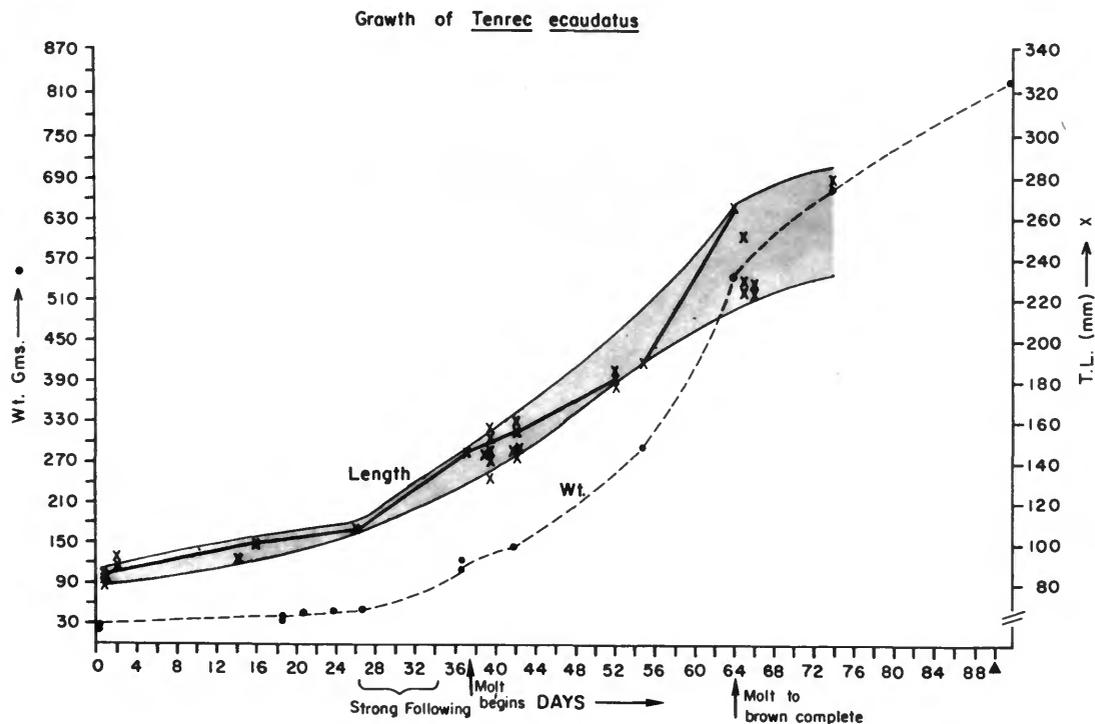


FIGURE 45.—Growth for *Tenrec ecaudatus*. Total length increases rapidly from 30 to 60 days beginning to plateau at that time. Molt begins at approximately 36 days and is completed at roughly 2 months of age. Shaded area represents the range of total lengths. Line connecting X's indicates the growth of the same individual.

subjected to motivational analyses. By a motivation analysis, we hoped to discern the circumstances of stridulation and the activity generally preceding and following its occurrence. We defined the motivational state of the animal in terms of the action that generally followed the stimulus. Thus, a group of behavior patterns or movements that could be associated with a subsequent tendency to flee were referred to as indicators of a flight motivational tendency. On the other hand, a set of movements and patterns associated with subsequent attack were termed indicators of an attack motivational tendency.

Juveniles were placed in a box and stimulated with a variety of foreign objects, light, touch, predator odor; and the occurrence of stridulation or nonstridulation was noted in conjunction with other movement components. From a series of some 30-odd trials, it was possible to conclude that stridulation in *Tenrec ecau-*

*datu* occurs over a narrowly defined range of motivational states in contradistinction to stridulation in *Hemicentetes* (see p. 102). Stridulation occurs in conjunction with crest erection and erection of the center quills. Generally the subject stands high on its legs and is oriented to a potential enemy. The half open mouth and hiss very frequently accompany stridulation. Stridulation does not occur when the animal is crouched even if the center quills be erected. If the animal exhibits a strong flight tendency or a tendency to flatten or burrow into the substrate, stridulation will not occur. It would appear that stridulation accompanies a tendency to attack coupled with a strong antagonistic tendency to withhold (Figure 46).

It should be noted, however, that the threshold for stridulation in wild animals is quite different from the stridulation threshold shown by hand-raised animals. A hand-raised specimen habituated to a hu-



FIGURE 46.—Subadult *Tenrec* (= *Centetes*) in typical stridulation posture: Quills and fur erect; *Tenrec* stands high on its legs. Note erection of long guard hairs.

man observer may exhibit stridulation when excited by the appearance of the handler. Stridulation during mild excitation on the part of the hand-raised *T. ecaudatus* would indicate a considerable lowering in threshold for the appearance of stridulation than that threshold displayed by wild-caught young. The exact significance of this cannot be interpreted.

In order to elucidate the possible function of this stridulating, two types of playback tests were conducted with *Tenrec ecaudatus* (see Appendix H).

**Playback test number 1:** In this situation, a female with her litter of seven was established in a large arena cage (4'×4'×4') with a nest box and a feeding location. A loudspeaker was placed alternately in several locations in the cage. Control stimuli, consisting of leaf rustling and background noise of the tape recording, were alternated with the sounds of (a) real stridulation produced by an aroused young and (b) artificial stridulation produced by stroking the dorsal quills of the young animal. The playbacks were run to the whole group under a variety of situations; however, we waited until the group was moving about in a relaxed fashion with no trace of defensive or offensive behaviors and then, on a signal, a given playback was offered whereupon a second observer noted the reactions of the group. Tests were run until the animals ceased to respond to any of the playback stimuli.

It was found that the animals would habituate to any given signal if it were presented four times in succession. Response to stridulation either real or artificial was more pronounced than response to the controls. The waxing and waning of responses to the various stimulus orders presented are included in Figure 47. When the responses during the first ten minutes of testing are considered, the following conclusions can be drawn. Control stimuli elicited no discernible response other than slight crest erection and shifting in seven animals; however, two fled. Eight tests with artificial stridulation resulted in four no discernible responses and four fleeing from the stimulus source. Out of 16 tests with real stridulation, 6 involved only crest erection and 10 involved flight from the direction of the speaker. From this it is possible to conclude that stridulation serves as a warning signal to members of the group resulting in arousal and attention. It may also serve as an indicator of identity and position of a juvenile that has been startled; however, as indicated, an identifier sound appears to involve the production of the "piff" sound. It is possible that the stridulation

promotes location of the young by the female and/or location of young by young but this experiment is not decisive in answering these additional questions.

**Playback test number 2:** The second playback experiment involved the use of a neutral arena where a single juvenile was released at one end and, as it walked past a loudspeaker, a signal of stridulation or control sound was played back to it. Responses to this playback were scored. With the exception of two subjects, each animal was subjected to two stridulation and two control playbacks. As a control the "huff" sound was utilized; 28 passes of stridulation were presented with 24 passes of "huff" giving a total of 52 playbacks. Thirteen subjects were employed, including one adult and 12 juveniles. In 34 of the 52 tests, there was no discernible response; 13 of these were to stridulation and 21 to the "huff" sound. There were 18 responses; 11 of the 18 responses were approach and were directed toward stridulation; 6 responses involved

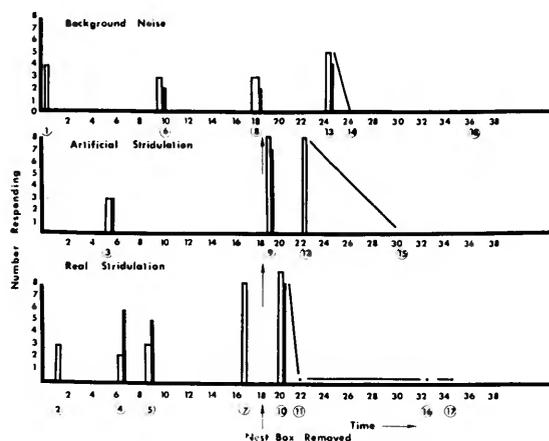


FIGURE 47.—Results of playback to *Tenrec ecaudatus*. Playback experiments indicate that any auditory stimulus is liable to produce an avoidance response on the part of a family group. Nevertheless, response level to the control playback are much less intense than those responses to the experimental playback. Following three replicas, the response intensity declines. The removal of the nest box from the testing arena in the 18th minute resulted in a temporary restoration of high response levels to the playback followed by a failure to respond to any playback in the 14th, 15th, 16th, 17th, and 18th trials. Abcissa indicates total time course of experiment in minutes. Circled numbers indicate order and time of presentation of the playback. Ordinate scale indicates number of animals responding to playback. Black=number fleeing from speaker. White=number of animals shifting their position as a group to a given playback but not fleeing.

moving away and 4 of the 6 were to stridulation. Out of the 18 responses, 15 were to stridulation.

This second experiment would indicate that in the novel arena, where the animal is already aroused, stridulation does not necessarily promote flight but may actually promote approach; thus, the nature of the response to stridulation is very much a function of the testing situation. If the animals are in a group and subjected to a sudden sound of stridulation, they become aroused and move away or avoid. If they are already somewhat aroused in a novel situation and stridulation is played to them, they may approach and investigate. Thus, we are not in a position to decide on the exact function of stridulation in *Tenrec ecaudatus*. It may be that it promotes arousal and serves to warn of a potentially dangerous situation which may lead to breaking, running, or scattering of the group. On the other hand, in already aroused animals, it may promote location of young by the female and/or location of the young by other young.

#### SOCIAL ORGANIZATION

From Rand's (1935) evidence and our own field studies, we may conclude that, with the exception of the mother-young group, adult *Tenrec ecaudatus* for-

age and hibernate alone. Pairing and the pair association must be brief and probably take place in the austral spring. After a 2-month gestation period, the youngsters develop in the burrow system and begin to accompany the mother on her foraging expeditions when they are approximately 3 weeks of age. Great cohesion is shown by the mother and her group of littermates. Linear following, aggregation to the female on being startled, and foraging with the female are all manifest over a rather prolonged period of time. Our observations would indicate that the female-young foraging unit may persist for 2 to 3½ weeks. During this time routes from the nesting area to the feeding ground and back are learned by the young. Selection of foodstuffs is potentiated by the association of the young with the female while she feeds. Coordination among the female and her young is ensured by the linear following tendency. The piff sound and perhaps stridulation are involved as identifiers and indicators of mood within the group. The littermates themselves may continue to associate in their foraging when about 2 months of age, although by this time the integrity of the family unit has broken down. Apparently the animals begin to take up residence alone at the time of hibernation only to re-emerge and initiate the cycle again in the austral spring.

## The Ecology of *Hemicentetes* (Mivart, 1871)

### INTRODUCTION

The genus *Hemicentetes* contains two species, *H. semispinosus* and *H. nigriceps*. These animals show a high tooth number, with a dental formula of  $\frac{3}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3}$  for a total of 40. The teeth, however, show a reduction in size and, when compared with that of the other genera, the skull is markedly elongate and delicate. *Hemicentetes* possesses quills scattered on its dorsum especially concentrated on the crown and in the light colored stripes extending the length of the body. The quills are barbed and detachable with the exception of the modified group of quills in the central posterior

region of the dorsum. This group of specialized quills, termed the stridulating organ, is described in the publications by Petter and Petter-Rousseaux (1963), Gould (1965), and Gould and Eisenberg (1966). These quills are enlarged and do not possess barbs and are less easily detached than the other quills on the body (see p. 102).

The animal has a boldly marked color pattern consisting of three main longitudinal stripes contrasting strongly with the black dorsal color. In the case of *Hemicentetes semispinosus*, the stripes and crown as well as a median stripe on the forehead are yellow. In the case of *Hemicentetes nigriceps*, there is no median



FIGURE 48.—*Hemicentetes nigriceps*. The black and white pattern apparently serves as a warning coloration for this nocturnal plateau-dwelling species. The dense underfur is apparent when a comparison is made with Figure 49.

central stripe on the forehead while the crown and body stripes are white. The venter of both species is almost free from spines. The claws on the forefeet are rather stout and some modification for burrowing is indicated (see Figures 2, 48 and 49). As was noted with the other genera, in addition to spines there is a soft underfur far more prominent in *H. nigriceps* than in *H. semispinosus*. In addition to fur interspersed with spines, long sensory hairs are distributed over the dorsum. The standard sensory hairs of the facial region are prominent including the mystacial, genal, super-orbital, and mental vibrissae.

The two species are allopatric and indicate slightly different environmental adaptations. *H. nigriceps* occurs from the vicinity of Manandroy south to Fianarantsoa. It appears to be confined to the central plateau edge. As one descends from the plateau into the true rainforest of the eastern escarpment, one finds *Hemicentetes semispinosus*. This form has been recorded

from Ivohibe to Maroantsetra. We can conclude that *H. semispinosus* is confined to the rainforest areas below the high plateau extending its distribution to the northern rainforests and south to an undetermined locality below Ivohibe. For convenience we propose to discuss the characteristics and ecology of these species under separate headings.

### *H. NIGRICEPS*—GENERAL ECOLOGY

#### Physical Description

This plateau-dwelling species is quite similar to the rainforest species with the exception of the difference in color and the fact that the pelage tends to be less spinescent. The underfur is dense and soft and the quills protrude from it so that, overall, the animal has a more woolly appearance. The quills comprising the stridulating organ are less in number on the average than is the case for *H. semispinosus* (Figure 50). The

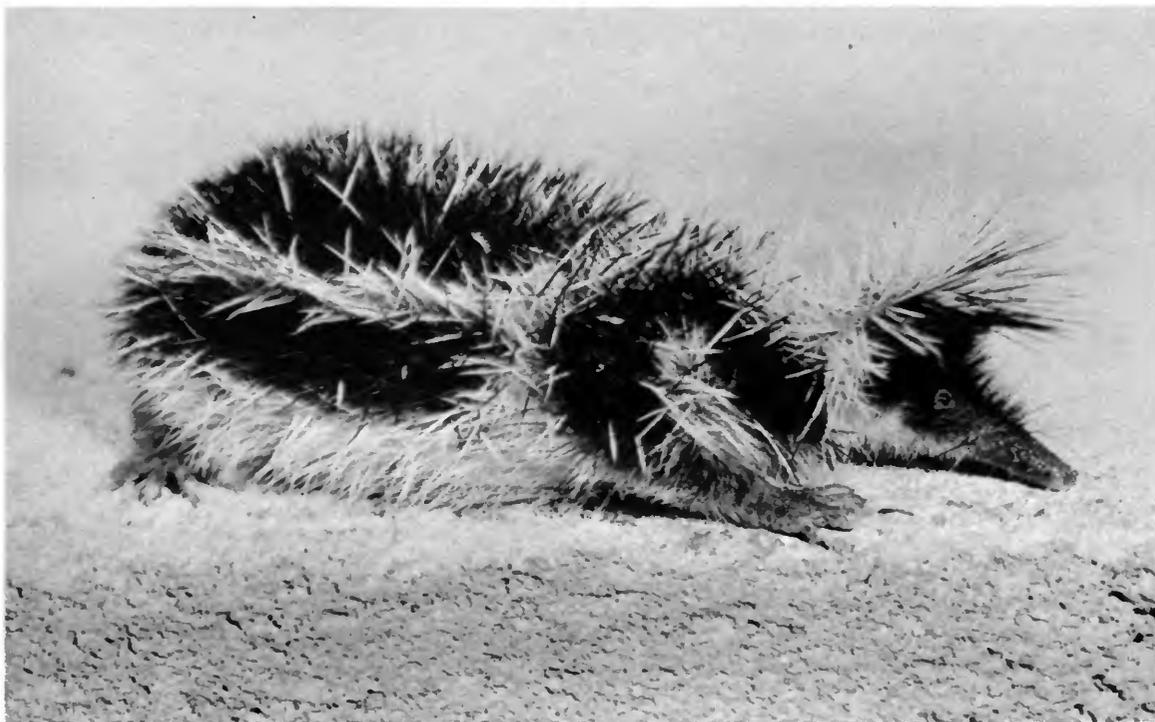


FIGURE 49.—*Hemicentetes semispinosus*. A typical form found throughout eastern lowland rainforest. Note the yellow and black warning coloration for this partly diurnal species. The spinescence is much more pronounced in *semispinosus* than is the case with *nigriceps*. Posture is full forward crest; the animal had been placed in bright sunlight.



FIGURE 50.—Stridulating organ of *Hemicentetes semispinosus*. Magnification is about 5 times. Surrounding body quills have been cut.

number of stridulating quills from a sample of 73 *H. nigriceps* ranges from a low of seven to a maximum of 17; the modal value was 11 quills. There is a difference when age classes are compared since younger animals tend to have more quills than older ones. Although the stridulating quills are replaced if lost, nevertheless, there seems to be a correlation between increasing age and a smaller number of quills (Figure 51).

There are no conspicuous differences between the sexes and the age classes may be defined on the basis of total length. The infant age class ranges from 58.5 to 60 mm for a minimum and 100 to 110 mm in total length at approximately 4 weeks of age. Females may breed at approximately 30 days of age when their total length lies somewhere between 120 and 130 mm. Maximum total length for adult specimens in the field was 180 mm. Field weights for adults range from 80 to 150 grams.

#### Distribution and Habitat

*Hemicentetes nigriceps* was taken in the plateau area between Manandroy and Fianarantsoa. Its habitat may be characterized as the plateau edge in the vicinity of the transition between eastern rainforest and plateau savannah. Burrows with animals may be found in the vicinity of brush and are generally never far from free water. The cultivation of rice has apparently opened suitable habitats for these animals and they are often found in the vicinity of paddy fields. When the animals utilize cultivated areas for foraging, they may adopt rather atypical habitats for burrow sites; indeed, in one area (i.e., Manandroy) almost all burrow sites were placed within an introduced eucalyptus forest but their foraging took place in the vicinity of the paddy fields and areas of cultivated manioc (see Figure 52).

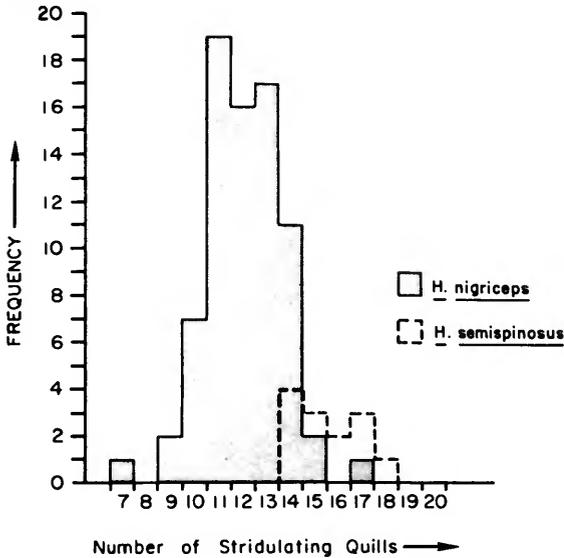


FIGURE 51.—Number of stridulation quills for *Hemicentetes nigriceps* and *Hemicentetes semispinosus*. *H. nigriceps* averages roughly four stridulating quills less than does *H. semispinosus*.

### Burrows and Microhabitat

From an examination of over 60 burrows, the following generalization can be made. Let us consider a typical case at Manandroy in the eucalyptus forest: Although located in a second growth habitat of eucalyptus, tree ferns and other primary elements are still to be found on the fringes of this introduced forest. The ground was covered with rotten logs, branches, and leaves, forming a mat of damp decaying vegetation. The following characteristics of the burrow were noted. It was located in the vicinity of a cultivated field under a rotten log. There was only one entrance to the burrow. The burrow was shallow, approximately 75 mm at the deepest point and around 450 mm long. The burrow entrance was plugged with leaves. Fresh feces were also noted there (Figure 53).

Coleopteran larvae, potential food items, were found in the rotten logs under which the animals tunneled. In addition, worms were found outside the eucalyptus mat in the red-brown soil near the paddy fields. The burrow provided a rather stable microhabitat for the tenrec. At Manandroy, burrow temperatures were measured for 21 locations. The ambient range was from 20.4° to 30.5° C. Burrow temperatures them-

selves ranged from 20.5° to 26.5° C. at a distance of approximately 150 to 200 mm from the burrow entrance.

### Activity and Thermoregulation

During the course of our field studies, observations were made from 0800 hours through 2300 hours in areas where *Hemicentetes nigriceps* occurred. Thirteen sightings were made between the hours of 1830 and 2300 hours. One additional animal was trapped sometime between the hours of 0200 and 0600. The field evidence would indicate that in this particular area *H. nigriceps* is almost entirely nocturnal with the peak activity in the early part of the evening. These observations were amply confirmed in captivity; however, under captive conditions the animals could be conditioned to feed during the daylight hours.

Studies of diel variations in thermoregulation were made in Madagascar both in captivity and in the field. Between the hours of 0900 and 1000, a captive group of five *H. nigriceps* showed a range of cloacal temperatures from 25.0° to 27.4° C. with an average of 26.3° C. over an ambient range from 23° to 24.2° C. A second series of morning readings was made over an ambient range from 16.8° to 20° C. *H. nigriceps* showed a cloacal temperature range from 20.8° to 26.4° C. with an average of 23.6° C. All of these measurements were made during the month of February when the animals are not torpid for long periods. A series of late afternoon temperature readings were made between 1500 and 1800 hours, when the cloacal temperature should be showing an increase. Over an ambient range from 21.3° to 24.3° C., a sample of 14 *H. nigriceps* showed a range from 26.0° to 31.5° C. with an average of 28.6° C. To compare with this series, several field measurements of body temperatures were made during the early part of April preceding the entry of the population into their seasonal torpid period. Over an ambient range from 22° to 26.8° C., a total of 12 individuals showed a range from 25° to 35° C. with an average of 30.3° C.

Our data would indicate that the animal shows a diel fluctuation in body temperature with the cloacal temperature rising in the late afternoon preceding activity. The burrow undoubtedly serves to aid in conservation of heat loss and to ameliorate the more drastic changes in the ambient temperature.



FIGURE 52.—View of rice paddy and introduced eucalyptus forest. This area was heavily populated with *Hemicentetes nigriceps*. The animals forage near the cultivated fields and paddies and found shelter within the introduced eucalyptus forest.

### The Annual Cycle and Reproduction

Annual variations in weight and activity were studied in the field and in the laboratory. From a period of 31 January to 3 February 1966, weights were determined for adult animals in the field. Eleven adults ranged in weight from 90 to 150 grams. Four *H. nigriceps* were returned to the laboratories at the National Zoological Park for further study. During the month of April our captive group of four attained weights from 135 to 187 grams. From the middle of April until July, this group ceased to feed, declined in weight, and did not significantly thermoregulate with the cloacal temperature remaining near the ambient. Minimum weights of 90 to 145 grams were achieved at the end of this period. Beginning in late July and early August, the animals increased their activity, began to feed, and new maximum weights were achieved in December of 1966, exceeding the previous maximum.

With no special manipulation of food or ambient conditions in the laboratories, the captive group began to show weight declines as early as December 1966 for one individual and as late as March 1967 for two others. These declines persisted until July of 1967 when the animals began to arouse, thermoregulate, and feed again. These captive data support previously recorded field observations. In the vicinity of Manandroy and Fianarantsoa, the population of *H. nigriceps* is generally torpid during June and July.

It would appear that the seasonal torpidity shown by *H. nigriceps* is in part under endogenous control, since the rhythm persisted through two seasons in captivity with no special attempt to manipulate environmental conditions. Thus, two types of thermoregulation are exhibited. During the breeding season extending from September on into February, the animals show a diel rhythm in thermoregulation but arouse during each 24-hour period to feed. In early

May the animals, having reached their full weight, enter a profound torpor which parallels the austral winter.

Population of *Hemicentetes nigriceps* were sampled in February of 1966 and 1967. The gestation for *nigriceps* is similar to that displayed by *H. semispinosus* which is about 58 days. *H. nigriceps* gestation exceeds 55 days and is less than 58 days; thus it seems reasonable to assume that it is approximately the same for the two species. The litter size for *H. nigriceps* in wild-caught individuals excavated from their burrows during the month of February 1966 ranged from one to three with an average of 1.4 for a sample of 14 litters. During the same season in 1967, the litter size ranged from one to five with an average of three for a total of six litters. Litter size determined from captive born animals for a sample of five ranged from two to four with an average of 2.8.

The age classes for *Hemicentetes nigriceps* have been determined from extensive captive studies. For the purposes of our discussion, we have referred to animals in the 60 to 90 mm total length size class as infants. Juveniles include the group from 100 to 130 mm total length and adults are all those animals exceeding 130 mm total length. Although the breeding for our population of *H. nigriceps* was not completely synchronized, the evidence strongly suggests that breeding begins in early September and most of the first born females in the population probably become pregnant from the period of December to early January. We infer this from a knowledge of the growth curve and of the gestation period.

For example, from 28 January to 7 February 1966, collections of individuals from Manandroy were marked and released. Of the 56 individuals measured, 10 fell in the infant class, 15 were juveniles, and 31 were adults. A similar sample of 33 taken at Manandroy from 6 to 7 April 1966 indicated 8 individuals in the juvenile age class and the remaining 25 as adults. In the following year from 4 to 5 February 1967, the Manandroy population was again sampled and a total of 48 individuals were measured. Of these, 9 were infants, 9 were juveniles, and the remaining 30 adults. This would appear to substantiate our contention that some breeding takes place in December; however, a consideration of the animals in the 130 to 150 mm age class (on the basis of pelage color and wear) suggests that some births may take place in early November. Thus, there must be a first breeding period in early



FIGURE 53.—Burrow site of *Hemicentetes nigriceps*. Burrow entrance center right at convergences of log.

September or the individuals in this size range have wintered over from the previous year having been born late in April of the preceding season. The latter hypothesis is doubtful in view of our knowledge of the growth curve. As indicated previously the Manandroy population was always marked and released. Collections for captive studies were made at Alakamisy Ambohimaha. We know from our captive records that animals may live to an age exceeding 2 years and 6 months. We know further from our sampling in 1966 and 1967 that marked individuals may survive to a minimum age of 15 months. Since females become sexually mature within 4 to 5 weeks of their birth, it is entirely possible that a given female will reproduce in two consecutive breeding seasons.

#### Feeding and Food Intake

In captivity, *Hemicentetes nigriceps* readily accepted earthworms. To a lesser extent, *H. nigriceps* would kill

and eat the larger coleopteran larvae found in the rotten logs under which it nested. Orthopterans were not taken. *H. nigriceps* could be induced to take some raw chopped meat in captivity, but the animals could be maintained in good condition only if considerable numbers of worms were fed. Two *H. nigriceps* were collected at night while feeding. Their stomach contents consisted almost exclusively of earthworms although an arachnid abdomen was identified. Some earth, evidently ingested with the worms, was present in both stomachs. Since earthworms appear to account for a large portion of the animals' diet, it seems desirable to review some of the characteristics of earthworm ecology and behavior.

#### EARTHWORM BEHAVIOR AND ECOLOGY

*Lumbricus terrestris* shows a minimum of activity between 0700 and 1100 hours. High rates of activity are shown before 0700 and after 1100 hours. Peak activity is shown in the early mid-afternoon lasting through early morning (Laverach, 1963). Favorable conditions for earthworms in the tropics include an undisturbed soil which has a regular and adequate water supply. Generally a fine soil texture is required but this is a concomitant of the physical availability of water since water will rise to a greater height in fine soils. In addition to these soil requirements, earthworms require a regular and adequate supply of organic material. Even though the layer of humus in tropical soils is very thin, earthworms can and do occur there and may be found even in the red sandy soils in the vicinity of paddy fields. Indeed, light and medium loams appear to carry higher proportions of worms than the heavier clay type soils or more gravelly sand and alluvial soil types (Guild, 1948). Local abundance of earthworms may be quite high. Biomass of earthworms may range from 6 kilograms per acre in a maize field to 2,339 Kg/acre in an artificial forest (El-Duweini and Ghabbour, 1965).

We sampled the earthworm population in the soils composing the floor of the eucalyptus forest at Manandroy and found earthworms to be practically absent. On the other hand, earthworms did occur in the vicinity of the paddy fields and other cultivated fields. This has led us to conclude that the eucalyptus forest served as a sleeping area rather than as a primary foraging area and furthermore the animals would need to move out each night into the vicinity of the fields in order to provide themselves with sufficient earthworms.

#### FOOD CONSUMPTION

Consumption of earthworms by captive individuals was studied in some detail. It was found that the average intake during a 15- to 20-minute feeding period to satiation for three specimens of *Hemicentetes nigriceps* ranged from 13.0 to 4.2 grams. The maximum intake was by an adult and the minimum by an infant. Yet the animals feed several times a day, and in order to determine average food intake for a 24-hour period, a sample of six *Hemicentetes nigriceps* were fed and weighed four times in each 24-hour period. This procedure was carried out for four days. The average increase in weight plus average consumption of worms for a 24-hour period could be calculated. Food intake for adults and juveniles averaged approximately 100 grams of earthworms in each 24-hour period, that is, the animal ingests approximately its own weight in worms daily. A young juvenile would tend to exhibit approximately 1.7 grams net gain in weight for each 24-hour period. This would indicate approximately 4.1 percent of the wet weight food intake was converted to net gain in weight for the animal feeding (see Figure 54).

The nutritional value of earthworms is rather high. The average dry weight of earthworms is about 15 to 20 percent of the wet weight. Protein accounts for the largest fraction of the dry weight and has been estimated between 53.5 and 71.5 percent of the total dry weight of *Lumbricus terrestris*. Measurements of *L. rubellus* and *Eisenia rosea* have a similar proportion of dry weight (16.38% which consists of 16.3% protein, 17% carbohydrate, 4.5% fat, with only 15% ash residue) (Laverach, 1963). The nutritional quality of earthworms is certainly adequate for rapid growth. In captivity, our *H. nigriceps* grew rapidly and, indeed, some question may be raised concerning the validity of our captive growth studies since we may have been feeding a diet with nutritional qualities far exceeding those in the wild. For example, total length could increase in captivity over a 30-day period by an increment of approximately 40 mm.

As we have previously stated, we had established a marked population of animals at Manandroy which were sampled in February and again in April 1966. By recaptures, we could estimate growth in the field and found that over a 2-month period a juvenile in the 104 mm age class could increase in total length some 31 to 36 mm. Larger animals first captured in the 141 to 148 mm total length class would increase in

total length over the same 60-day interval by approximately 14 to 15 mm. This indicates that although we may have slightly accelerated growth in captivity, we certainly did not distort too far from the field situation since increase in total length is certainly very rapid, even under field foraging conditions.

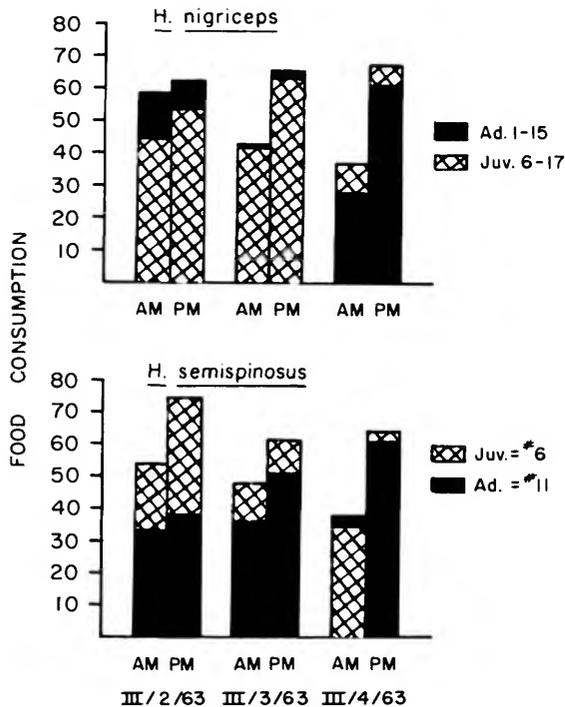


FIGURE 54.—Food consumption in grams for three consecutive 24-hour periods by *Hemicentetes nigriceps* and *H. semispinosus*.

## H. SEMISPINOSUS—GENERAL ECOLOGY

### Physical Description

As noted previously, *H. semispinosus* differs from *H. nigriceps* by the possession of a more spinescent pelage. Even the venter is sparsely covered with spines and it is only on the venter that true hairs persist in the adult. An underfur of nonspinescent hairs is present in juveniles on the dorsum but virtually disappears with continued growth. The stridulating quills are more numerous in *H. semispinosus*. A sample of 13 gave a range of 14 to 18 in number with a mode of 14 (see Figure 51). Older animals may show some wear with

respect to the stridulating quills and even a loss of the same.

There are no conspicuous differences between the sexes; males may be identified by manual expression of the phallus from the cloaca. The teats are very conspicuous in both males and females being surrounded by a darkly pigmented area. Age classes may be arbitrarily defined on the basis of total length. Infants range in size at birth from 60 to 66 mm total length. A juvenile is defined as an animal able to forage about and in the stage of being weaned. At this time it is approximately 90 mm in total length. A female can conceive when approximately 120 to 130 mm in total length; hence, the adult age class has been defined as any total length exceeding 125 mm. Linear growth begins to taper off at approximately 3 months of age or at a total length of 140 to 150 mm. The maximum size of a wild caught adult male was 172 mm in total length. Adult weight shortly after capture and in good condition ranged from 125 to a maximum of 280 grams. Adult animals during torpor may fall to a weight of 70 to 90 grams.

### Distribution and Habitat

*Hemicentetes semispinosus* characteristically inhabits rainforest areas. Its denning sites may be either in primary or second growth forest. Den sites were examined at Ambitolah, Ranomafana, and Perinet. These sites may be near cultivated fields or rice paddies. On the other hand, in more mature forests, the burrow is generally located near a stream or other body of water (see Figure 55). Feeding appears to be executed in natural clearings such as areas where a landslide has been overgrown with forbs and grasses or, in one case, at the site of an abandoned village.

### Burrows and Microhabitat

It is convenient to consider two types of burrows: (1) a burrow inhabited by a single individual or small family unit and (2) an extended burrow system inhabited by a large family group or colony. The following description is of a burrow uncovered at Ranomafana on 27 January 1966: A family of seven animals including an adult male, an adult female, and five young was removed from the nest. The burrow was characterized by a single entrance to a tunnel approximately 18 inches long. The burrow was very shallow



FIGURE 55.—Multistratal evergreen forest which is typical of the habitat for *Hemicentetes semispinosus*.

averaging 2 to 3 inches in depth. It was located above a stream on a rather steep slope of approximately  $45^\circ$ . The burrow contour followed in part a tree root. The forest floor in the immediate vicinity of the burrow was covered with leaf litter and the following invertebrate types were noted in the soil: Millipedes, *Nasutitermes*, a large flightless cricket, ants, and the shell of a land snail. The soil included a thin layer of humus overlying a reddish earth.

An example of a burrow system inhabited by a colony of some 19 individuals was as follows: The burrows were located on a south facing, steep bank with naturally formed terraces of humus and leaves (see Figure 56). At the foot of the bank was a fairly level area of moist humus covered with grass. The burrow complex included three subcomponents, the first being a burrow running some 3 meters in length following the contours of the bank and ending in a chamber approximately 2.25 meters from the entrance. An extended tunnel system proceeded beyond the nest

chamber for approximately 71 centimeters. Not directly connected with the major burrow was a second tunnel about 40 centimeters away. The tunnel was some 69 centimeters in length ending blindly in a nest chamber. Some 19 meters from this second burrow was a burrow system approximately 1.8 meters long ending blindly in a nest chamber. Although these were not interconnected, individual animals were seen to move from one tunnel to another, and we may conclude that this colony involved considerable interchange of the members actually found in the three component burrows. A total of two adult males, two adult females, and 14 juveniles were removed from this colony.

To summarize, a total of five burrow sites in the vicinity of Ranomafana exhibited the following characteristics: The burrow was generally located on a bank above a stream or damp area. Although a burrow may range from 1 to 6 feet in length, it generally has one entrance with a nest formed of leaves lying some



FIGURE 56.—Locus of *H. semispinosus* burrow. The burrow entrance was at the base of a steep bank in the upper center of the photograph and framed by the curved vine. Nineteen individuals lived in the complex of burrows.

1 to 2 feet beyond the entrance. The burrow tends to follow the contour of the slope upon which it is located or it may run along a root or under a stump. If rocks are present, the burrow may be quite intricate and pass between the larger stones. An entrance of an active burrow is generally plugged with leaves. Feces may be deposited near the entrance. The following commensals have been found within the burrow system: land snail, millipede, spittle bugs, and a small frog. The potential food supply in the immediate vicinity includes wingless crickets, millipedes, earthworms, and perhaps land leeches.

#### Activity and Thermoregulation

At Perinet a family group consisting of a female and five babies was installed in a large observation enclosure (see Figure 4). A photocell device with an op-

eration recorder was installed at the entrance to the nest (see Appendix F), and for 48 hours the activity of the family group was monitored by counting the number of departures and returns to the nest. The following activity pattern was discernible: From 0900 to 1300, there is sporadic activity with a major peak directly after 1200 hours. (In Herter's publication (1963b), he portrays an activity diagram by one of three subjects which also showed a peak of activity around 1200 hours.) Sporadic activity began again between the hours of 1700 and 2100 with the highest peak of activity recorded during a given 24-hour period falling between 1800 and 1900 hours. Throughout the night other peaks were noted between 2200 and 2300 hours, at 0300 hours, and an extended peak from 0400 to 0600 hours.

Field observations which included two nights at a burrow near Ranomafana yielded eight sightings of

tenrecs. Five sightings were made between the hours of 1300 and 1400 and three sightings between 1800 and 2015 hours. Our field observations coupled with our seminatural activity recording suggest that *Hemicentetes semispinosus* does feed during the day as well as in the evening and early morning hours. This activity pattern conforms fairly well to the known activity patterns of earthworms and, since earthworms are probably its major food resource, this may be an overall adaptation to their prey. Although *H. nigriceps* does not show such a diurnal activity peak, this may be related to the more exposed nature of its habitat on the high plateau which renders such diurnal foraging more dangerous. As with *H. nigriceps*, *H. semispinosus* can be trained in captivity to feed at various times during the day.

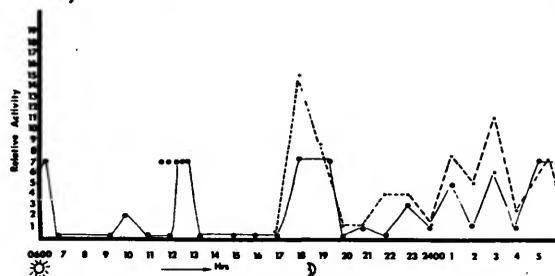


FIGURE 57.—Activity for *H. semispinosus*. Solid line indicates inferred number of individuals active outside the burrow for one 24-hour period. Dotted line indicates for two days the average number of interruptions of the photocell set at the entrance to the burrow system. Unconnected dots from 1100 to 1300 hours indicate the range of diurnal activity observed for a 4-day period. The diurnal peak of activity is clearly evident.

Herter (1962a) in his Figure 9 showed a double peak in body temperature for a captive *H. semispinosus* with a high of 30° C at noon falling to 26.8° C at 1800 hours, only to rise to almost 30° C between 2400 and 0200 hours followed by a decline to 28.2° C at 0800 hours. Although his activity data for this individual did not parallel the body temperature fluctuation, this thermoregulation pattern parallels our field activity data.

### The Annual Cycle and Reproduction

Some controversy exists concerning the seasonal variation in activity and the seasonal torpor of *H. semispinosus* (see Gould and Eisenberg, 1966). Unfortunately, we studied the thermoregulation of *H. semispinosus*

very little. In our captive group, held at Madagascar during 1966, the cloacal temperatures of eight animals were measured during February yielding a range from 28.5° to 31.2° C with an average of 29.7° C. These measurements were made in the morning during the theoretical low of the diel activity cycle. During April a sample of three taken at 1515 to 1530 hours ranged from 29.5° to 31.5° C at an ambient of 22° C.

In general, during the austral spring and summer, the animals maintain a reasonably stable temperature but in captivity a tendency for seasonal torpor is shown. Torpor was exhibited in the colony at the National Zoological Park during their first captive season in 1966. From late April to late July, four individuals from a sample of six showed a decreased tendency to feed and a loss in weight; however, this trend was not synchronized since two other individuals during the same period showed weight gains. During 1967 the situation was even less synchronized. Therefore, we conclude that, although individual *Hemicentetes semispinosus* can and do exhibit torpor, their tendency to pass into torpor is in part a function of the state of their fat reserves as well as ambient conditions. When animals become torpid, their body temperature falls very close to the ambient, there is decreased activity, and virtually no feeding.

For example, during the first season of captivity while in a period of torpor, one male passed from a 160 gram high in April to 130 grams in late July. An early July reading of cloacal temperatures showed a range from 22.1° to 33.8° C for our captive group of six over an ambient range of 21.0° to 27.5° C. Torpid animals invariably showed a cloacal temperature less than 1° C above that of the ambient. The evidence suggests that, depending upon local food abundance and temperature condition, *H. semispinosus* shows a facultative ability to exhibit torpor.

Gestation for *H. semispinosus* is 58 days. The litter size is variable. At Ambitolah three families were collected showing a litter size range from five to eight with an average of 6.3. In the vicinity of Perinet (Anevoka), four families were collected showing a litter size range from five to eight with an average of 6.2. Litters born in captivity in our Madagascar colony showed a litter size range from seven to eleven with an average of 8.8 (sample size of four families). Age classes were defined as for *H. nigriceps*; 60 to 90 mm total length, infant; 100 to 130 mm total length, juvenile; 130 mm and up, adults. Females can con-

ceive at an age of approximately 35 days. Based on this knowledge, we can make some generalizations concerning reproduction at Perinet.

During 1967 in the months of February and March, a total of 42 *Hemicentetes semispinosus* were collected of which 18 were infants, 13 juveniles, and 11 adults. These data suggest that the population at Perinet initiates breeding in October and that conceptions occur through December. Reproductive activity is depressed in Perinet during the month of July; however, local populations at lower elevations (e.g., Rogez) may be active and breeding (see Gould and Eisenberg, 1966). Again, we are forced to conclude that the timing of reproduction in *H. semispinosus* is a function of local conditions including temperature and abundance of prey.

### Feeding and Food Intake

Feeding tests in captivity indicated that *Hemicentetes semispinosus* readily takes worms, coleopteran larvae, and some ground meat. It would appear that earthworms are its primary prey in the wild. We have already considered the activity and local abundance of earthworms in the section for *H. nigriceps* and these points will be utilized in the following discussion for *H. semispinosus*.

In the vicinity of Perinet, earth samples at four localities were taken in order to determine the local abundance of earthworms. The earth sample sizes were 2,500 square centimeters in area and 20 centimeters in depth. *H. semispinosus* does not forage much more than a centimeter below the surface but we took a deep sample of earth in order to obtain the worms which may be available in a reasonable volume of soil since

we assumed that most of the worms in such a soil sample would move to the surface for feeding at least some time during their 24-hour activity period. Four such samples yielded 21.4 grams of earthworms. We may extrapolate then and assume that, if our sample is fair, this area could have 83.8 kilograms of earthworms per acre. This is well within the published density range for earthworms (El-Duweini and Ghabour, 1965).

Food intake for captive *H. semispinosus* was similar to those results cited for *H. nigriceps* (Figure 54). One juvenile was observed over a period of three days and consumed an average of 104.4 grams of earthworms per day. An adult sampled over a similar period averaged 85.5 grams of earthworms per 24-hour period. This is in reasonable agreement with the results that Herter published (1936b) where his one subject averaged 99.4 grams of food over a 24-hour period. If we assume that the previous estimate of worm density is nearly correct and that our captive food consumption approximates the normal food consumption in the field, then we can assume that a *H. semispinosus* would consume up to 1 kilogram of earthworms in a 10-day period. Given these assumptions, if the earthworm population in an area were not replacing itself, a prime area of one acre would support 10 animals for 83 days. This is a reasonable estimate, since a family group is somewhat in the neighborhood of seven to ten animals, and it would appear that they range over an area of approximately an acre.

Growth in captivity for *H. semispinosus* was similar to that described for *H. nigriceps* and is in reasonable agreement with the growth curve published by Herter (1963b; see also pp. 97–99 on Ontogeny).

## The Ethology of *Hemicentetes*

Because the behavior patterns of *Hemicentetes semispinosus* and *H. nigriceps* are so similar in their component parts, the general description of the behavior patterns for both species will be undertaken as a single unit. Some information concerning the behavior patterns of *H. semispinosus* has already been published by Herter (1963b) and by Gould and Eisenberg (1966).

### GENERAL MAINTENANCE BEHAVIOR

*Locomotion.*—*Hemicentetes* locomotes by employing the diagonal coordination pattern of limb movement. In running, the heel may be lifted off the ground, but in general the animal is plantigrade. The animal seems to have little ability to jump but during the offensive and defensive behavior patterns it is able to buck and pivot on its hind legs giving the appearance of a slight hopping movement. At times a short bounce as a concomitant of pivoting or bucking may occur but this movement is in no way comparable to a springing jump as defined for quadrupedally ricocheting mammals.

The animal is capable of climbing by employing a crossed extension pattern but there is little ability to grasp with the individual digits. It certainly does not climb often and could in no way be considered as arboreal as *Setifer* and *Echinops*.

Swimming, employing a diagonal limb coordination pattern, has been described by Herter (1963b) and we have observed an animal, startled in the vicinity of a paddy field, swim across a small body of water. The animal swims rapidly with the nose and head held above the surface.

*Exploration and utilization of living space.*—When placed in a novel environment, the animal will generally show some hesitancy and begin to move about slowly, testing the air by lifting its head and wriggling its mobile nose. The animal will then proceed to move forward in an elongate posture pausing to sniff the substrate and test the air. The role of "tongue clicks" as a possible means of echo-locating has been experimentally verified by Gould (1965).

In a novel situation, the slightest change in background stimulation will cause the animal to show spinal erection; especially prominent in the nuchal crest erection (see p. 93). The nose is utilized to probe in the substrate; apparently earthworms are recognized by tactile and olfactory stimuli. In the large observation pens, the animals have been observed to explore extensively before settling down to a set pattern of space usage. Generally a defecation point is selected in the environment which is used over and over again. A burrow site is selected and subsequently a nest is built of leaves and grass.

Foraging activity appears to be a function of the proximate environmental conditions. In general the greatest foraging activity could be elicited in areas of the pens where the earth was soft, moist, and to some extent shaded. Sunlit areas were not necessarily avoided if sufficient leaves lay on the ground to permit some shade for small invertebrates.

Our observations on both *H. semispinosus* and *H. nigriceps* indicate some shifting of nest sites. In our capture-mark-and-release program, burrows were opened and, on subsequent days of sampling in the same area, animals could be found that had moved. Of course, their movement could be attributed to the fact that the burrows had been disturbed. Nevertheless, in those cases where burrows of *H. semispinosus* were not disturbed and the animals were observed by inspection of the tunnel from the outside, we found some shifting at the end of a 10 to 15 day period. Turning to *H. nigriceps*, we have found with our marked population at Manandroy that, with a year interval and given six recaptures of animals marked during the previous year, den site shifting ranged from 50 to 800 feet. It would appear that an individual *nigriceps* will settle in an area and utilize den sites in an opportunistic fashion. Breeding females set up a deeper more permanent burrow. Neighbors may move in and nest with each other under certain conditions.

Within any given foraging area, den sites appear to be limited. For *H. nigriceps* the principal denning sites

were in the eucalyptus forests bordering the cultivated fields. Within the eucalyptus forests definite preferred loci for denning could be discerned. These were generally areas containing a great number of fallen logs which provided a ready shelter under which the burrows were constructed (see Figures 53 and 58). As noted earlier for *H. semispinosus* (p. 85), a given denning area may be utilized for some period of time and an actual colony may be formed. Although a denning

area may be established and a small colony set up, within the denning area actual burrow sites may be utilized off and on depending on the density of ectoparasites in the nest and other physical factors.

*Rest and sleep.*—*Hemicentetes* will sleep by curling into a ball and tucking its head ventrad beneath the abdomen resting most of its weight on the head and hind legs. On the other hand, the animal may rest lying on its side and lactating females habitually lie in

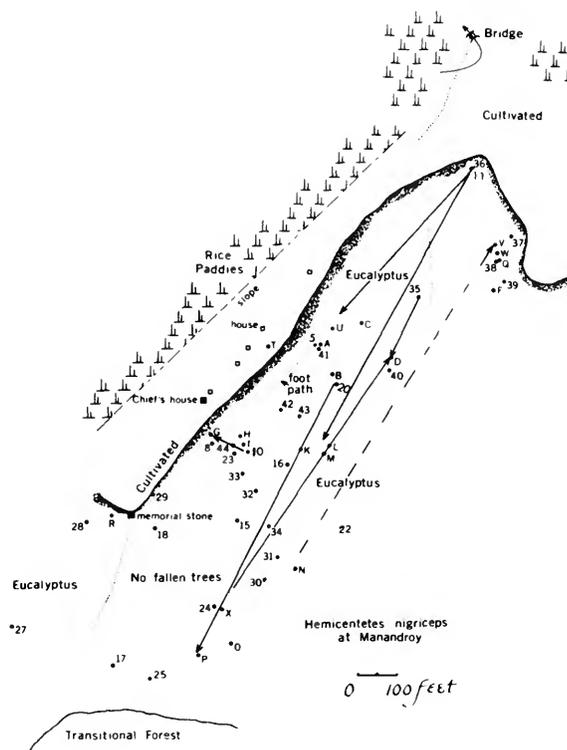


FIGURE 58.—Denning sites and movements for *Hemicentetes nigriceps* population studied at Manandroy. Study area equals about 14 acres. The clustering of nesting sites reflects the availability of cover in the form of rotten logs on the ground. Areas of low density are areas lacking in fallen logs. Lines indicate direction and distance, to scale, that animals moved between 1966 and 1967. Dashed line represents the movement of one individual in one day. Five other movements that occurred during a period of 3 months of 1966 were: 4 to 25, 8 to 35, 5 to 20, 20 to 35, and 13 to 29. "Missing" numbers or letters are due to empty burrows or burrows found outside the mapped area.

Composition of burrows—1966

5	1 individual	30	1 juvenile
8	1 adult male	31	1 subadult female
10	1 adult male	32	1 adult male
11	1 adult male, 1 adult female, 2 infants	33	1 adult female, 1 subadult female
15	1 adult female, 1 adult male	34	1 adult female
16	1 adult female	35	3 adult males, 4 adult females, 1 subadult female (6 April)
17	1 adult female, 1 juvenile female	36	1 adult female, 1 adult male, 4 infants
18	1 adult female, 1 juvenile male	37	1 adult female
20	2 adult females, 2 juveniles	38	7 adult male
22	1 adult	39	1 adult male
23	1 subadult	40	1 adult female
24	1 adult female, 1 juvenile female	41	1 subadult
25	1 adult male, 1 adult female	42	1 adult male
27	1 adult female	43	1 adult male
28	1 adult male	44	1 individual, 1 adult male
29	1 adult male		

Composition of burrows—1967

- A 1 adult female, 3 infants (about 1 week old)
- B 1 subadult, 1 infant (about 1 week old)
- C 2 males, *Setifer*
- D 1 adult male, 1 subadult, 2 juvenile males, 2 juvenile females
- F 6 infants (TL 58-61) including 1 albino
- G 2 adults
- H 1 adult male, 1 subadult female
- I 1 adult
- K 1 subadult male
- L 1 adult female
- M 1 subadult male
- N 1 adult male
- O 1 adult female
- P 2 subadult males, 3 juveniles
- Q 1 subadult female
- R 1 adult
- T 1 adult female, 1 adult male, 3 juveniles
- U 1 subadult, 1 adult male, 1 adult female, 3 infants
- V 2 adults
- W 1 adult female, 1 juvenile male
- X 1 adult

this position when the young are suckling. The animals have also been observed to sleep on their backs but, when torpid, they generally curl in a semicircle lying on one side within the nest.

*Marking.*—Urine and feces may be deposited at the burrow entrance. An animal does not venture very far from the burrow when defecating during the day, and at this time the feces may be deposited within 1 or 2 inches of the entrance itself.

*Hemicentetes nigriceps* has been noted, during encounters with conspecifics, to drag its perineal region on the substrate. Once an animal was noted to rub its ventrum by extending and flexing the body in the substrate. *Hemicentetes semispinosus* has been noted to extend and flex its body while lying on its side in the soil—this action is termed a “side rub.” The perineal drag is also exhibited during an encounter situation or when exploring a novel environment. All of these scent depositing movements together with the locus specific urination and defecation are of potential significance in chemical communication.

*Care of the body surface and comfort movements.*—In addition to the patterns of yawning, stretching, and shaking, *Hemicentetes* exhibits scratching as a primary means of dressing its pelage and spines. The hind foot may reach the head and a good portion of the anterior part of the dorsum and ventrum. After a bout of scratching, the animal will often turn and nibble at its toenails. The face-wash exhibited by *Setifer*, *Echinops*, and the *Microgales*, is present only in an abbreviated form in *Hemicentetes*. One forefoot may occasionally be used to wipe the side of the face, but the animal never sits upright or exhibits a stereotyped face-washing pattern employing both forepaws simultaneously. The teeth and tongue are utilized as a cleaning organ by licking parts of the ventrum and the cloacal region.

*Urination and defecation.*—As noted previously, *Hemicentetes* tends to defecate near the burrow entrance. Defecation generally involves a freezing movement while partially extending the hind legs. At the conclusion of defecation, the animal frequently kicks back. *Hemicentetes nigriceps* will, on occasion, bury its feces with movements similar to those described for *Tenrec ecaudatus*. This pattern consists of moving somewhere away from the burrow entrance to a pre-

ferred locus, probing in the substrate, and digging with the forepaws to create a small depression. After turning around and orientating its posterior over the hole, it defecates and kicks back, partially covering the feces with earth. Such a ritualized kicking back and covering movement has not been noted for *H. semispinosus* although all the basic behavioral elements are present for its complete expression.

*Nest building and burrowing.*—*Hemicentetes* is a rather good burrower possessing well-developed claws on its broad forepaws. Burrowing movements typically consist of selecting a site, generally under a log or near a rock, and commencing to dig at some intersection between the log and the substrate. Alternate movements of the forepaws are employed and the accumulated earth is kicked back with the hind feet. Simple burrows are constructed and, when a tunnel about a foot long has been excavated, the animal begins to transport nesting material. Leaves and blades of grass are seized in the mouth and carried to the nest where they are deposited. If blades of grass are being selected, the animal may grip them quite tightly with its teeth and shake its head from side to side. It is customary when *Hemicentetes* enters its burrow, at the conclusion of a foraging bout, to re-emerge and seize leaves lying in the vicinity of the entrance, pull them in, and deposit them to one side of its body. The net result is that the burrow entrance is effectively plugged when the animal retires to the inside.

*Foraging and prey capture.*—Since the principal food of *Hemicentetes* is earthworms, we will attempt to describe the location and capture of worms for both species. As indicated in the section concerning utilization of the living space, the animals tend to be selective in the areas in which they exhibit foraging behavior. The extent to which odor is involved in the detection of earthworms is difficult to determine; however, soil that has been impregnated with earthworm scent generally stimulates activity at that spot.

The animal, when foraging on a grassy or leaf-littered ground cover, will insert its nose at the roots of the grasses or under leaves. Upon detecting a worm, it will hesitate and then attempt to bite at the worm with its mouth while simultaneously loosening the earth to either side of the worm by scratching movements. These may be directed backwards or slightly to one side. Once the worm has been seized, it is frequently shaken and seized again. The animal exerts

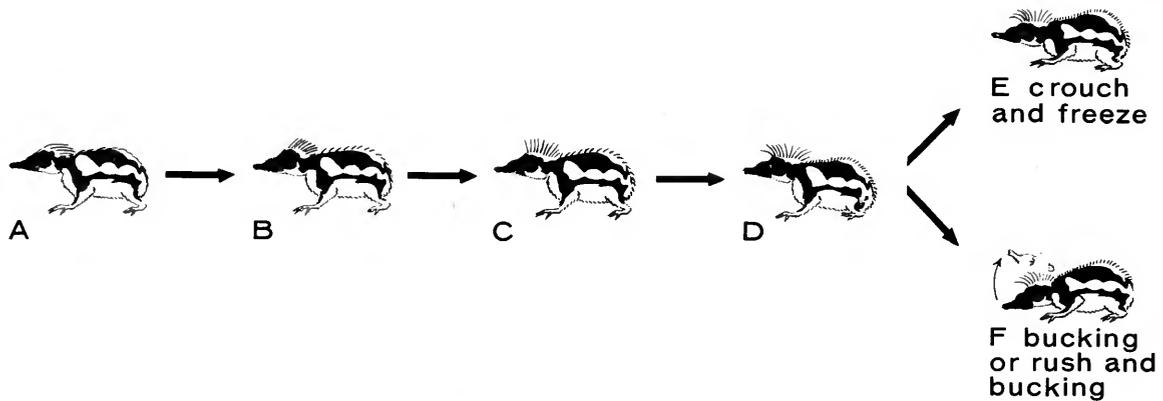


FIGURE 59.—Degree of crest erection displayed by *Hemicentetes*: A, Crest not erect; body quills not erect; B, Crest half erect; body quills erect; C, crest fully erect; body quills erect; D, Crest forward; body quills erect; E, Same spinal erection but crouching and freezing; F, Same spinal erection but bucking and/or rush and bucking.

a strong pull while bracing its forefeet and pulling back with its neck muscles. It will then proceed to relax the tension while shaking its head from side to side, and then initiate a new bite while stroking downward on either side of the worm with its forepaws in a very characteristic patting motion. It is interesting to note that this pattern of seizure with the mouth, shake of the head, and patting with the forepaws is displayed toward other foodstuffs such as raw meat even when these movements are no longer necessary to aid in prey capture. The sequence is quite stereotyped and is displayed whenever initially seizing any foodstuff, regardless of its nature. (See also *Solenodon* Eisenberg and Gould, 1966).

Some observations on the capture and consumption of coleopteran larvae are useful at this point since these large grubs have pincers and can afford some discomfort to *Hemicentetes* when they are being eaten. Since the grubs are quite large, juveniles have special difficulty in killing them. For example, a juvenile sniffed and attempted to pick up a grub in its mouth up to nine times. During each attempt it was unable to effect a grip and finally left the grub and walked off. As another example, an adult approached a grub, bit it, and immediately exhibited the head shake and stamping movement thereby succeeding in tearing the grub open. It then commenced to chew, and consumed the grub completely except for the head and

pincers. Some adult *Hemicentetes* would not eat grubs. This could in part be attributed either to a lack of experience and an avoidance of a novel prey object or to the possibility that the animal had been pinched before and was deliberately avoiding the grub.

*Offensive and defensive behavior.*—When startled in the field, *Hemicentetes* generally will exhibit spinal and crest erection followed by either flight or offensive behavior patterns. The animals are capable of running quite rapidly and during our speed tests we clocked six individuals of *semispinosus* over a range of 1.6 to 2.7 feet per second. One individual *H. nigriceps* achieved a speed of 1.5 feet per second. As will be discussed later, any marked change in the background environment induces offensive or defensive behavior on the part of the animal, but the odor of predators such as *Galidia elegans* or *Fossa fossa* is especially effective in inducing an offensive reaction.

Defensive behavior consists of erecting the quills especially those on the head (nuchal crest). The degree of crest erection is in part a function of the degree of stimulus contrast<sup>7</sup> and may range from partial erection to full forward where the spines of the head are directed anteriorly forming a circle around the head of the animal (see Figure 59). During defensive re-

<sup>7</sup> Throughout, "stimulus contrast" will be used in the sense defined by Andrew, 1964.

sponses the animal utters typical vocalizations: Mild arousal is accompanied by the putt-putt sound; stronger arousal involves the crunch sound plus bucking. Bucking consists of contracting the epaxial muscle plus extending the forelimbs causing the head to lift. Alternate contraction of the neck muscles causes the head to bob up either independently or in conjunction with the foreleg movements. This movement effectively serves to drive crest spines into the nose or paws of a predator. The animal is quite capable of pivoting on its hind legs and will orientate immediately toward any disturbing stimulus and continue bucking. The barbed detachable quills make this defense quite effective.

If aroused by predator odor, the animal will not only erect quills and buck but will also run towards any disturbing object bucking all the while. When disturbed in the nest, a nontorpid animal generally responds with the full-blown defense pattern and, in the case of colonies such as those formed by *Hemicentetes semispinosus*, all members will be aroused and give a concerted attack on any intruder in their nest or tunnel system.

*Hemicentetes* rarely bites but may do so when disturbed in the nest. The extreme reduction in tooth size makes biting a less adequate defense than defense involving spines.

Other offensive and defensive patterns are displayed toward conspecifics and are discussed on pages 94–95 under Social Behavior.

#### SOCIAL BEHAVIOR

*Communication.*—Auditory communication is prominent in *Hemicentetes*. Nonvocal communication includes the general sounds which accompany the animal's foraging activity including the stamping of the feet as an earthworm is pulled from the ground and the chewing sounds. In addition sounds are produced when the animal stridulates (Gould, 1965; see also p. 102 ff). During offensive and defensive patterns of behavior, characteristic vocalizations are produced.

The "crunch" sound which is homologous to the sound produced by *Setifer* and *Echinops* generally accompanies nuchal crest erection, body spine erection, head bucking, and/or body bucking. It may be produced with half to full crest erection prior to a startle

response leading to flight. The "putt-putt" sound is generally displayed when the animal shows full-body spine erection. The nuchal crest need not be fully erected. This sound is generally produced when the animal is disturbed in the nest box or during the initial phase of an encounter. A sharp inhalation and exhalation may be produced when the animal is exhibiting bucking. A "piff" sound similar in tonal quality to that produced by *Tenrec* is shown but the circumstances cannot be specified. There is a graded series of squeaks including a grunt sound, a squeak, and a twitter which are produced during social contact. These are the only sounds that show a true harmonic structure. During courtship as the male approaches the female, he may lift his nose and bend the terminal tip dorsad as he exhibits a nose to ear. At this time he may utter a prolonged "hiss" which is strongly associated with courtship (see Table 8).

Chemical communication is implicated by the marking movements and the locus-specific deposition of feces and urine.

Tactile communication is involved in all contact-promoting behaviors such as naso-anal, naso-nasal, nose to ear, nose to body, crawling over, and nose to nape. During offensive and defensive behavior toward conspecifics, the animal may rump another, buck, or bite.

*The encounter.*—The behavior patterns employed during encounters with conspecifics are similar to those described for the other genera of Tenrecinae.

Offensive and defensive behavior toward conspecifics: (1) striking with the nose; that is, suddenly swinging the head to one side and pushing at a conspecific with the snout; (2) rumping; that is pivoting on the forelegs and pushing the rump into a partner; and (3) while standing quadrupedally with the heel off the substrate, darting the head at a partner while attempting to bite. The nuchal crest may be raised during this latter movement.

While fighting, males will attempt to bite one another in the flank or shoulder. If the body axes are oriented in opposite directions when they are standing side by side, they may mutually bite each other in the flank and roll over. In seeking to grasp one another they may bind together in a grapple and tumble about for some time. On rare occasions the agonistic behavior may involve raising the crest and actually attempting to buck and drive the crest quills into a partner.

Contact promoting behaviors include nose to anal or inguinal region, nose to nose contact, nose to ear, nose

TABLE 8.—Physical properties and circumstances of occurrence for some vocalizations of *Hemicentetes*\*

Sound Type	Sample Size	Note Structure	Temporal Patterning	Frequency Range (Hz)	Dominant Frequency Range (Hz)	Duration (seconds)	Circumstances of Occurrence
Clear tones Squeak**	1	Single note with harmonics	Single note	1,500–3,000	2,000	.08	Response to pain.
Noisy sounds Crunch	3	No harmonics, noise	Repetitive	50–6,000	50–2,000	.03–.05	During attack bucking with full forward crest.
Putt putt	19	No harmonics, noise	Repetitive .07–.10 sec. interval	50–2,000	50–500	.05	During mild arousal and threat context while in nest.

\*Sound types similar for *H. semispinosus* and *H. nigriceps*.

\*\*Indicates recording from *H. nigriceps*, all others for *H. semispinosus*.

to the side of the body, nose to nape, and crawling over and crawling under. Sexual behavior includes mounting by the male and lordosis by the female. The mount is prolonged in *Hemicentetes* and may exceed 20 minutes in duration. The gape reaction is absent in *Hemicentetes*. This loss correlates with the decreased tendency to bite and the reduction in tooth size.

The form of the encounter may be specified in part by a knowledge of the age and sex classes engaged in the interaction:

Male-male encounters are characterized by an initial contact-promoting session involving nose to anus, nose to ear, and nose to body; generally followed by moving away and/or offensive and defensive behaviors including bucking. Young males maturing in a family group may be tolerated by older males and no agonistic interaction will occur, but if two adult males who are unknown to each other are introduced in the presence of females, some severe fighting may ensue. In addition, groups that have been kept together through the torpid period during the austral winter will upon emerging often exhibit considerable agonistic behavior in the austral spring (see Gould and Eisenberg, 1966). As described previously, male fights may involve biting and locking and grappling.

Female-female encounters generally involve preliminary contact of nose to crest, nose to nose, nose to ear, nose to body, followed by moving away and avoidance.

The nature of the male-female encounters depends upon the female's sexual receptivity. In general the male will always initiate a great deal of contact promoting behavior followed by an attempt to mount. The most frequent contact-promoting behaviors are nose to nose and nose to body. Crawling under, and head-over head-under, have been exhibited only rarely. The females generally show less contact-promoting behavior but do engage in all of the patterns noted for the male with the exception of attempted mounts (Figure 60). If the females are unreceptive, they will move away. If the male persists in his mounting attempts, females will buck and show crest erection. Eventually the male will desist under these circumstances; however, moving away and bucking on the part of the female do not necessarily indicate that she will not receive the male, and the male may persist through two or three bouts of bucking and rebuttal from a female before he finally mounts her. The following protocols give some idea of the interaction sequence.

Example 1—*Hemicentetes nigriceps*: Male and female come together nose to nose. Male exhibits a nose to her crown or ear; female stands and then exhibits a nose to the side of the male and a nose to his crown. Male demonstrates lip curl and hisses in her ear. Female exhibits nose to side. Male exhibits nose to side, nose to crown, and nose to rump of female, and initiates following as the female moves away. He at-

## CONTACT AND MATING HEMICENTETES

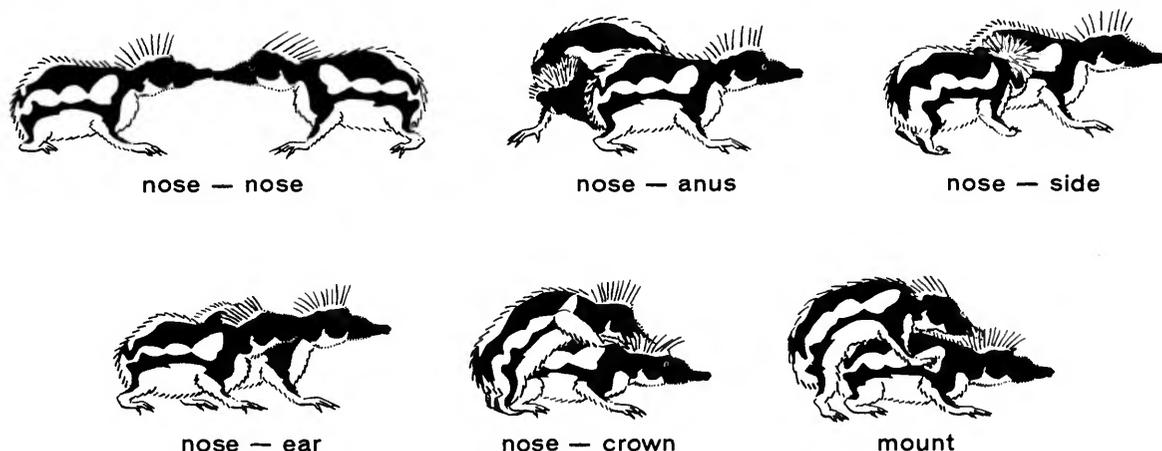


FIGURE 60.—Contact and mating behavior in *Hemicentetes nigriceps*. Contact configurations include touching nose to nose, nose to anus, nose to side, nose to ear, nose to crown, and mounting by the male. (Nose to anus is equivalent to nose to posterior portion of cloaca.)

tempts to mount. The male will also drag his perineum and ventrum in the substrate between encounter attempts.

Example 2—*Hemicentetes semispinosus*: Male approaches; female stands. Male exhibits nose to ear followed by a nose to ear by the female. Male shows lip curl and hisses in her ear again. Female shows nose to ear of male. Break. Male approaches from the rear, exhibits nose to cloacal region of female; female stands. Male attempts mount and exhibits nose to crown. Male achieves mount and grasps the quills of her nape in his mouth.

Because *H. semispinosus* frequently dwells in colonies during the reproduction season, several tests were run by introducing adult males to females with half grown young. Two different males were introduced separately to a group composed of two females and eight juveniles. During a 44-minute encounter period, Male A showed the following patterns toward the adult females: Nose to crown, nose to nose, nose to cloaca, nose to ear with hissing, nose to body, attempted mounts, and finally two separate mounts. Mount durations were 10½ minutes with Female No. 9 followed by 21 minutes with Female No. 10. The mount included intromission by the male and thrusting. Adult females showed moderate contact responses to the male

including nose to cloaca, nose to nose, and nose to ear. Initially the females showed moving away and some bouts of bucking but were quite docile once they had encountered the male at least twice. The second male (Male B), upon introduction, was unsuccessful in his attempts to mate with the adult females and confined most of his activities to the juveniles. Contact promoting behaviors were shown to juveniles and three times he attempted to mount juvenile animals. The juveniles reciprocated only with nose to nose contact and upon attempts to mount they bucked or squealed with an erect crest.

During Male A's mating with the adult females, the juveniles would congregate around the coupling pair in a circle or semicircle. The number of young concentrated around the mating pair varied throughout the 44-minute encounter time. During the first minute, there were two young. The number of young increased to a maximum of eight young after 11 minutes and then waned to an average of three young for the remaining 16 minutes of the encounter.

We may note the following characteristics of the mating pattern of *Hemicentetes*: Contact promoting behaviors are very similar to those described for the other genera of tenrecs. The neck grip confined to the nuchal crest area is still present in *Hemicentetes* males. The mount duration is protracted. Receptive females

initially show a period of agonistic behavior toward the male followed shortly by quiescence. Figure 60 illustrates the mating ritual of *Hemicentetes nigriceps* and this may be compared with that portrayed for *Microgale* in Figure 29. The great similarities in the tactile and olfactory exchange configurations is immediately apparent.

#### PARENTAL CARE BEHAVIOR

Some days prior to parturition and on through the day of parturition, female *Hemicentetes* exhibit an increased tendency to build a nest. They assiduously collect leaves in the vicinity of the nest and transport them there in their mouths. Nest defense increases markedly during the initial period of rearing the young. "Putt-putt" sounds may be made upon initial disturbance. Further disturbance of the nest results in a crunch sound, full forward crest, bucking while stamping the feet, and even rushing. *H. nigriceps* will bite occasionally as will *H. semispinosus*; however, biting appears to be of much rarer occurrence in *H. semispinosus*. Female *Hemicentetes* lick and clean their young utilizing the tongue until the young are 10 days of age. Retrieval of young to the nest by the female persists until at least 10 days of age. From 10 to 15 days of age, the female will still exhibit attentive behavior to the young but by the time the young are 2 weeks old attentive behavior has begun to wane. Until the infants are 15 days of age, the female will extend toward a youngster, place her nose over it, and draw it under her body (see Gould and Eisenberg, 1966). The female will attempt to stand over the litter until they are approximately 15 days of age. Suckling begins to wane from 18 to 22 days.

#### ONTOGENY OF BEHAVIOR

*Hemicentetes nigriceps*.—The young of *H. nigriceps* mature very rapidly (Figure 61). Until approximately 14 days of age, they are very much oriented to the nest. At birth the young can both squeak and suckle and will attempt to locate the teat by switching the head from side to side. The "crunch" sound is generally shown at approximately 4 days of age. Neonates can crawl using a crossed extension pattern with some hind leg coordination but the ventrum drags until approximately 10 days when they begin to lift the ventrum from the substrate. Fully coordinated locomotion is well developed by 20 days of age. The righting response or the capacity to turn over when placed on

their backs, is present by the second day. The meatus is closed until the 7th day of age. The eyes generally remain closed until the 8th day. Teeth are detectable at approximately 5 to 6 days of age. The animals will exhibit a bucking response at approximately 1 day of age. When displaced from the nest, a shiver reflex is demonstrated until approximately 9 days of age when it wanes. The nipples are visible in the young from approximately 3 days on. Hair and spines begin to show after 24 hours and develop together reaching a maximum development at approximately 20 days of age. The stridulating quills appear from 2½ to 5 days.

The young first emerge from the den at approximately 9 days of age only to return, never proceeding very far from the entrance. The young begin to accompany the mother from 12 days on and from the age of approximately 17 days they may be found foraging quite far from one another in the field. The scratch reflex begins to appear at 7 days but at this age they tumble to one side while scratching and only exhibit fully developed scratching from 15 days on. The young begin to feed on solid food at approximately 13 days of age and depend more heavily on solid food from about 17 days on. Spontaneous defecation is shown at 4 days of age. Young *nigriceps* will begin to dig a hole, defecate, and cover the feces at approximately 16 days of age.

From approximately 13 days to 22 days of age, the young will follow the mother loosely and cluster around her when she stops. Following begins to wane at about 20 to 30 days. First estrus is shown by females at roughly 32 days of age. Nest building is first shown by the young from 16 to 20 days only to wane and then reappear again at approximately 30 days of age. Clustering around the female is dependent on the nursing association and as lactation wanes so does clustering. The period of family group foraging may be as short as 3 to 5 days.

The young at birth are roughly 60 mm in total length. At approximately 30 days of age, they show a total length of from 110 mm to 130 mm. Growth begins to plateau at about 40 days of age. The animals are dependent on milk from birth until approximately 22 days of age when they may be weaned on solid food (see Figures 62 and 63).

*Hemicentetes semispinosus*.—The description of behavior ontogeny for *H. nigriceps* fairly well describes the situation of *H. semispinosus*. At birth *H. semi-*

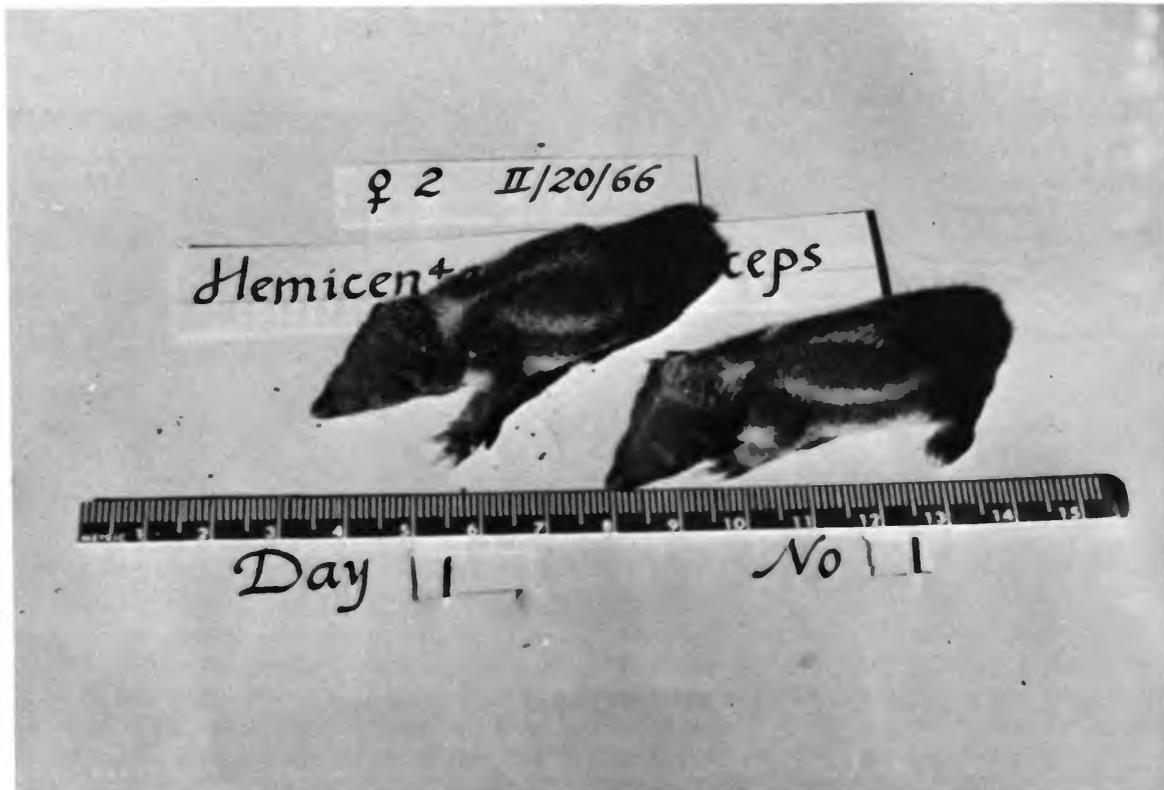


FIGURE 61.—*Hemicentetes nigriceps*, 1 day old.

*spinus* is 60 to 70 mm in total length and, at the conversion to solid food from 18 to 22 days, the animals are approximately 90 to 100 mm long. From this point on, growth is extremely rapid beginning to plateau at approximately 40 days of age when the animals may be anywhere from 140 to 150 mm in total length.

At birth the meatus and the eyes are closed. The meatus opens at approximately 6 days of age; eyes are open at roughly 7 to 8 days of age. Spines and hair are visible shortly after birth and begin to become especially prominent around 5 to 15 days of age. Stridulation is loud and clearly detectable at 16 days of age.

The youngsters begin to emerge from the den and cluster around its entrance at approximately 9 days of age and initiate following of the female from about 12 to 22 days of age. The following response is most pronounced from day 16 to 18. First estrus is estimated to occur at between 35 and 40 days of age.

#### SOCIAL ORGANIZATION

*Hemicentetes nigriceps*.—Our marked population of *H. nigriceps* at Manandroy provided us with much information concerning grouping tendencies in the field. In February 1966, 28 burrows were examined and the range in group size per burrow was one to four with an average of 2.05. The April 1966 series included 22 burrows with a range of one to seven animals and an average of 1.6 animals per burrow. The February 1967 samples for 21 burrows indicated a range from one to eight with an average group size of 2.7 animals per burrow. The most consistent grouping pattern was the female with juveniles or infants. This grouping included 14 of the total burrow systems examined. Solitary males occurred 10 times; solitary females occurred 15 times. A male with adult females occurred 13 times; these females may or may not have been accompanied by juveniles. Male-male and female-female as-

# MATURATION RATES

*H. NIGRICEPS*

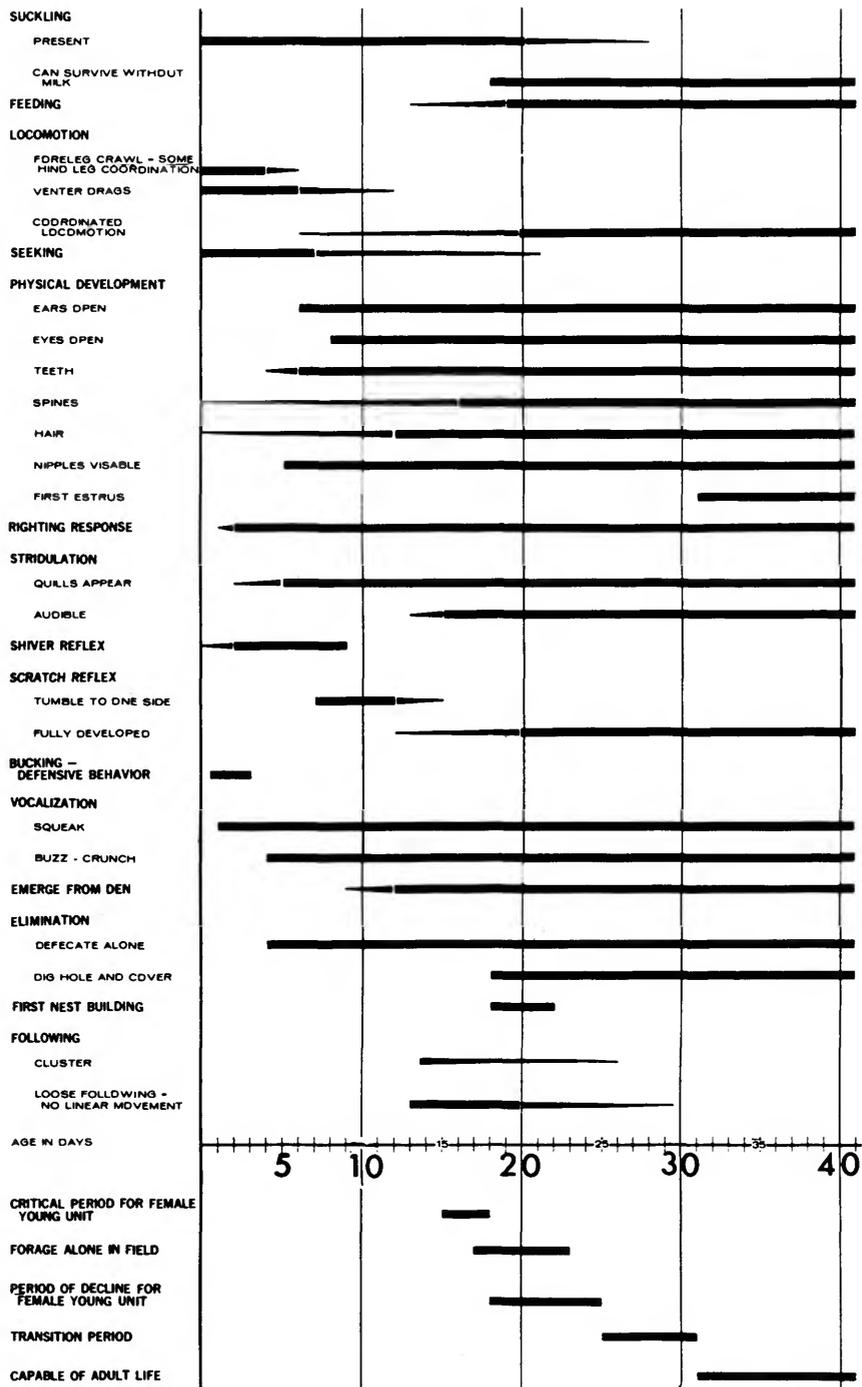


FIGURE 62.—Maturation rates for *Hemicentetes nigriceps*. The black bars indicate the onset and cessation or onset and continuation of the various measurements of behavioral and morphological maturation.

Plots of Age Class Limits based on Total Length

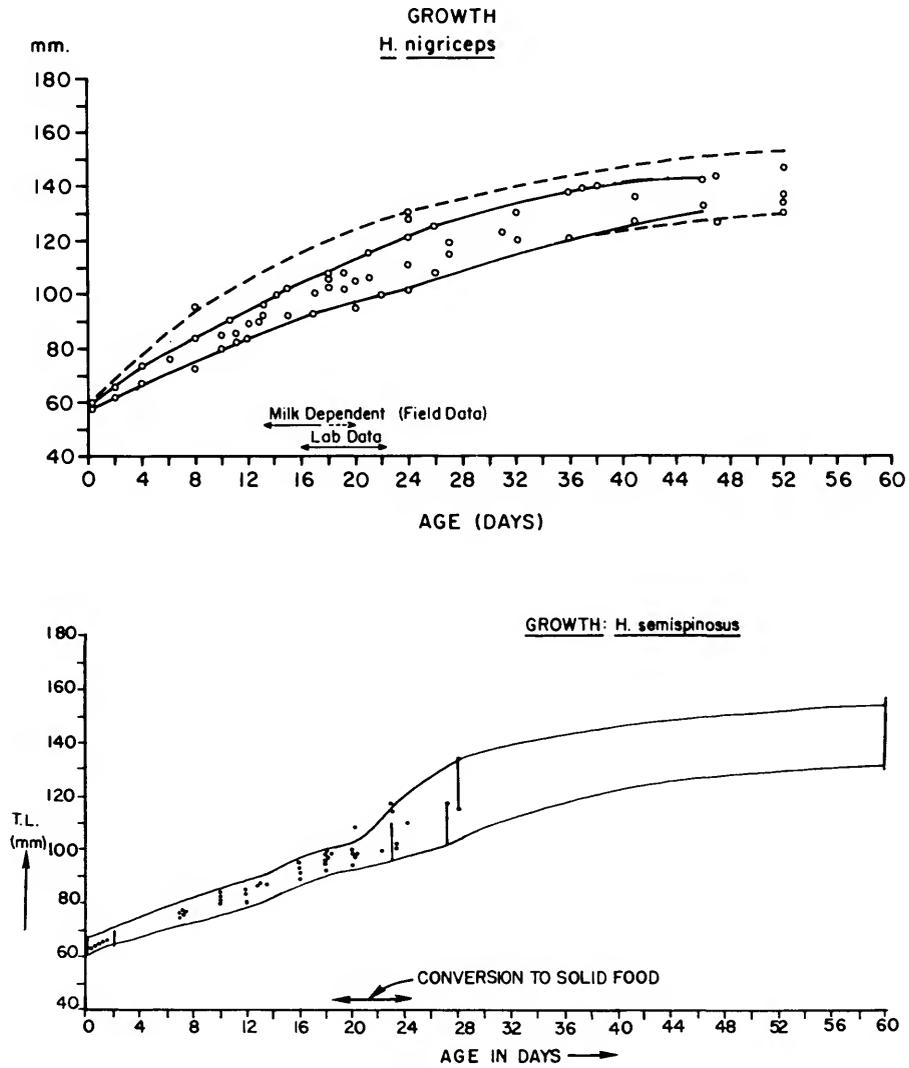


FIGURE 63.—Comparison of growth for *Hemicentetes nigriceps* and *Hemicentetes semispinosus*. Total length increases uniformly until approximately 40 days of age when it begins to plateau. The slight deflection in the *Hemicentetes semispinosus* curve is a reflection of slower initial growth rates probably because of the larger litter size in *H. semispinosus*. Solid vertical lines connecting dots of *H. semispinosus* graph is range at that age: two enclosing lines represent total range. Solid lines on *H. nigriceps* graph connect measurements of the same individuals; dashed line represents the range of total length.

sociations were very rare, including two instances each.

In captivity tests were conducted by introducing alien males to groups composed of a female and her young. In general after the young were 19 days of age, the adult female showed little defense of the nest. As noted in experimental encounters, the female will respond by bucking if a male attempts to mount unless she is quite receptive. The young animals generally cluster around an alien but the cluster formation is temporary. In one of the encounter tests, the intruder definitely avoided the nest box of the female and young, denning separately, but in three other encounters, the intruder denned with the female and juveniles from the first night. The juveniles are definitely more prone to become aroused and show a forward crest at first contact with a strange male. Adult females are far more tolerant in their arousal patterns.

From these observations and from studies of the marked populations, we conclude that within a given community of *Hemicentetes nigriceps* adult females tend to den alone prior to parturition. After parturition they show active nest defense, tolerating no aliens. Males, however, may enter when the young are approximately 2 weeks old, and perhaps mate again with the female in the following week. In one case we noted a male persisting in association with a female through the birth of her young. Juveniles apparently are tolerated indiscriminately in the den or burrow with the female and infants. Adult males do not associate habitually with one another nor do adult females. From our observations in captivity, we have the definite impression that adult males are aggressive to one another and this probably accounts for some spacing. Juvenile males on occasion will form small bachelor groups occupying the same burrow system.

*Hemicentetes semispinosus*.—A total of eleven dens were examined in 1966 and 1967 in both the area of Ambitolah-Ranomafana and Perinet. As described previously (p. 86) one of these groups consisted of an extended colony of 18 individuals including 2 adult males, 2 adult females, and 14 juveniles. If we discount this maximum colony size of 18, then the groups fall accordingly to the following descriptions: (1) Solitary

individuals included two instances of juveniles which were sheltering in what appeared to be temporary burrows and one pregnant female in a well-constructed burrow. (2) Two instances of two individuals denning together were noted; in one, two females both pregnant, in the other a male and a pregnant female. (3) The other five burrows noted included one group of seven including a female and her young; one group of seven consisting of two females, one with infants and the other pregnant; one group of eight consisting of a male and a female with their offspring; one group of seven consisting of a male and a female and five offspring; one group of nine consisting of a male and a female with seven infants. The larger groups of *H. semispinosus* when compared with *H. nigriceps* in part result from the larger litters produced. There does appear to be a marked tendency for males to associate with females and their juveniles even when the adult female is pregnant. Our evidence from an examination of the colony of 18 indicates that some male-male spacing must occur since the number of adult males was rather disproportionate compared to the number of juvenile females available for impregnating.

Experiments in captivity indicate that a female with young of approximately 14 days of age, will readily allow an alien male to enter her den after an initial rebuff. Further observations on colonies of *H. semispinosus* indicate that females approaching parturition do tend to shift to a more isolated portion of the burrow system or to a separate den nearby. After the first week or so, females are rather tolerant with respect to the entrance of conspecifics but it would seem essential that the female isolate herself somewhat with her litter in order to maintain some continuity in parental care.

Potentiality for colony formation does exist in *H. semispinosus* and, in part, is a function of the increased litter size and a tolerant attitude on the part of the female with young of approximately 2 weeks of age. It is evident that for both *H. nigriceps* and *H. semispinosus* adult males may associate with the female for shorter or longer periods during pregnancy and nursing.

## Stridulation in *Hemicentetes*

### THE PHENOMENON OF STRIDULATION

#### Introduction

As noted in the preceding sections, sounds may be produced by the specialized quills in the posterior mid-dorsal region of both species of *Hemicentetes*. A description of the quill structure is included in Petter and Petter-Rousseaux, 1963. Rand (1935) first noted that this group of specialized quills could be moved independently of the other body quills. Gould (1965) first recognized that the quills produce ultrasonics and described the physical characteristics of a stridulation pulse series. Frequency analysis was obtained by feeding stridulation signals from a tape loop on the Precision Instrument tape recorder into a Hewlett Packard Wave Analyser (No. 310A) and then to a Bruel and Kjaer Level Recorder (No. 2305). A stridulation sound shows little harmonic structure. It is organized into a train of pulses and, within each pulse, the energy is broad band noise from about 2 KHz to 200 KHz. Three to five peaks of energy usually occurred in groups, probably a result of three to five primary loci of contact among the three rows of interdigitating stridulating quills. Energy peaks clearly show up at 200 KHz. There was little difference between energy peaks between 50 KHz and 150 KHz. There was an abrupt drop at 150 to 200 KHz. The study by Wever and Herman (1968) indicates that *Hemicentetes* can hear stridulation within the lower range of the stridulation energy distribution (i.e., up to 18 to 20 KHz). The sensitivity of the ear is sufficient to permit coordinated responses to stridulation at a distance of about 4 meters.

The signal varies in its physical characteristics with respect to duration, amplitude, and the repetition rate of pulses. Some of the variations in pulse characteristics may be correlated with the mood of the stridulating animal, the individual animal, or the species of *Hemicentetes* which is stridulating. Young individuals of *Hemicentetes* generally produce a lower intensity sound when they are between the ages of 14 to 17 days. By about 17 days of age the intensity of

stridulation is very near adult level. Intensity of 3 adult *Hemicentetes semispinosus* (two females and one male) ranged between 61 and 63 db re  $2 \times 10^{-4}$  microbars; intensities of two juveniles 29 and 30 days old were 60 and 61 db. Distance from the microphone to the stridulating organ was approximately 3 inches. Tape-recorded stridulation sounds were displayed on an oscilloscope and the signals were photographed using a 35 mm oscilloscope camera; these photographs were analyzed for changes in duration, pulse repetition rate and relative differences in intensity. Depending on the degree of arousal displayed by the animal, two signal types may be discerned: (1) slow intermittent stridulation and (2) fast, loud stridulation. A random sample of stridulation pulses of two *H. semispinosus* and two *H. nigriceps* while exposed to different stimuli such as dim and bright light and teasing, revealed a much higher rate of shorter duration pulses in *H. nigriceps* (Table 9). Range of durations was the same for both species. Probably the fewer number of stridulation quills (Figure 51) on *Hemicentetes nigriceps* accounts for their shorter duration and lower intensity.

#### The Motivational Basis for Stridulation

Stridulation is accomplished by erecting the stridulating quills and moving them back and forth so that they strike against one another and thereby set up a complex wave system. The erection of stridulation quills is generally accompanied by some partial erection of the other body quills. This immediately suggested to us that there could be some correlation between the degree of spinal erection shown by the animal and the degree or quality of stridulation. As we have outlined before, the crest is composed of specialized quills for driving into an enemy. Thus, crest erection was analyzed to determine whether stridulation correlated with the degree of spinal erection.

Such an undertaking necessitated the establishment of a behavioral classification so that, as a first step, spinal erection could be correlated with the types of behavior that the animal was engaged in. As we have

TABLE 9—Duration of stridulation pulses over a 140-second period during three different light stimulus tests

Duration of Stridulation Pulses (in milliseconds)	<i>H. semispinosus</i>		<i>H. nigriceps</i>	
	No. of Pulses	%	No. of Pulses	%
7 to 40	35	50	54	81
40 to 60	21	30	3	5
60 to 100	14	20	9	14
Total	70		66	

outlined in the preceding sections, the behavior of each species was examined in detail so that a complete inventory of its behavioral repertoire was available to us. This permitted us to establish a functional classification; that is, a classification of behavior which grouped together those behavior patterns which appeared to be involved in the same adaptive process (Hinde, 1966, p. 12). Thus, we could accept as a starting point the sleeping animal exhibiting little arousal and no spinal erection. From this we could consider a class of activities termed maintenance activities which would involve subcategories such as: simple locomotion, care of the body surface, urination and defecation, searching for foodstuffs, ingestion and such related activities as digging and nest building.

A second major functional category, overlapping somewhat with the preceding, included those behavior patterns associated with exploration and foraging in the environment. It is within this class of activities that we may note the tendency either to approach or withdraw on the part of a given animal when encountering an unfamiliar object. Approach could lead to a variety of other actions falling under the first class of maintenance activities, such as feeding, or it could lead to new functional categories of behavior such as contact-promoting and sexual behavior toward conspecifics. Pure withdrawal involves, ultimately, the manifestation of flight behavior. If the object encountered were not a prey object or a conspecific, offensive and defensive behavior or flight behaviors could be shown depending on the quality of the stimuli received. Which course of action the animal took would in part depend on its internal physiological state and the quality of environmental stimuli impinging on it.

For the moment, let us consider the degree of crest

erection as a manifestation of the degree of defensive spinal erection since the erection of the crest never occurs unless some body spines are also erected. Further, let us briefly survey those categories of behavior that may be occurring when the crest is erected. After a long period of observation, we established that no crest erection was associated with activity during relaxed locomotion or during flight. A relaxed crest with partial erection of body quills often occurred while the animal was foraging or exploring a slightly unfamiliar environment. Crest half erect with body quills erect occurred during agonistic contexts with respect to conspecifics or during exploration in a novel environment. Full crest erection with partial erection of body quills could occur during exploration or when moving into the sun from shade. Either full crest erection or forward crest (which involves a rolling forward of the brow accompanied with butting or bucking and the crunch sound) was generally exhibited during extreme offensive or defensive activities, seldom with conspecifics but more often with potentially dangerous stimulation. The behavior associated with active offense including bucking has been described previously (see p. 93). By noting the degree of crest erection and the associated circumstances, we were led to attempt a method of quantifying the degree of crest erection shown and correlate this with a known stimulus input.

#### Light Intensity and Crest Erection

Since crest erection would be shown to a change in the intensity of illumination, we proposed to investigate the relationship between change in incident illumination and the degree of crest erection shown by the animal. Four arousal states were defined in terms of the behavior of the animal. These were crest half erect, crest fully erect, crest forward, and crest forward plus bucking (see Figure 59).

The experiments were run as follows: The subject was placed in a box open at the front and having a background of ruled paper. The animal would then be photographed during exposure to a defined amount of light. By examining the printed photographs after the experiments, one could with the aid of the ruled background determine the angle formed between an arbitrary line drawn from the tip of the nose through the eye and the leading edge of the crest. Thus, the degree of crest erection could be expressed in terms

of a measurable angle and this degree of crest erection could then be correlated with the change in light intensity.

The first series of measurements involved placing the animal in the observation box with 10 seconds exposure to four known stimuli. The first stimulus or condition consisted of low illumination (<5 foot candles), the second to dim light (32 foot candles), the third to bright light (500 foot candles), and the fourth to bright light plus mechanical stimuli (i.e., touching the animal's facial vibrissae with a stick). After each of the 10-second exposures to the defined preceding four stimuli, four pictures were taken at four frames per second. Later one could measure the degree of spinal erection as a function of four increasing stimulus intensities set arbitrarily at 1 to 4. Both *H. semispinosus* and *H. nigriceps* were tested using eight subjects of the former and six of the latter. The data are portrayed in Figure 64.

Our conclusions based on this study were: (1) crest erection is in part independent of body-quill erection; (2) *Hemicentetes nigriceps* is more sensitive to change in background light than *H. semispinosus*; and (3) the degree of crest erection is directly proportional to the increase in stimulus intensity.

A qualitative inspection of our data indicated that under the first condition, that is low illumination or less than 5 foot candles of light, the animals were prone to exhibit movement and investigatory behavior with some body-quill erection and either no nuchal crest erection or half erection. Under the second condition at 32 foot candles, the animals still moved and explored with body quills erect but there was more of a tendency to show from half to full nuchal crest erection. Under the third condition of 500 foot candles of light, there was still some gross movement with body quills erected but there was a marked tendency to show a full forward nuchal crest. With the addition of tactile stimuli to the bright light, the nuchal crest was maintained at the forward position and the animals showed a tendency to buck and/or crouch low to the ground. *H. nigriceps* displayed a pronounced tendency under the third condition to attempt to dig or burrow into the floor of the test box. To express the data another way, it was possible to say that the erection of body quills has the lowest threshold and there is an increasing threshold as one considers crest half erect, crest fully erect, or crest forward. The highest threshold of all appeared to involve bucking and crunching. With higher thresholds for actions, an increasing strength of

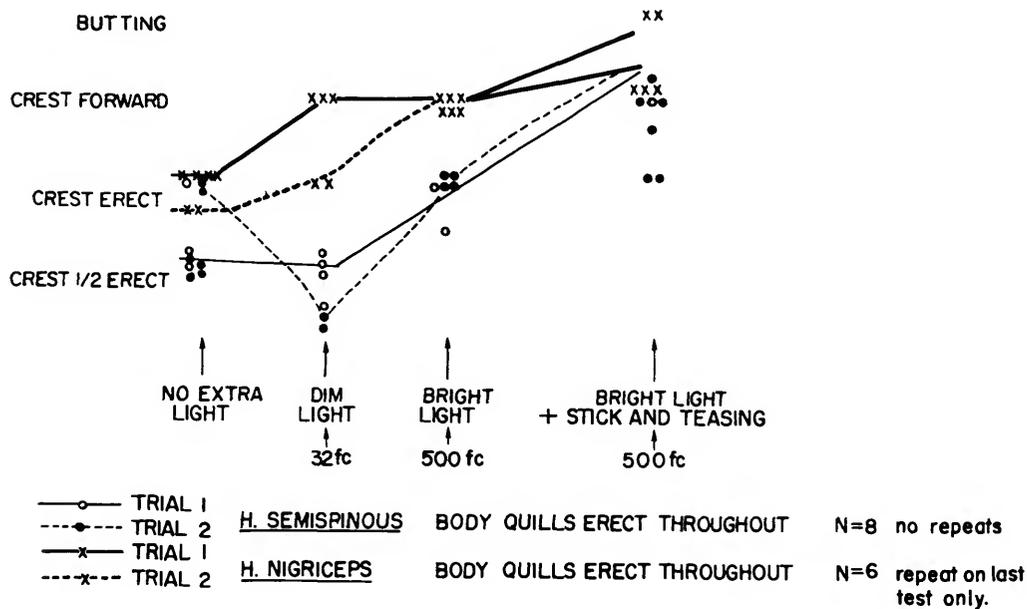


FIGURE 64.—Response strength of *Hemicentetes* to various light intensities.

TABLE 10.—Crest erection responses to four successive changes in light intensity

Species and Trial	22 f.c.*	32 f.c.	1,000 f.c.	1,000 f.c. plus Mechanical Stimuli
<i>H. semispinosus</i>				
Trial 1	No crest	Half erect	Full erect	Full erect
Trial 2	No crest	No crest	Full erect	Full forward
<i>H. nigriceps</i>				
Trial 1	Half erect	Erect	Forward	Forward
Trial 2	Half erect	Erect	Forward	Forward (buck)
Trial 3	Half erect	Erect	Forward	Forward

\*Foot candles.

the stimulus is necessary to elicit the response (Table 10).

### Arousal and Stridulation

The next set of experiments endeavored to clarify whether there were a relationship between the stridulation produced by the animal, the degree of crest erection, and the change in background stimulation. The subject was placed in an arena and the observer sat in front of the arena describing its appearance and behavior by speaking softly into a microphone. The stridulation was recorded simultaneously utilizing the second channel on the tape. In order to arouse the animal, the 1,000 foot candle lamp was switched on during the observation period; thus, the subject and his condition could be verbally recorded while the stridulation rate was recorded and then the change in the background light intensity could be correlated with changes in the stridulation rate and changes in crest erection and behavior. The data from these recordings and observations are portrayed in Figure 65.

The general conclusions were as follows: (1) The position of the crest is *not necessarily* an indicator of stridulation rate. (2) Low intermittent stridulation can occur during moderate arousal<sup>8</sup> even though the animal is immobile, *if* the animal is engaged in some activity such as exploring the substrate with its nose, or testing the air. (3) Low intermittent stridulation can occur when a highly aroused animal is moving in a jerky hesitant fashion. (4) Loud and rapid stridulation

occurs when the animal is highly aroused but not frozen into immobility. (5) A sudden stimulus contrast such as a change in the ambient lighting may cause a sudden increase in stridulation rate and intensity followed by a quiet interval as the animal apparently chooses a course of action. (6) The animal does not stridulate while defecating, chewing, or when "frozen" into immobility following an initial massive change in stimulus contrast. The animal stridulates almost continuously when moving and active. Figure 66 shows actual stridulation rates with associated crest position.

### Sound Intensity and Crest Erection

In order to investigate the relationship between the degree of crest erection and spinal erection shown by the animal and the change in background noise, the following observational procedure was established: The observer sat in front of an arena with a light-proof hood covering the arena and the observer's body. The animal was observed and notes were taken by means of a tape recorder while a given sound was played back to the animal. The degree of crest erection shown by the animal could be noted before and after the sound input. Thus a known sound input was given to an animal in a known state of arousal as evinced by its degree of crest erection. The sound was a recording of stridulation by a *Hemicentetes*. This test was necessary as a precursor to our playback experiments, since it gave us some idea of the range of variability in response by an animal in a known motivational state to a known playback input. Four *Hemicentetes nigriceps*

<sup>8</sup> Degree of arousal defined by degree of crest erection.

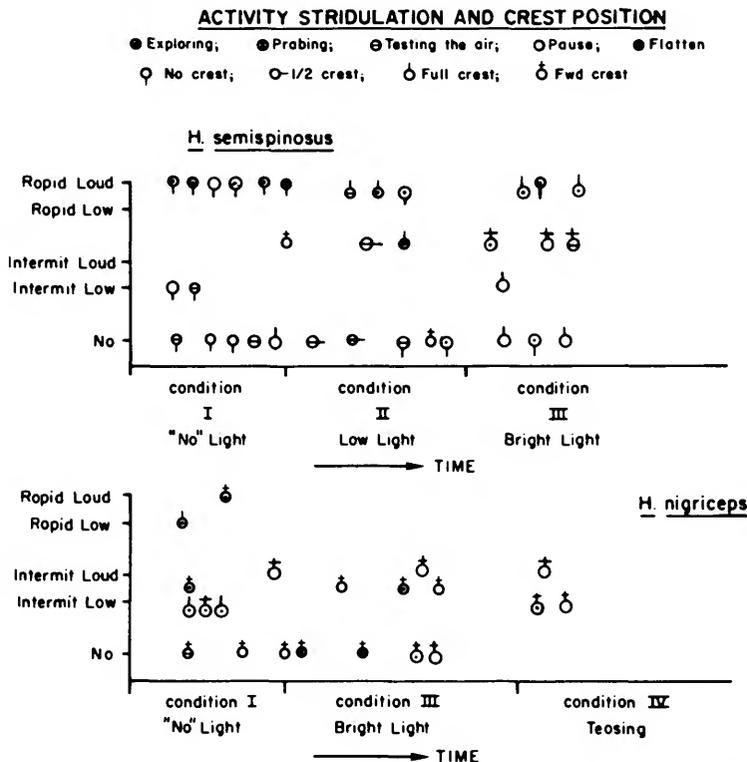


FIGURE 65.—The form of stridulation as a function of crest erection and activity. Little correlation can be seen between the degree of crest erection and the quality of stridulation.

were selected as subjects. The total duration of playback was greater than 3 seconds but less than 15 seconds. This was necessary to avoid a habituation effect. Analysis of the data indicated that, given the same input, it would appear that if the degree of crest erection is known beforehand, the animal after perceiving the known input will exhibit the next stage of crest erection and arousal as an initial effect. The data by which we reached this conclusion are portrayed in Table 11.

**Stridulation and Circumstances of Occurrence**

The animals could be observed in the various arenas and their activity monitored by means of the ultrasonic microphone (see Appendix H). By observing and monitoring with earphones, it was possible to make the

following correlations: The maximum probability of stridulation occurs when the animal is half aroused or at the stage 2 level of arousal (i.e., crest half erect, center quills erect, no crouching, and active movement of the head), but it can occur during full erect and forward crest if the animal is engaged in offensive behavior. Stridulation occurs while feeding, during social contact, during courtship behavior and when the male is mounted on the female, during exploration activities, and during flight activities, or when moving away. When an animal is actually eating, it rarely stridulates, but will stridulate when it extends to pick up a worm, when it shakes a worm, or when it is pulling a worm from another animal. Subjectively speaking, the stridulation is a low intensity single burst or 2 or 3 brief pulses. If an animal is startled and flees, it stridulates loudly with a continuous train of pulses when it

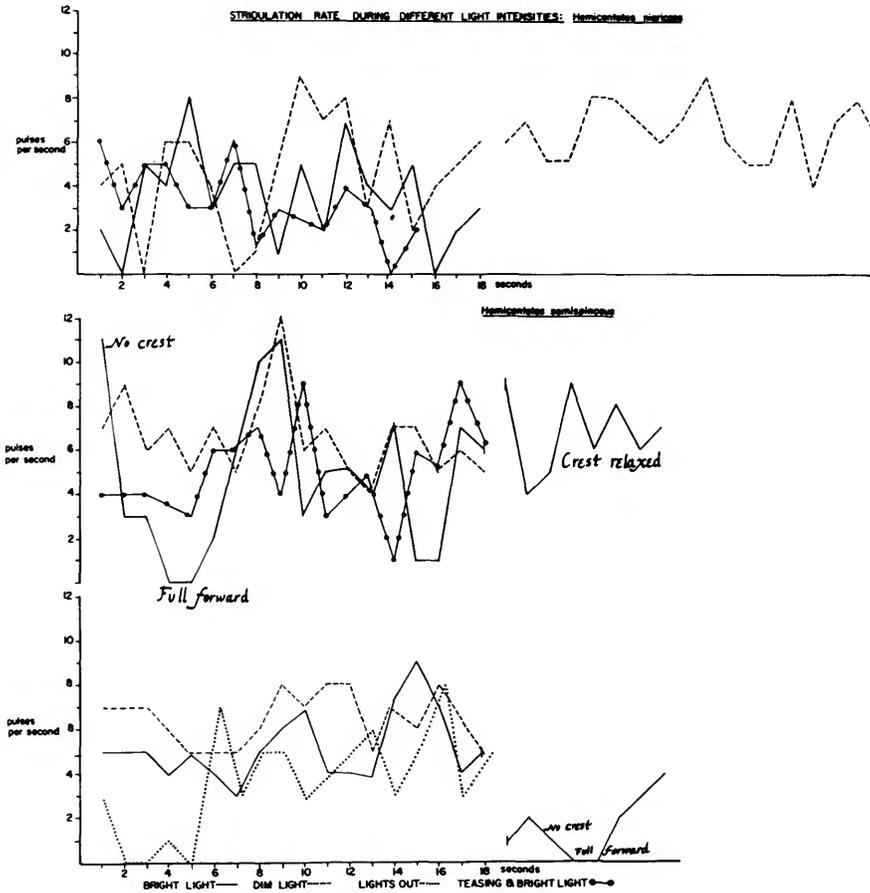


FIGURE 66.—Stridulation rate during different light intensities and associated crest position of *Hemicentetes semispinosus*. Note that during dim light, stridulation is relatively stable, about 5 to 8 pulses per second; during bright light and teasing, rates are highly erratic from 0 to 11 per second. In these and other records, full forward crest is frequently associated with bright light. "Lights off" is frequently associated with slower stridulation but relaxed crest. Each set is a consecutive series, that is, stridulation was recorded with dim light immediately followed by bright light; teasing occurred during bright light. Lights out followed bright light.

Each line of data begins at the start of the new light condition. The order of administering the stimuli was: dim light, bright light, no light, teasing and bright light.

The upper set of *H. semispinosus* data represents the stridulation rate of the same animal. The lower set of data pertains to a second animal. All the data under *H. nigriceps* are from the same animal.

Crest condition of *H. semispinosus*, upper set of 3 lines:  
 Dim light: No crest  
 Bright light: 0-3.5 sec. no crest  
 3.6 sec. 18 full forward crest.

The break in the line represents an omission of 1.1 seconds. The remainder of stridulation is associated with no crest. Teasing and bright light—full crest, not forward. (Comment during observations and recording: "very docile.")

*H. semispinosus*, lower set of 3 lines:  
 Dim light: No crest erection

Bright light: No crest erection until stridulation rate dropped to zero; just as stridulation stopped full forward crest. Break in the line omits 3 seconds.

*H. nigriceps*:  
 Dim light: Full crest not forward  
 Break in the line omits 15 seconds; entire remaining rate associated with full crest, not forward. Note that stridulation rate tends to stabilize with habituation. Bright lights: full forward crest, belly flat on the substrate.  
 Teasing and bright light: full forward crest.

TABLE 11.—Degree of crest erection by *H. nigriceps* as a function of sound input

Preceding Playback	Immediately Following Playback			
	None	Half	Full	Forward
None	—	3	—	—
Half	—	—	6	1
Full	—	—	—	3
Forward	—	—	—	—

finally initiates flight. If an animal is grasped, the pulses are rapid, loud, and repetitive.

The general conclusions from the light experiments and the sound playback experiments were as follows: (1) An unspecific change in the background stimulation, such as change in light intensity or change in sound input even if it be stridulation, will produce a general arousal in the animal. This arousal is manifest by the degree of spinal and crest erection. (2) One cannot predict what the subject will do next, but one can say that all playback experiments would be profoundly influenced by the degree of arousal exhibited by the receiving animal. (3) Hence, any standardization in playback experiments would necessitate a standardization of the degree of arousal displayed on the part of the receiving animal. (4) One of the better methods of determining arousal was to note the degree of crest erection shown by the receiving animal prior to playback.

Stridulation occurs during a wide range of activities. Low intermittent stridulation generally occurs when the animal is active and doing a variety of activities but not exhibiting strong offensive-defensive or escape reactions. Upon being presented with a sudden change in background stimulation, the animal will begin to show offensive and defensive behaviors with the preliminaries being strong crest and body spine erection. At this time, stridulation may pass through a period of being loud and rapid, then quiet, and then loud and rapid, and finally waning as the animal's degree of arousal wanes. Hence, there is only a restricted correlation between the degree of arousal shown by the animal and the quality of the stridulation. The degree of defensive arousal shown by the animal is in part a function of rather unspecific stimulus inputs. An exception to the preceding generalization is the profound

arousal and active offensive behavior demonstrated by an animal when presented with the odor of a predator such as *Galidia* or *Fossa* (see p. 94).

The answer to the original question: "Is there a correlation between degree of spinal erection and stridulation?" can best be answered by saying that *Hemicentetes* stridulates over a wide range of motivational states. The degree of crest erection is not necessarily an indicator of the quality of stridulation being produced. Stridulation may be produced whether or not the crest is erect, whether or not the animal is crouched or high on its forelegs, whether or not the animal is exhibiting active offensive or defensive behaviors. The only necessary correlation between stridulation and spinal erection is that the middorsal line of quills be erect when stridulation is occurring. Further, the form of the stridulation whether it is soft and intermittent or loud and rapid is in part a function of arousal but not absolutely correlated with any degree of crest erection. Rather it is correlated with the degree of stimulus contrast that the animal has just received. Full forward crest position was most frequently associated with a halt in stridulation when *Hemicentetes* responded to the bright light stimulus. "Lights out" also halted stridulation but the crest usually relaxed from its former position. Stimulus contrast which leads to an elevation in the arousal state but not an elevation to the tertiary or quaternary states (i.e., defensive-offensive) is liable to involve the production of loud stridulation. Low intermittent stridulation is more liable to occur when the animal has not experienced any drastic change in background stimulation but is going about its activities with no profound alteration in autonomic activity.

## THE PLAYBACK EXPERIMENTS<sup>9</sup>

### Introduction

Considering the preceding information, the following points are cogent to the design of playback experiments: (1) The initial state of the receiving animal is important. Arousal to the point of exhibiting flight, avoidance, approach, or offensive and defensive systems of behavior including crest erection, is in part unspecific when the stimulus is considered, and all of

<sup>9</sup> An outline of playback techniques is discussed in Appendix H.

these arousal forms may be shown to a wide variety of changes in the stimulus field including a shift in the intensity of the stridulation which is being played back to the animal. Thus, (2) the selection of the type of stridulation is important if we know the arousal state of the recipient; however, the state of arousal in the receiving individual could be estimated only imperfectly. (3) In nature, the stridulation signal constantly varies in output. Stridulation amplitude and repetition rate can be grossly correlated with the arousal state and activities of the presumptive sending animal. (4) During playback care must be exercised not to habituate the presumptive recipient to the signal (see Figure 67).

**Preliminary Tests**

The following preliminary tests were set up for an initial analysis of the behavior of *Hemicentetes nigriceps* and *H. semispinosus* to playback stridulation. A loudspeaker was placed in an arena which was inhabited by an established group. For example, two families of *Hemicentetes nigriceps*, a female and four babies, and a female and two babies were each established in a 4x4 foot arena. (This will be designated as the "small arena.") A further example would be the *Hemicentetes semispinosus* family in a study cage 18x4 feet. In these established cages, the animals were allowed to move freely and when they were in the vicinity of the speaker or feeding near the speaker, an observer signaled a second man who played back a known signal to the animals. Tape loops were prepared of several types of stridulation including record-

ings of (1) an animal moving about in a sound insulated box with the microphone held within an inch of its stridulating organ, (2) an animal which was hand held in front of the microphone while producing rapid, loud stridulation, and (3) artificial stroking of the stridulating quills. Control sounds were used including (1) background noise of the recording and (2) the sound of rustling leaves. In order to sample the responses of animals according to their age, females with young were chosen for *H. nigriceps* as indicated in the preceding paragraphs, and for *H. semispinosus* a family of five adults and four juveniles were tested.

The results of our preliminary playback indicated considerable variability in response; however, if we consider only the responses to the first presentation in a given test series to a designated individual, then the following results were obtained:

Eight *H. nigriceps* received 24 stimulus presentations. Twenty-one presentations of loud stridulation were played back to the eight subjects. Ten animals avoided the loudspeaker or fled. In seven tests the animals stayed in the vicinity of the speaker exhibiting varying degrees of crest erection. In three cases the animals approached the speaker. Three presentations of low stridulation were offered which resulted in three responses which involved remaining in the vicinity of the speaker with little or some crest erection. Four presentations were made of the control stimulus which evoked no responses.

Five adult and four juvenile *H. semispinosus* were subjected to 15 playbacks. There were six presentations of loud rapid stridulation which resulted in six avoidance or flight responses to the loudspeaker. There were nine presentations of low intermittent stridulation plus the hiss sound which were made during a male courtship. These nine playbacks resulted in five approaches to the speaker, one stay in the same position, and three avoidance or flight responses.

An interpretation of the above results is somewhat difficult but they indicated the possibility that stridulation contains the following information: (1) It indicates the position of another *Hemicentetes*; (2) it indicates the mood of the sender, that is, either the sender is greatly excited or not greatly aroused, but active. Thus, the receiving animal is disposed to approach, ignore, or avoid, depending on its own motivational state.

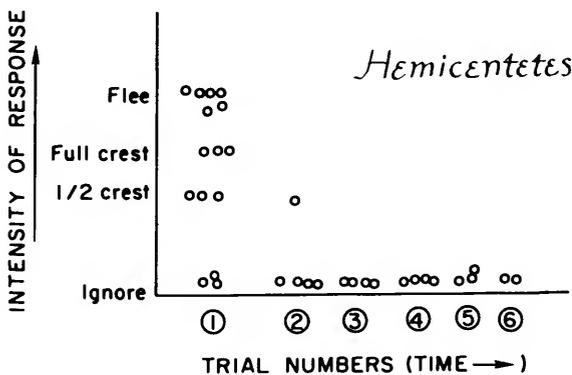


FIGURE 67.—Habituation by *Hemicentetes* to the same stimulus input presented on consecutive playbacks.

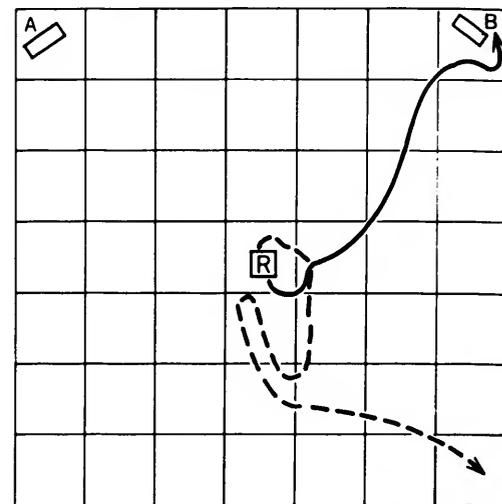
### The Orientation Test

An experiment was conducted with a series of infants during their phase of attachment to the female. We endeavored to test if the mother's stridulation served in any way to coordinate their movements and serve as an orientation cue, since stridulation could indicate the position of the mother to the infants. In order to test this hypothesis, we used families of *Hemicentetes semispinosus*.

An arena was set up measuring 7×7 feet. The floor of the arena was divided into 49 squares, 1×1 foot. Observations were carried out in darkness during the early part of the evening utilizing an infrared viewer. Either one or two speakers were involved. If we employed two speakers, they were placed in diagonally adjacent corners; when utilizing one speaker, we placed it in one of the four corners of the arena. The position of the speakers was changed after each trial. An animal was tested in the arena only once in a given evening and given only one test per recorded sound type. A variety of preliminary trials were run including tests where the animal was released in the center of the arena from a small box and permitted to wander about during 60 seconds of playback.

The young showed no special interest during playback and only occasionally went to a speaker producing stridulation sounds. We detected some tendency to approach the speaker when the playback ceased; therefore, we established the following delayed response test: A young infant was placed in a box in the center square of the grid. By means of a piece of string, the box was lifted only after the infant had been subjected to playback of either stridulation or control sound for an interval of time varying from 15 to 30 seconds. No more than two passes of the same tape were permitted to a given individual, thus avoiding the habituation phenomenon. Then, the animal's movements could be traced on a sheet of paper by referring to the square of the grid to which it moved upon being released at the cessation of playback (see Figure 68). Only one playback speaker was involved in this test. Thus, the inference was that the animal would be attracted to the corner from which the stridulation had emanated. After each test with an individual, the position of the speaker was rotated so that on all subsequent tests, the speaker was in a location different from that of the preceding test.

The age of the subjects ranged from 9 to 19 days. Twenty-four individuals were tested in a series of 30



--- → Response to A-control sound  
 ——— → Response to B-stridulation  
 III/13/67

FIGURE 68.—Example of movement patterns displayed by *Hemicentetes semispinosus* juveniles to playback in an arena. Playback of control sound results in avoidance upon release from the center square of the grid; however, playback of stridulation leads to approach toward the loudspeaker upon the release of the responding animal.

trials. There were four replicates of a test series or, if we consider the age of the subject to be a variable, there was one replicate at an age of 15 days (see Table 12). Of the 30 playbacks, 19 involved the playback of stridulation; the remaining 11 playbacks were controls. The control sounds were the background noise of the tape. Of the 19 playbacks of stridulation,

TABLE 12.—Summary of delayed response playbacks to *H. semispinosus*

Conditions	Response		No Response	Total
	Approach	Avoid		
Experimental stridulation	15	1	3	19
Control (Background noise)	—	9	2	11
Total	15	10	5	30

15 of the 19 infants made a direct approach to the corner containing the speaker. One showed direct avoidance of the speaker and in three of the trials the infant's movements were not conclusively oriented with respect to the speaker. In the control series, nine avoidances and two undetermined responses were recorded. The results of this delayed-response test conclusively demonstrated that (1) in the presence of stridulation an infant explores with little reference toward the loudspeaker aside from an occasional approach; (2) at the cessation of stridulation playback, an infant will orientate to and move towards the previous source of stridulation.

A test was run using the same arena with two loudspeakers to determine if there were any preference for the mother's stridulation over the stridulation of another female. Our results indicate that, upon cessation of stridulation, the animals would orientate to the location of the stridulation last heard. If stridulation were played back from the upper right corner in the first series followed by stridulation in the lower left corner in the second series, then when stridulation ceased the infant would move towards the source of the last heard stridulation regardless of whether it was the mother's stridulation or not.

### THE ROLE OF THE MOTHER'S STRIDULATION IN NATURE

Experiments were run employing the large outdoor enclosure with the overhead platforms (see Figure 4). In this large enclosure, a female with a group of infants would be established in a nest box and fed and observed for some days. The floor of the enclosure was divided into a grid so that the exact location of the female and her young, when foraging together, could be noted. As previously indicated in the section on *H. semispinosus*, this animal will forage during the day; therefore, most of our observations were made between 1100 and 1400 hours to coincide with the midday foraging activity.

We know from our ethological studies and long periods of observation that linear following, so typical of *Tenrec ecaudatus*, is not displayed by the infants of *Hemicentetes*. Rather, the young remain in the vicinity of a female while she forages and drift with her in a loose formation, but young animals may be as much as 9 to 10 feet away from a female during this activity. Furthermore, our observations indicated that as the

young mature the female has a decreasing influence on their position in space and loose clusters of juveniles may be formed rather than a tendency to orientate toward the mother herself. Apparently the young learn routes to the feeding area and back to the nest and learn specific feeding loci by associating with the female over a period of approximately 4 days. Thus, the learning period and the phenomenon of attention to the mother only persists in this species for some 4 days whereupon they begin to forage in a more and more independent fashion (see p. 97).

Thus, with the grid pattern in the large outdoor enclosure, it was possible to plot the position and estimate the distance of the female to the nearest young or the distance for a given young to the nearest sibling. These inter-individual distances were plotted as a function of the distance of a given individual from the nest.

The following tests were run utilizing young of an equivalent age: (1) The female with an intact stridulating organ was observed and the positions of the young with respect to her and the nest box plotted. (2) The female was caught, her stridulating organ glued or cut, and the subsequent deployment of the young with respect to the mother was noted. The results of these experiments are included in Figures 69-72. Clearly, the young stay near the female and/or each other, if the female's stridulating organ is immobilized. Thus, they depend on other cues such as the odor of the mother or the sound she makes while foraging; these secondary cues apparently preclude foraging at the distance of 9 to 10 feet as in the case when the mother's stridulating organ is intact.

A second test was run whereby the mother, during her foraging, was induced to enter a small box with worms in it and the box itself was controlled by a system of strings to the overhead platform. Thus, the door on the box could be closed and the box itself lifted and shifted overhead to a new position above the arena. The movements of the young and their deployment in space could then be studied as a function of whether the mother who was shifted in the box had an intact stridulating organ or a glued stridulating organ. The results are presented in Figure 73 and indicate that a displaced female with an intact organ will induce the young to drift gradually in the outdoor enclosure to the vicinity below her new locus.

A preliminary experiment approached the problem of sound deprivation when the infants were very young. The stridulating organ of one female *Hemicentetes*

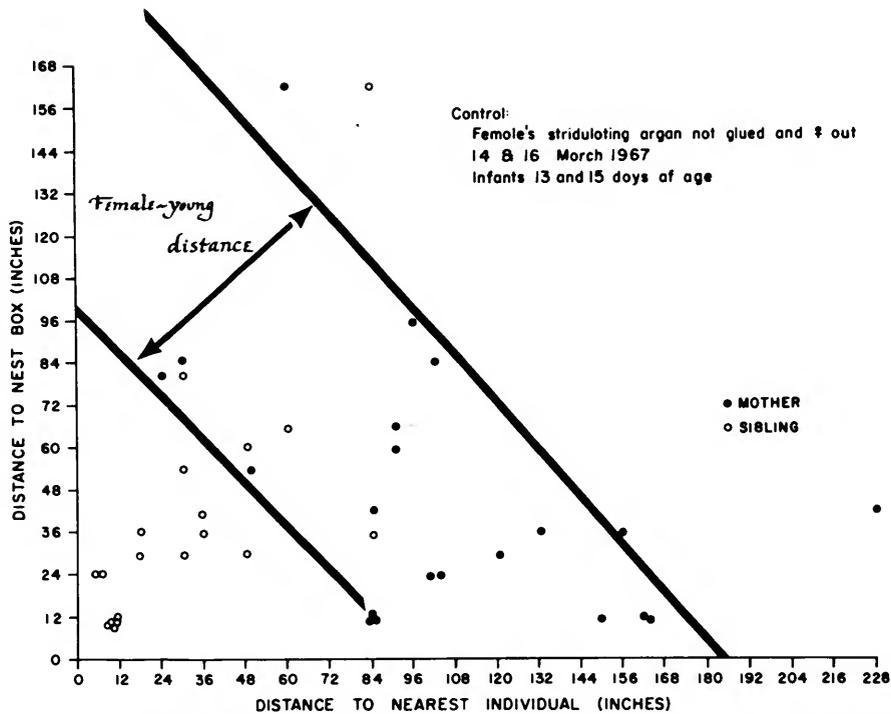


FIGURE 69.—Relative clustering tendencies by *Hemicentetes semispinosus* juveniles when foraging with their mother. The mother's stridulating organ is active. Glue was placed on the back but none interfered with the stridulating organ. As the animals move farther from the nest site, the intersibling distance and distance from the mother increases to reach a maximum of approximately 180 inches.

*semispinosus* was cut when her young were 3 days of age. At 10 days of age the infants were seen wandering over the entire outdoor enclosure and showing no signs of being able to locate their mother. At this age they ordinarily would be clustered near the female or each other and within a few feet of the nest box.

We conclude from the preceding experimental series with *H. semispinosus* that stridulation serves in the female-young unit as an identifier of the female's locus. The unanswered question is whether a shift in intensity of the female's stridulation influences the behavior of the young. We have on numerous occasions observed in the large outdoor enclosure that the female upon being frightened will hesitate, then begin to stridulate rapidly and flee. The youngsters in her vicinity will generally assume upright crests, attentiveness, and flee with her to the nest box. The flight is not uniform and

may take over a minute and a half before all young have moved to the nest. We are unable to determine whether the young flee because they are alerted and frightened by the same stimulus that acted on the female or whether, indeed, they are further activated by the change in intensity of her stridulation, or they are induced to flee because of the sounds the female makes as she crashes through the underbrush racing toward the nest. Probably all these things have an effect on the general arousal of the young and potentiate the flight response and serve in some way to direct it. The experimental resolution of this problem remains incomplete.

#### OTHER FUNCTIONS OF STRIDULATION

There are other possible functions for stridulation, some of which we have investigated and others which we

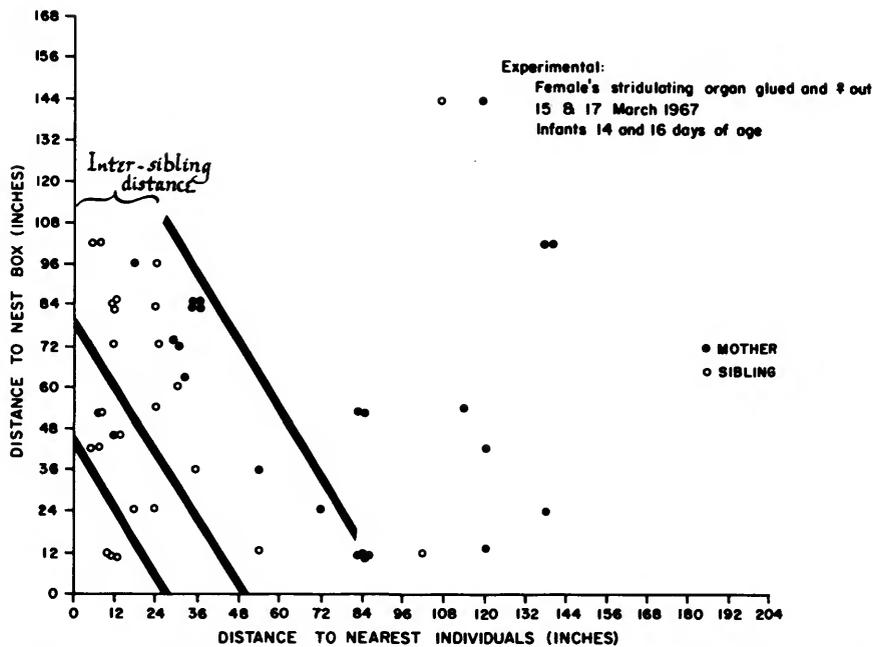


FIGURE 70.—Clustering tendencies by *Hemicentetes semispinosus* juveniles to their mother when the mother's stridulating organ is immobilized. As the animals move farther from the nest box, the inter-sibling distance remains clumped and, as the mother moves farther from the nest box, there is little relationship maintained by the young with respect to the mother's position.

have only partially attempted to clarify. It had occurred to us that stridulation might be involved in echo-location. Gould's work in 1965 indicated that *H. semispinosus* can orientate in the absence of visual cues and locate objects in space. The animal can accomplish this when its spines have been clipped, therefore it would seem that stridulation is not entirely essential to echo-location and the animal seems to do rather well with tongue clicks.

Nevertheless, the possibility that stridulation might be involved in echo-location was not dismissed. A predator approaching *Hemicentetes* from behind might conceivably distort the sound field to the rear of the animal resulting in an increased echo return of the stridulation pulses, thus warning the animal of an object behind it. *Hemicentetes* was tested in an arena by stimulating it with predator odor to exhibit the full offensive and defensive reaction. Then various objects on the end of a stick were placed behind it and the turning frequency of the animal measured either

with or without an object behind it. No special alteration in its turning tendency could be noted.

The possibility that stridulation serves as an anti-predator signal was considered. Since the predator tests indicate that the detachable, barbed quills are a considerable deterrent to predation, although not a complete guarantee of freedom from the activities of predators, the boldly marked patterns of *H. nigriceps* and *H. semispinosus* are undoubtedly warning colors which serve as an antipredator mechanism. We conducted some playback experiments with one *Galidia* out of our group of three which would consistently kill *Hemicentetes* and found that the signal of stridulation could serve to orientate the *Galidia* to the *Hemicentetes* rather than warn it away. This does not exclude the possibility that stridulation could be a warning signal to predators, since it may be effective with those predators which have had an adverse experience with the *Hemicentetes*. Certainly the sound of stridulation is not a deterrent to a predator that has

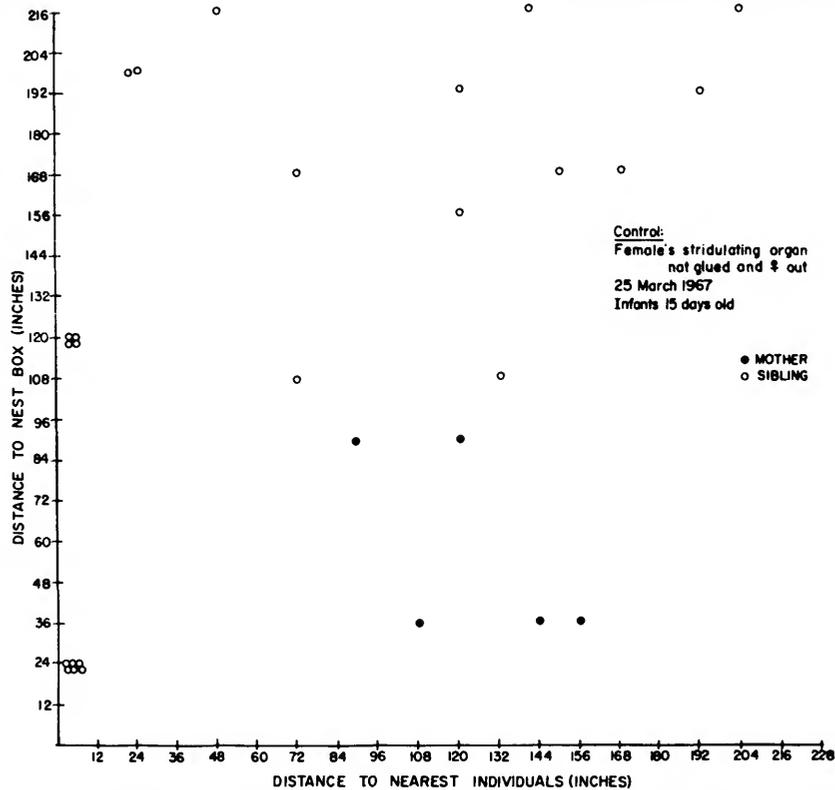


FIGURE 71.—Control: This litter was a different litter from those described in Figure 69 and 70. The mother was held in the transfer box on the ground so that her position could be controlled.

learned a technique to kill *Hemicentetes* (see Figure 13).

We considered the possibility that stridulation may be a mechanism for attracting earthworms to the surface of the ground. This would seem a bit far fetched when one considers the position of the organ and dispersion of the sound about the animal; nevertheless, we did play back the sound of stridulation to two species of Madagascar earthworms on several occasions employing a continuous playback loop. We could discern no tendency on the part of the earthworms to come to the surface.

Finally, we should consider once again the situation in *Tenrec ecaudatus* juveniles where a stridulating sound is produced. Our experiments with *Tenrec ecaudatus* were not extensive and our results were somewhat inconclusive. It may well be that stridula-

tion in *Tenrec ecaudatus* serves to coordinate the movements of juveniles during the following of the female; however, our evidence indicates that stridulation is associated with high levels of excitement and not with low levels, as exemplified by peaceful foraging. This would appear to rule out a similar function analogous to that in *Hemicentetes semispinosus* and *H. nigriceps*. Therefore, we are forced to consider the possibility that stridulation in *Tenrec ecaudatus* juveniles may have been selected for because it mimics stridulation in *Hemicentetes*.

Consider the following possibility. Stridulation may have been evolved in *Hemicentetes* as a means of communicating the position of one adult to another and may be involved in the location of mates but is principally involved in the following and clustering activity of the infant *Hemicentetes* during the initial

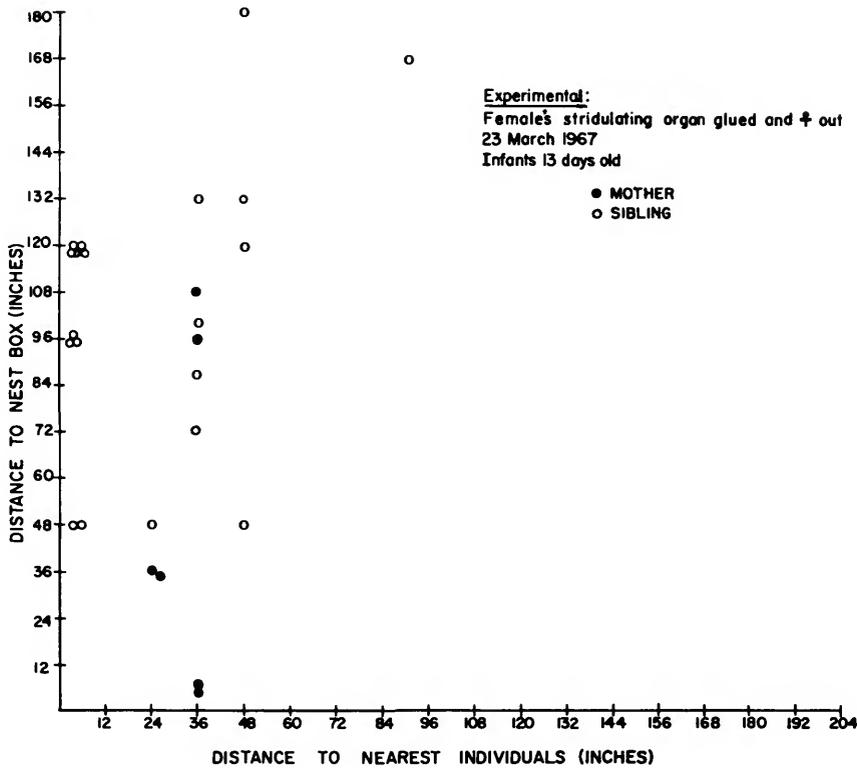
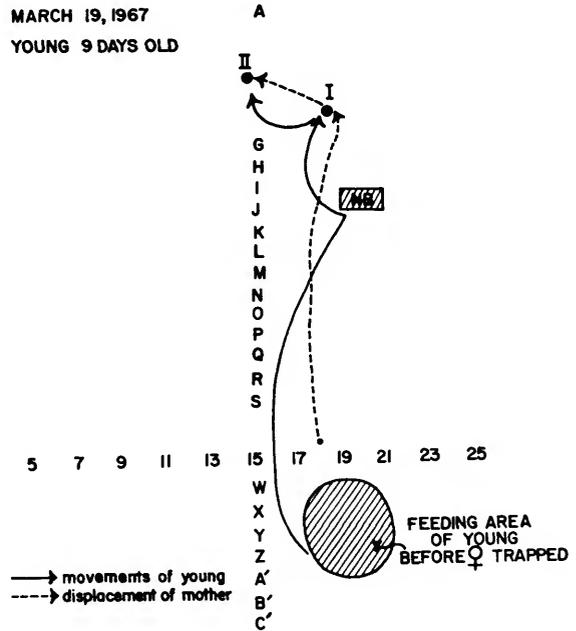


FIGURE 72.—Experimental: Note clustering when stridulating organ was glued. Mother was free-ranging (not in the transfer box).

foraging phase with the mother. It may secondarily serve as a warning signal to predators. Thus, the color and spinescence of the juvenile *Tenrec* might be a partial mimicry of *Hemicentetes* and further set the stage for selection favoring stridulation on the part of *Tenrec ecaudatus* young when menaced by a predator. The stridulation would enhance further the mimicry between juvenile *Tenrec ecaudatus* and adult or infant *Hemicentetes*. This final question may never be completely resolved until further studies on the role of stridulation in *Tenrec ecaudatus* have been undertaken.

FIGURE 73.—Response of *Hemicentetes semispinosus* juvenile to mother who has been displaced in an open field foraging situation. As can be seen, upon displacement of the mother to two different loci, the young at first return to the nest and then proceed to move in accordance with her new position.



## Comparisons and Extensions

### EVOLUTIONARY TRENDS AMONG THE TENRECIDAE

If we assume that the ancestral tenrecid was small in size and similar to *Geogale*, then we could imagine an animal with a hair-covered body; a naked tail approximately 75 to 100 percent of the body length; perhaps an imperfect homeotherm; cryptic in its behavior; and an insect-eater with some ability to forage on the forest floor as well as climb. While occupying an environment with little competition, speciation and adaptive radiation would take place whenever sufficient geographical isolation had been achieved. The initial modifications in morphology and behavior would include: (1) differentiation into small terrestrial surface foragers; that is, a head and body length less than 120 mm; and (2) evolution into forms that were more fossorially or aquatically adapted. Within the Oryzoricinae the upper extremes in size would then occur in those groups which had adapted to the least conspicuous mode of habitat utilization, i.e., the aquatic and fossorial forms; and even today, these are the forms that show the greatest head and body length (130 to 170 mm).

Aside from structural modification to enable the animals to utilize the extremes of the environment, there would be little modification of the basic behavioral repertoire. The greatest departure in the evolution of the tenrecs occurred when adaptive radiation began to give rise to the subfamily Tenrecinae. The general trend in the evolution of this group is toward a larger body size and, as a result, a loss of inconspicuousness and the development of rather elaborate antipredator behavior. The evolution of the subfamily Tenrecinae further involved the loss of the tail.

Two discernible foraging types evolved including (1) a terrestrial and semi-arboreal form in the deliberate climbers, *Setifer* and *Echinops*, and (2) the almost completely terrestrial genera with an increased digging ability and modification of the forepaws including *Hemicentetes* and *Tenrec*. Both *Setifer* and *Echinops*,

although feeding on invertebrates, tended to become generalized omnivores as did *Tenrec ecaudatus*. On the other hand, *Hemicentetes* became much more specialized in its feeding techniques until it had specialized as an earthworm feeder with modifications in its skull and tooth structure.

The subfamily Tenrecinae, in the course of its evolution, early acquired a spinescent coat. It would appear that the acquisition of spines in *Echinops*, *Setifer*, and *Hemicentetes* has resulted in profound modifications of their antipredator behavior and offensive-defensive behavior syndrome. For example, *Echinops* and *Setifer* are able to roll the brow forward and buck with the head or to roll completely into an impregnable spiny ball. *Hemicentetes* evolved barbed detachable spines and has capitalized on rolling the crest forward thus exposing a crown of spines, and by employing a rushing, bucking, and pivoting technique its spines can be driven into a predator. *Tenrec ecaudatus*, although related to *Hemicentetes* (see Borgaonkar and Gould, 1965) and still partially spinescent, has tended to lose its spines and as an antipredator device to rely more on size and speed coupled with its ability to stand and fight. The juvenile *T. ecaudatus*, however, greatly resembles *Hemicentetes*. Indeed, the resemblance including the stridulatory spines is so remarkable that one is tempted to believe that in a way *Hemicentetes* is a specialized, neotenic *Tenrec ecaudatus*.

In the course of *Hemicentetes*' evolution the striped pattern has passed from a protective color pattern, as would appear to be the case in the young *Tenrec ecaudatus*, to a warning color which is part of its antipredator syndrome. The black and white pattern of *H. nigriceps* is a very effective nocturnal warning coloration whereas the yellow and black is a more versatile warning coloration for the rainforest adapted *H. semispinosus* which is also to some extent diurnal. With the exception of the aquatic *Limnogale*, the genus *Hemicentetes* is the most specialized in its feeding habits and in its antipredator behavior.

## A COMPARISON OF BEHAVIOR CATEGORIES

It is instructive to consider the functional categories of behavior and to trace the evolutionary trends within each category for all the species of tenrecs included in this study.

The categories of "comfort movements" and "marking movements" exhibit considerable uniformity when the family is surveyed as a whole. The face-washing pattern is present in *Microgale* and is obviously a conservative pattern. It is retained in the specialized Tenrecinae within the genera *Echinops* and *Setifer*, but in the genera *Hemicentetes* and *Tenrec* this pattern is no longer present. This loss may in part be related to the fact that it is awkward for these tailless forms to sit upright in a crouch, but it is more probable that this loss is related to the specialization of the hand in *Tenrec* and *Hemicentetes* as a digging organ. The forepaw is wide, bearing stout claws, which reduces its use as a cleaning organ. Nevertheless, the propensity to use the forepaw to wipe at the face is still present in a modified form in both these genera. The ritualized wiping pattern and simultaneous stroking while sitting upright, so prominent in the other genera, has disappeared as a complex complete pattern in *Tenrec* and *Hemicentetes*.

The perineal (= cloacal) drag as a marking movement is present in all species examined. Defecation near the burrow entrance is prominent in the subfamily Tenrecinae. Digging in the substrate, then backing into it, depositing the feces, and covering them with fresh earth is unique to the genera *Hemicentetes* and *Tenrec*. In the latter genus, this behavior pattern is carried to its most ritualized form.

Foraging behavior in the Tenrecidae is rather similar. The long flexible nose is inserted in crevices and cracks and in the substrate. If an invertebrate is located, it is seized with the mouth. The use of the forepaws in prey capture is minimal. Forepaws may be used to brace or may be used to hold the prey down while it is torn apart, but aside from pinning, the forepaws are not involved in a primary prey-catching movement. In *Tenrec ecaudatus*, the forepaws may be used to pin a prey object before the bite is delivered but the mouth itself is often the primary capture organ and the forepaws are involved only secondarily. This is also true of *Hemicentetes* when it forages for earthworms.

Offensive and defensive behavior patterns, as stated

previously, have undergone great modification within the family. Biting is universal but has tended to pass out as an active pattern in *Hemicentetes*, especially with respect to interspecific defense, although it is still retained in intraspecific fighting behavior. The gape reaction which probably evolved from an intention movement to bite is present throughout all genera of the family with the exception of *Hemicentetes* where it has waned and is not shown as a display pattern.

Head bucking, pivoting on the hind legs, and stamping with the forepaws have arisen as a form of defensive behavior in the subfamily Tenrecinae. This is especially effective in the very spinescent genera where the quills on the head may be jabbed into an enemy. Such a bucking pattern is still present in *Tenrec ecaudatus* even with the lack of formidable spines on the head. Here, however, the buck is combined with the open mouth and slashing bite. Rolling into a spiny impregnable ball is a correlate of the completely spinescent dorsum with nondetachable spines which one finds in the specialized genera *Setifer* and *Echinops*.

Turning to the patterns involved in social interaction, we have seen that the contact-promoting behaviors displayed during initial, amiable encounters involve placing the nose or mouth in glandular areas on the body. These tactile configurations are quite uniform for the whole family from *Microgale* through *Tenrec ecaudatus*, and only minor variations are shown. In sexual behavior, licking the fur of the partner or nipping at the partner are common and shown throughout all genera. The neck grip is employed by all males while mounting the female. The mount in the family Tenrecidae is prolonged especially when one compares mount duration with those demonstrated by males of the genera *Suncus* and *Blarina* in the insectivore family Soricidae. The brief mounts of soricids are reminiscent of the brief mountings of many of the common cricetine and murine rodents. The long mount in tenrecids is reminiscent of the long mount in the genus *Dipodomys* of the heteromyid rodents (Eisenberg, 1963).

Nest-building patterns are very similar for all species of the tenrecids. The nest defense syndrome involves elements of the defensive behaviors originally discussed in the preceding paragraphs. The *Microgales* typically gape and attempt to bite. *Setifer* and *Echinops* produce "putt-putt" sounds and attempt to buck and drive spines into the offender's body. *Hemicentetes* exhibits a similar pattern of "putt-putt" sounds, crunching,

## SUMMARY OF YOUNG ANIMALS' RESPONSE TO MOTHER

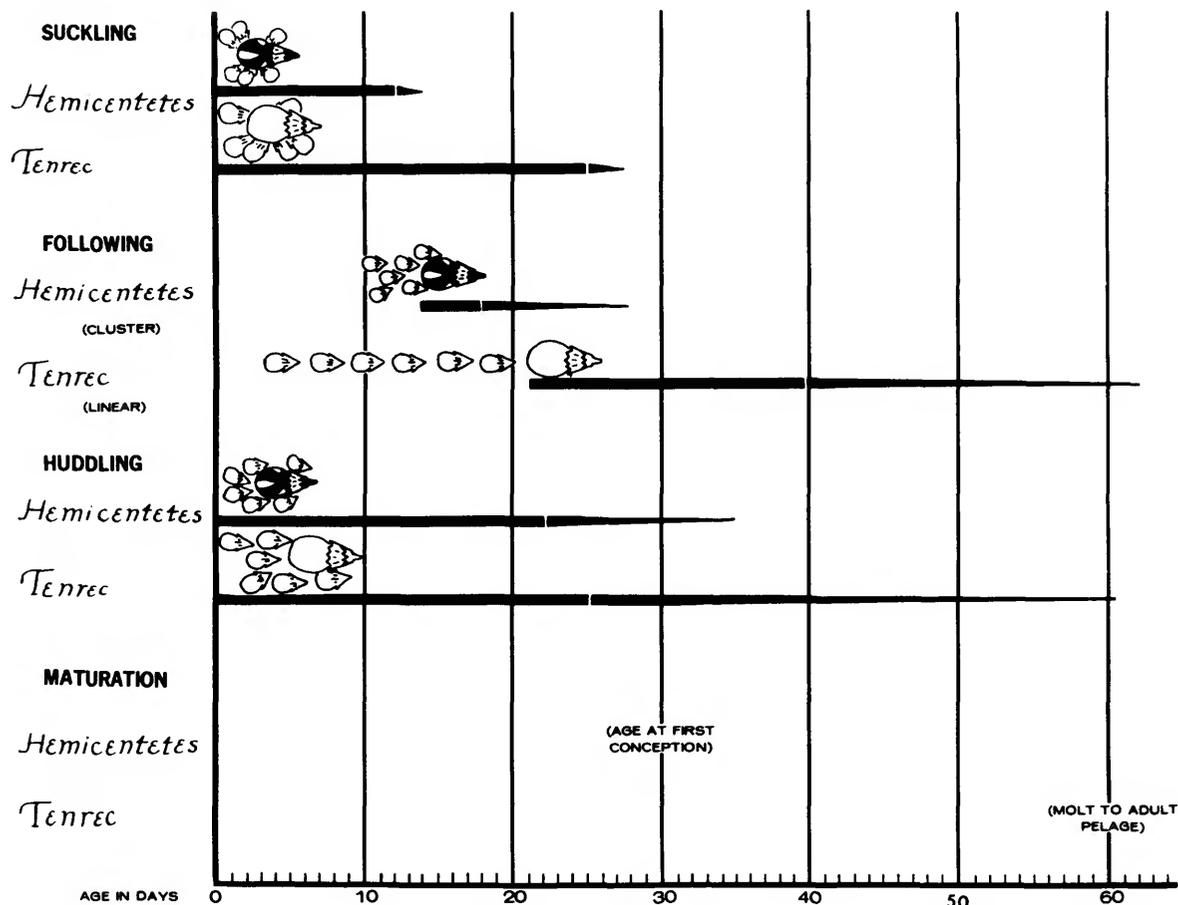


FIGURE 74.—Comparison of *Hemicentetes* and *Tenrec ecaudatus* with respect to the juvenile's response to the mother. Suckling in *Hemicentetes* is relatively shorter than is the case for *Tenrec ecaudatus*. Following persists for only a short time for *Hemicentetes* whereas it persists until 40 days for *T. ecaudatus* and then begins to wane. Strongest following response for *Hemicentetes* is only about 4 days. *Hemicentetes* maintains a cluster phenomenon with distances up to 10 feet between mother and young. *Tenrec ecaudatus* young tend to be linear in their following response. Huddling when the mother is stationary wanes earlier in *Hemicentetes* than in *Tenrec ecaudatus*.

erect crest, bucking, and stamping. *Tenrec ecaudatus* hisses, foot stamps, and with an erect crest and half open mouth attempts to bite and slash at an intruder.

The vocalizations, when one compares all species of the family Tenrecidae, exhibit remarkable uniformity. There is, first of all, a class of noisy sounds showing little harmonic structure. One set of sounds is related

to rapid inhalation and exhalation and may be referred to as the hiss and puff. This hissing is to be found in all genera studied. The very rapid "putt-putt" sound with high overtones is characteristic of *Hemicentetes*, *Setifer*, and *Echinops*. The buzz or crunch sound which again exhibits little harmonic structure is to be found in all genera studied.

TABLE 13.—*Reproduction of tenrecoid insectivores*

Species	No. of observed periods	Length of gestation period (days)	No. of Captive Litters Studied	Eyes Open (days)	Age at weaning (days)
<i>Tenrec ecaudatus</i>	3	58-64	1	9-15	25-30
<i>Hemicentetes semispinosus</i>	4	57- $\leq$ 63	10	7-9	18-25
<i>Hemicentetes nigriceps</i>	3	$\geq$ 55	5	7-8	18-25
<i>Setifer setosus</i>	2	65-69	3	9-13	15-20
<i>Echinops telfairi</i>	5	62-65	18	7-9	18-22
<i>Microgale dobsoni</i>	1	62	2	-	$<$ 24
<i>Microgale talazaci</i>	1	$\leq$ 63	2	8	-

The second class of sounds exhibits some harmonic structure with clearcut overtones. These would include the soft squeaks and the chirps or a repeated series of brief squeaks which we term a twitter. The note form in these vocalization types may be linear or may approximate chevron form as defined by Andrew (1964). In addition to these rather harmonic clear sounds, another voiced sound, showing overtones but nevertheless a great deal of noise, can be termed the grunt. This sound has been noted for *Tenrec ecaudatus*, *Hemicentetes*, and *Setifer*. At high-intensity stimulation the chirp itself may show blurred harmonic structure with a great deal of noise being introduced into the sound.

The female's response to her young is similar for all the species studied, involving licking and cleaning the young; retrieving the young by mouth transport if they stray from the nest; and drawing the young under her body employing the nose. The young are huddled over and suckled—these are of course basic mammalian patterns. The response of the young to the mother appears to be similar for all genera studied in that the young follow the mother for the first few nights on their foraging excursions. The genus *Hemicentetes* shows the most specialized mode of communication between the female and young and, in conjunction with this, the most specialized feeding habits, thus necessitating perhaps increased guidance of the young in their initial foraging trips (see Figure 74).

When the basic data concerning the reproduction of the Tenrecidae are compared in tabular form (see Table 13), we again find remarkable uniformity in duration of gestation, rapidity of development by the young, and lactation time.

In summary, then, the Tenrecidae exhibit interesting variations on a common behavioral repertoire. As stated in the introductory paragraphs, the more prominent variations are concerned with behavioral specialization for feeding and antipredator mechanisms.

#### THE INSECTIVORA: A CONSIDERATION OF EVOLUTIONARY LIMITS

The isolated condition of the Madagascan landmass permitted an extended adaptive radiation by at least four Orders of mammals which reached the island independently and enjoyed a lack of conventional competitors. The original invaders of Madagascar were conservative in their body plan, especially the insectivores and primates. The muscle systems, dentition, brains, and sense organs reflected an unspecialized morphology.

If we consider the Insectivora, the primitive ancestral form showed a triconodont dentition; undifferentiated muscle slips in the head region and arm; a lissencephalic brain; audition and olfaction as the primary sensory modalities; and a reduced eye which could process little complex, visual data. Complexity and specialization in morphology reached its climax with the evolution of *Hemicentetes* and *Tenrec*. Complexity and specialization of behavior patterns are reflected in the communication system of *Hemicentetes* and its more complex social structure. *H. semispinosus* exhibits colony formation. Colony formation generally results from the selection of a favorable denning site with respect to a convenient feeding locus. Colony formation leads to the utilization of the same denning space by several females, probably related by descent, and a male. Such a related colony may not persist

through the adverse winter season and/or a prolonged period of torpor.

The communication system evolved by *Hemicentetes* permits indication of position by an individual (generally the mother to her infant). This system evolved from simple spinal erection and the rubbing together produced as a concomitant of autonomic arousal and was enhanced by selection favoring spinescence rather than hairs alone. Originally, it was probably a warning signal to a predator and secondarily it had the possibility of being a warning signal to associated individuals. It was potentially an indicator of arousal in response to a change in the ambient conditions. Later, as selection for enhancement of the signal promoted the evolution of stridulating quills, a concomitant selection favored the lowering of the threshold for stridulation; and, instead of being a warning signal alone, it became a signal indicating the position of an adult, generally the mother. She produced the sound whenever she exhibited general arousal or activity. The primary selective advantage for the enhancement of this signal and the lowering of the threshold probably was increased survivorship of the offspring of a female which produced a more audible signal with a lower threshold. The young probably survived better because they were able to learn the loci of foodstuffs and learn easily the route to the feeding area and back to the nest. The information conveyed in the signal is unspecific; nevertheless, it serves as an indicator to the young of the position of the female.

The time when stridulation is of crucial importance in the life of the animal is short, since the female-young feeding systems may last as little as 4 days; however, complex female-young interaction systems may be quite intricate over an equally short space of time in other insectivores. For example, the reader is referred to the references by Herter (1957) and Dryden (1968) concerning the caravan formation in *Crocidura* and *Suncus*. Here a female, upon emitting a specific twittering sound, causes the young to grasp her tail or one another's tail to form a continuous chain so that the mother, as she flees from the nest, can guide them to a new nesting site. Furthermore, the following response exhibited by a number of primitive mammals involves specific selection for capacities on the part of the young to respond to specific inputs from the female's body itself. This following response has evolved repeatedly and must be of extreme importance to the survivorship of the young even though it persists only a brief time.

The simple following response which one sees in *Tenrec ecaudatus* and to a lesser extent in *Setifer setosus* or *Echinops telfairi* is not enough to insure efficient foraging in the case of *Hemicentetes* when one considers its increased specialization in feeding habits. In *Hemicentetes*, eye size reduction reaches its maximum and the snout is in the ground as the animal probes for worms. Hence, if the young are to be effective in feeding, they cannot smell the mother nor can they see her; thus, the sound produced by the mother provides far greater efficiency in permitting the young to maintain contact with her while still foraging on their own. The communication system and colony formation exemplified by *Hemicentetes semispinosus* are a current limit in social complexity and communication for the Order Insectivora.

It is instructive to look at the evolutionary limits reached by other Orders of mammals which have undergone adaptive radiation on Madagascar. As in the case of the tenrecs, morphological diversity has been achieved in other Madagascar mammals which started from a conservative morphological framework. For example, in the Lemuridae, the original progenitor of the lemurs on Madagascar was probably a small nocturnal form; probably capable of estivation, and exhibiting a slightly unstable thermoregulation pattern. Through adaptive radiation diverse forms were developed including large terrestrial browsing primates, the Megadapidae, diurnal leafeaters such as *Indri*, and diurnal frugivores such as *Lemur* and *Propithecus*. Diurnality and a departure from an insect diet to a fruit or leaf diet was concomitant with the evolution of complex social organizations that included adults of both sexes in the case of the genus *Lemur*, or family groups as in the case of *Indri* (see Petter, 1962, and Jolly, 1967). Specialization in foraging habits and concomitant specialization in social structure characterizes the evolution of primates in the Old and New World. Thus, as a given line evolves away from the conservative stem form and by adaptive radiation develops new feeding mechanisms and diurnality, the trend leads inevitably to specialization in the form of social organization and the communication systems.

The Carnivora arrived in several independent invasions on Madagascar and have undergone less dramatic radiation but one can see again the same specializations for occupancy of feeding niches, so that a large arboreal cat-like form has evolved from primitive viverrid stock

and resulted in the fossa, *Cryptoprocta ferox*, of today. In a similar manner, a nocturnal digitigrade fox-like species, *Fossa fossa*, has developed on Madagascar, in marked contrast to the arboreal and diurnal forms such as *Galidia elegans* and *Mungotictus lineatus*.

If a mammalian order on Madagascar has had a long enough evolutionary history and its evolution was initiated with an unspecialized stem form possessing a conservative body plan; then, through natural selection, adaptive radiation has resulted in a rather uniform occupancy of the feeding niches available. Indeed, when the Madagascan forms are compared with continental mammals, equivalent feeding niches are filled, thus typifying complementarity as outlined by Darlington (1957). The adaptive radiation in the absence of conventional competition has allowed a rather conservative order, the Insectivora, to achieve surprising levels of social complexity.

### CONFIGURATIONS IN SPACE AND TIME

The study of the tenrecs brings up several points of interest to students of mammalian behavior and evolution. When considering the evolution of mammalian behavior, one must consider the sense organs and the "inner world" of the subject. For the tenrecs, the sense of smell, the sense of sound perception, and the sense of touch are of primary importance. We have demonstrated how, in the absence of discrete visual perception, one genus of tenrec, *Hemicentetes*, has elaborated auditory communication as a means of group integration.

To appreciate the significance of many behavior patterns, one must consider again the tempo of the life cycle. Tenrecs are small mammals with a very rapid growth which achieve sexual maturity within a short time after birth. They can pass through a life cycle in a matter of months with generations renewing themselves on an annual basis. To the student of large mammals, it is a serious handicap to have to adjust one's time sense to the scale imposed by such small mammals as tenrecs. As outlined in the previous section, a 4-day period where the female is guiding the young to and from the feeding areas may be of vital importance in providing the selective impetus for the evolution of a complex communication system such as the stridulating organ of *Hemicentetes*.

In a similar manner, configurations of small mammals in space may be overlooked as trivial because their time of occurrence is brief. When, for example, a

novel stimulus, such as an alien individual, is introduced to a colony of *Hemicentetes*, the animals orientate toward the stranger and form a semicircle or circle about him; thus, giving a configuration that is very similar to the orientation response of herds of ungulates to, for example, a newcomer. At other times, if the stimulus object is of a sufficiently strong valence and a mother tenrec is accompanied by her young, the mother may extend toward the stimulus while the young hang back. This again is analogous to the type of configuration one sees in an encounter situation with many of the social ungulates. For example, with elephants, an old female will move toward an alien stimulus such as a man, and the younger females and infants hang back (see Figure 75). Furthermore, as pointed out under the

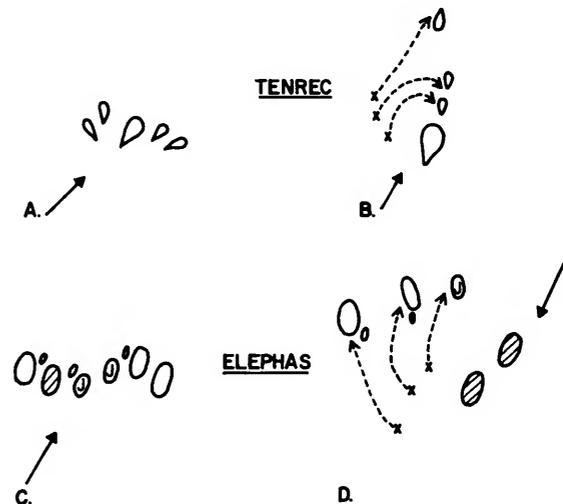


FIGURE 75.—Comparison of spatial configurations during response to alien stimuli by *Tenrec ecaudatus* and *Elephas maximus*: A, Orientation of female Tenrec and four young to a mildly disturbing stimulus indicated by arrow. The mother and young faced together the stimulus source with the young somewhat behind the mother. B, Input of a stronger stimulus intensity may result in the female holding her position whereas the young may flee or move to a position behind her. C, Configuration of *Elephas maximus* female herd to a mildly disturbing stimulus. Cross-hatching indicates oldest adult female. Adults tend to range in a line somewhat oriented toward the stimulus source. Young remain to the side or fall back. Juveniles and young tend to be towards the center. D, A stronger stimulus intensity indicated by the arrow results in an orderly dispersal of the group with the juveniles and mothers with infants leaving first and a male if present or older female holding position with respect to the stimulus source. In all cases a very intense stimulus results in flight by the entire group.



FIGURE 76.—Nuclear herd of *Elephas maximus*. Compare the formation with that in Figure 77. An old female leads a group of her daughters with their offspring. Such a cohesive social grouping displayed by the elephant is nevertheless based on a family group related by descent.

discussion of antipredator behavior in *Hemicentetes* and *Tenrec ecaudatus*, if a predator odor is wafted toward a group consisting of a mother and her juveniles, they will orientate toward the source and may exhibit attack behavior in unison.

Again, consider the similar behavior patterns that have been noted on the part of elephants and large ungulates with respect to predators. These configurations in space displayed by the tenrecs bear a remarkable similarity to those shown by larger mammals and yet, because they occur briefly and are seldom observed, they tend to be neglected. While much is made of the mobbing behavior or concerted group attacks on predators by primates, such behavior on the part of tenrecs would be brushed over: (1) because it is not known to occur or (2) because it occurs for only a few minutes and then is not repeated.

Let us consider again the configuration shown when a female forages with her infants. In *Tenrec ecaudatus*

the female leads a long chain of youngsters following behind her in regular order. Compare this spatial configuration with that shown by an elephant herd on the march (see Figures 76 and 77) or consider the subtle clustering of the young *Hemicentetes* remaining approximately 9 feet from the female within hearing range of her stridulating organ. The configuration here indicates a cohesion which would never be guessed at if the existence of the stridulating signal were not known.

Given the sensory limitations of the Tenrecidae and the minor role of visual displays in their interactions, the basic behavioral repertoire of the tenrecs is common to many other mammalian Orders and, indeed, forms the fundament of behavior patterns from which most mammalian patterns are derived. The behavior patterns of more highly evolved or specialized mammals do not differ markedly from the behavior patterns of primitive or morphologically conservative

mammals such as the tenrecs. Rather, more highly evolved mammals are larger, have larger brains, take a longer time to mature, and their life cycle and life timing is more similar to our own. As a result, the larger forms of mammalian life are able to assimilate a greater variety of data from their environment, store it in their nervous systems, and retrieve it for use later on. As a consequence of the prolonged association of the young with these larger mammals, the young have a longer time to acquire and process information

handed down to them through the activities of their elders. It is this protocultural transmission of information; it is this degree of differentiation by the more highly evolved sense organs; it is the ability to conserve and transmit more complex information that separates higher mammals from such conservative forms as the tenrecs; but, with respect to the basic configurations in space and time and the basic behavioral repertoires, the tenrecs exhibit the fundament which is common to essentially all terrestrial Mammalia.

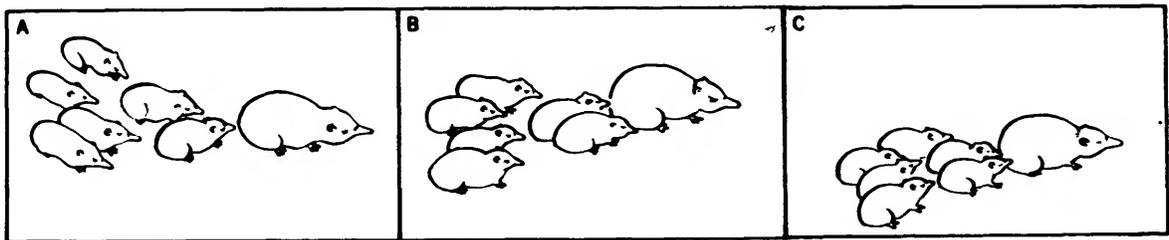


FIGURE 77.—Female *Tenrec ecaudatus* leading her young. Note the linear following tendency for this family group. Such a foraging unit may persist until the young are over 40 days of age. Drawn from 16 mm color film.

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## Appendixes

### Appendix A. List of specimen sightings and collections.

Species	No. of Specimens	Remarks	Species	No. of Specimens	Remarks
1967: PERINET REGION			1967: ANTSINGY REGION—Con.		
Insectivora:			Primates:		
<i>Tenrec ecaudatus</i>	63	Abundant	<i>Propithecus verreauxi</i>	—	Feeding on flowers
<i>Hemicentetes semispinosus</i>	47	Abundant	<i>Lemur mongoz</i>	—	Two bands
<i>Setifer setosus</i>	2	Rare	1967: MORONDAVA REGION		
<i>Microgale talazaci</i>	18	Live trapped	Insectivora:		
<i>Microgale cowani</i>	1	Live trapped	<i>Tenrec ecaudatus</i>	15	Including mother and infants in the wild
<i>Suncus murinus</i>	7	Live trapped	Carnivora:		
Rodentia:			<i>Mungotictis</i>	1	Pet infant
<i>Nesomys rufa</i>	1	Live trapped	Primates:		
<i>Eliurus myxonus</i>	1	Live trapped	<i>Propithecus verreauxi</i>	4	In the forest
<i>Rattus rattus</i>	11	Live trapped	<i>Microcebus murinus</i>	3	
Carnivora:			1966: RANOMAFANA REGION		
<i>Galidia elegans</i>	3	Sighted	Insectivora:		
Primates:			<i>Tenrec ecaudatus</i>	24	Abundant
<i>Lemur fulvus</i>	18	Sighted in 2 bands of 8 and 10	<i>Hemicentetes semispinosus</i>	34	Abundant
<i>Hapalemur griseus</i>	11	Sighted in 3 bands of 3, 3, and 5	<i>Microgale talazaci</i>	2	Live trapped
<i>Indri indri</i>	7	Sighted 3 times in groups of 1, 3, and 3	Carnivora:		
<i>Propithecus diadema</i>	3	One sighting	<i>Galidia elegans</i>	4	Live trapped
<i>Microcebus murinus</i>	10	Solitary or female and young	<i>Fossa fossa</i>	3	Live trapped
<i>Cheirogaleus medius</i>	22	Solitary, pairs, or trios	<i>Viverricula indica</i>	6	Live trapped
1967: MANANDROY REGION			Primates:		
Insectivora:			<i>Lemur fulvus</i>	5	Sighted in 1 band
<i>Tenrec ecaudatus</i>	1	Incidental collection	1966: MANANDROY REGION		
<i>Hemicentetes nigriceps</i>	58	Marked and released	Insectivora:		
<i>Setifer setosus</i>	3	Incidental collection	<i>Tenrec ecaudatus</i>	8	Not systematically collected
1967: MANOHILAHY REGION			<i>Hemicentetes nigriceps</i>	77	Marked and released
Insectivora:			<i>Setifer setosus</i>	2	Scarce
<i>Tenrec ecaudatus</i>	3	Torpid	<i>Microgale dobsoni</i>	11	Live trapped
<i>Hemicentetes semispinosus</i>	—	Reported torpid	1966: ALAKAMISY AHIMAHASOA REGION		
<i>Microgale dobsoni</i>	17	Abundant	Insectivora:		
<i>Suncus murinus</i>	3		<i>Hemicentetes nigriceps</i>	12	
Rodentia:			<i>Setifer setosus</i>	27	
<i>Rattus rattus</i>	5		1966: FIANARANTSOA REGION		
Primates:			Insectivora:		
<i>Microcebus murinus</i>	7	Abundant	<i>Hemicentetes nigriceps</i>	11	Moderately abundant
<i>Lemur rubriventer</i>	4		<i>Setifer setosus</i>	24	Abundant
1967: ANTSINGY REGION			<i>Suncus murinus</i>	—	Numerous
Insectivora: (All Tenrecidae torpid in May.)			Rodentia:		
<i>Suncus madagascarensis</i>	3		<i>Rattus rattus</i>	—	Numerous
Carnivora:					
<i>Galidia elegans</i>	—	Several sighted			

**Appendix A.** List of specimen sightings and collections—Continued

Species	No. of Specimens	Remarks
1963: MORONDAVA REGION		
Insectivora:		
<i>Tenrec ecaudatus</i>	—	Abundant
<i>Echinops telfairi</i>	—	Abundant
Rodentia:		
<i>Hypogeomys</i>	4	Pets of natives
Carnivora:		
<i>Mungotictis</i>	4	Feeding on carrion along the road; 2 infants and 2 adults
Primates:		
<i>Propithecus verreauxi</i>	—	Pets
<i>Microcebus murinus</i>	1	
1963: ROGEZ		
Carnivora:		
<i>Viverricula indica</i>	1	Live trapped

**Appendix B.** Collecting localities and study areas visited by Gould in 1963 and by Gould and Eisenberg in 1966 and 1967.

EASTERN RAINFORESTS.—*Perinet* (18° 54' south, 48° 26' east) 18–22 January 1963; 10–17 March 1963; 9 February–27 April, 1967. *Rogez* (18° 46' south, 48° 54' east) 27 July–5 August, 1963. *Ampansandrano* (19° 37' south, 47° 04' east) 14–18 June 1963. *Ranomafana* (21° 14' south, 47° 28' east) and *Ambatolah* 7–10 July 1963; 17, 27, 31 January 1966; 8, 9, 12, 17, 28 February 1966; 3, 11 March 1966; 4 April 1966. *Ambodivoangy* (12 kilometers north of Rogez) 27 July–5 August, 1963.

EASTERN PLATEAU ECOTONE.—*Manandroy* (21° 07' south, 47° 17' east) 29, 31 January 1966; 2, 8, 12, 28 February 1966; 3 March 1966; 6–7 April 1966; 4–5 February 1967. *Alakamisy Ahimahaso* (21° 19' south, 47° 13' east) 30–31 January 1966; 3 February 1966. *Fianarantsoa* (21° 28' south, 47° 04' east) 24 January–11 April 1966. *Manohilahy* (17° 16' south, 48° 01' east); 22 kilometers west of Morarano Sud, with D. S. Borgaonkar; also 3.6 kilometers north of Manohilahy on the slopes above the Sahasambena

River; 17–19 April 1967. *Ambatondrazaka* (around 20 kilometers north, near Anjoja) 5–7 March 1967.

WESTERN COAST AND PLATEAU.—*Morondava* (20° 14' south, 44° 17' east) 23–30 January 1967 (also Mahabo and Beraboka); 24 June–22 July 1963. *Antsingy Region* (18° 37' south, 44° 56' east); about 15 kilometers east of Antsalova, with S. Parcher; 5–16 May 1967.

**Appendix C.** Thermoregulation techniques and criteria.

In attempting to study the thermoregulation rhythms displayed by the Tenrecidae, we employed the following criteria and equipment. Readings were made with a telethermometer manufactured by the Yellow Springs Instrument Company. A rectal probe was employed. Before each series of trials, the calibration of the telethermometer was checked against a standard mercury thermometer. The ambient temperature at which the animal had been previously maintained was recorded; then, the animal was carefully picked up, turned upon its back, and the rectal probe was inserted to a distance of not less than 10 mm in its cloaca. Readings were made at the first stable point recorded by the telethermometer. Such a reading was always made with less than 30 seconds insertion time. The total handling time for the animal including recording of its cloacal temperature was less than 90 seconds. We attempted to make readings during different parts of the animal's daily cycle; that is early morning readings, afternoon readings, and early evening readings. In captivity each animal had a designated number and all measurements could be correlated with a given individual. This was especially important in studies of long-term thermoregulatory changes and torpor.

Burrow temperatures were recorded either by inserting a probe from the telethermometer into a burrow to a measured depth or, in the case of 24-hour monitoring, a Rustrak assembly was employed. A Rustrak Model 133 B, 24-volt powered electric thermometer was coupled to a 24-volt storage battery, Rustrak Model 154–24–1900. This electric thermometer comes equipped with two probes, one which may be left outside for ambient recording and the other inserted to a determined depth in a burrow system for continuous monitoring of the burrow tempera-

ture. The Rustrak electric thermometer is equipped with a continuous recording chart assembly.

#### Appendix D. Encounter techniques and open field tests.

In order to study the social interaction of the various tenrec species, a standard encounter technique was developed. Several different size arenas were utilized for staging the encounters. For *Tenrec ecaudatus* the arena floor area equaled 8 meters square. The smaller species of the Tenrecinae, such as *Setifer*, *Echinops*, and *Hemicentetes*, were studied in arenas having 1.5 square meters floor area. The genus *Microgale* was also studied in arenas having a floor area of approximately 1.5 square meters; in addition, a box measuring 1.8 by 0.6 by 0.6 meters divided into two equal parts, with a small door in the center divider, was employed to stage territorial encounters.

Encounters were run during the active part of the animal's 24-hour period. Animals selected for encounters were not torpid and were apparently healthy. The animals were observed under red light. We found that bright light would severely inhibit activity by any of the tenrec species.

Several types of encounters were run: The simultaneous encounter involves the introduction of two animals into an arena with which they have had no previous experience. Very often in a simultaneous encounter the two interacting individuals were introduced while still in their respective nest boxes. This gave each animal a familiar reference point from which it could venture to explore the novel environment.

Two types of territorial encounters were run: (1) A resident was established in an arena for over 24 hours and then an alien was introduced. (2) An arena was established with a center divider giving each animal access to half of the arena for approximately 24 hours whereupon the center divider was removed allowing the animals to encounter while still maintaining a reference area with which they were familiar.

The various encounter types were run with all age classes and sex classes of individuals; thus, juvenile to adult encounters, adult-adult encounters, male to female, male to male, and female to female encounters were staged. By employing the various encounter types with the different age and sex classes, we were able to estimate the influence of familiarity with the locus on the outcome of an encounter, differentiate between

adult and juvenile encounter behavior; differentiate between predominately male patterns, and further differentiate female responses from male responses with respect to the various age and sex classes.

All encounters were observed either behind a screen or the observer was a sufficient distance away to prevent biasing the movement patterns of the animals. The observer spoke softly into a microphone coupled to a tape recorder; thus, obtaining a continuous verbal description of the interaction patterns. The recorded tape was then at a later date played back and, by employing a stop watch, the time course of the encounter studied. The verbal transcription from the tape was transcribed on paper in a semicoded fashion. These protocols could then be subjected to a quantitative analysis and such information as the frequency of acts or duration of acts could thereby be recorded.

Various observations were conducted using an infra-red viewer, Varo Detectirscope, model 5500C, produced by Varo, 5574 N. Northwest Highway, Chicago, Illinois, 60630.

Open field tests employed a simulated natural habitat in arenas of approximately the same dimensions as noted above. Arena size included a 1.2 by 1.2 meter floor area for the smaller species and a 4.6 by 0.9 meter floor area for *Tenrec ecaudatus*. The arena floors were covered with earth, and various artifacts including rocks, tree limbs, and prey objects could be placed in the arena. The animals were again observed during their active cycle under red illumination and descriptions of activity patterns of the animals were tape recorded. By employing such an open field test, such behavior patterns as prey catching, locomotion, care of the body surface, marking, nest building, digging, etc., could be noted and described in some detail.

In addition to the formal encounters and open field studies employing a verbal description of the behavior patterns, we ran a follow-up series of observations and filmed the activity patterns of the animals employing a 16 mm Bolex cine camera. Tri-x film was utilized and, by maintaining light at the lowest possible intensity, a great deal of interaction could be recorded on film with little disturbance to the animals. Such films were later analyzed on a film editor and some of the more discrete patterns could be examined frame by frame. In the text, Figures 25, 29, 59, and 60 were drawn from single frame analysis of 16 mm film.

### Appendix E. Speed tests.

In order to study the maximum running speed of a tenrec, a long runway was employed. Speed trials were run over a distance of 4.6 meters. *Tenrec ecaudatus* and *Hemicentetes semispinosus* were resident in holding pens measuring approximately this distance. As a result, the nest box for the specimens was maintained at one end of the run so that when they were displaced from the box to the opposite end of the holding pen, their flight reaction would be directed toward the nest and no difficulty occurred in obtaining a maximum straight line run to shelter. One observer remained at the nest box with a stop watch while the second observer carried the animal to the opposite end of the run and, at a given signal, released it. *Setifer setosus* was never maintained in a holding pen with this linear dimension, and all trials within such a pen had to be employed with animals which were slightly naive with respect to the environment. As a result, directed runs were infrequent and many trials had to be executed before three acceptable attempts by *Setifer* were obtained within the same testing situation.

### Appendix F. Activity measurements.

The activity of captive tenrecs in large seminatural holding pens was monitored employing a four-channel operations recorder (Rustrak, Model 92, 6 volts). Motor power for the chart drive was delivered from a Rustrak Model 154-3.6-1900 6-volt assembly. The operations recorder was coupled to a Rustrak amplifier (Model 922, 24 volts). Power for the amplifier was supplied by a 24-volt DC storage battery or alternatively four 6-volt dry cells which provided sufficient power for some 14 hours running time. The same 24-volt source was utilized to power the photocell and light source assembly. The photocell light source assembly was obtained from the Farmer Electric Company of Nattuck, Massachusetts. Both photocell and light source were powered from the Rustrak amplifier. The photocell assembly could be placed in the vicinity of either a feeding station or the burrow entrance. As an animal passed in or out of a burrow or fed, it would obstruct the light source and trigger the operations recorder. Very low light intensities could be employed with the photocell at a distance of approximately 15 cm separating light source from

photocell. At these intensities the tenrecs seemed little inhibited in their behavior.

### Appendix G. Predator odor tests.

Captive specimens of *Fossa fossa*, *Galidia elegans*, and *Viverricula indica* were maintained in captivity for several months. Both urine and feces could be collected from the cages of the various carnivores. Urine or feces could be soaked or smeared onto small pieces of absorbent cloth which were then tied to a slender stick. In an open field testing arena, various species of tenrecs were presented with the chemical stimuli and their reactions noted. The strength of the response by the tenrec could be quantified in terms of degree of spinal erection, attack behavior, flight behavior, or biting at the test object.

In addition to the preceding method, a cloth pad was left in the cage of one of the captive *Galidia elegans*. This cloth pad was repeatedly marked by the *Galidia* and could be removed and used as a test object. The cloth, when wrapped around the end of a stick, was waved in front of the test animal thus producing an odor in the immediate vicinity. There was no control over the exact chemical traces left on the cloth but in the main it consisted of glandular exudates from the anogenital region of the *Galida* with little urine or feces. As with the previous tests, the strength of the response of the animal could be noted. Repeated presentations of the same test stimulus was also valuable in estimating the degree of waning in the responsiveness of the animal upon repeated presentations of the same stimulus.

### Appendix H. Sound recording and playback techniques.

During all recording and playback techniques, power was supplied from a 60-cycle, 120-volt, gasoline-powered generator (Onan, model AJ). A voltage regulator ensured a constant power input. Recordings of stridulation were made with a Bruel and Kjaer (B and K) quarter-inch microphone coupled to a B and K microphone amplifier (Type 2604); the recorded pulses were passed through a Krohn-Hite variable band-pass filter (model 310C) and led ultimately to recording channel one of a Precision Instrument tape recorder (model 202). Recording speed was 30 inches

per second. During stridulation recordings, an observer could describe the activities of the animal by speaking into a voice microphone coupled to channel two of the Precision Instrument tape recorder thus permitting a simultaneous recording of input from the animal and a verbal description by an observer.

In addition to this recording technique, the ultrasonic sounds of the animals could be monitored by employing an ultrasonic microphone, monitor, and earphones. The ultrasonic microphone and transducer complex allowed one to hear rectified ultrasonic sounds (see Bertolini, 1960; McCue and Bertolini, 1964; and Kuhl, Schodder, and Schroder, 1954). Sounds could be played back from the tape recorder into a Tektronix portable oscilloscope (model 321A). The oscilloscope permitted continuous monitoring of the tape recordings as the recordings were made and, in addition, it served as a check monitor during playbacks. By means of cross checking with the oscilloscope, a section of tape could be selected for playback. Playback loops during preliminary tests (see p. 109) were prepared in the standard manner cutting an appropriate section of tape, splicing it, and utilizing the Precision Instrument playback loop. Playbacks to *Hemicentetes* infants (see Figure 68 and Table 12) were prepared with two Precision Instrument tape recorders, thus permitting placement of different signals on the two channels of a given length of tape loop. In this way, the original recording was preserved.

Playbacks were made utilizing the Precision Instrument tape recorder, passing the sound through a band-pass filter to a d.c. on-and-off switch (designed by Mr. Robert Glacken) that minimized distortion or loss of the signal, thence to a 70 watt amplifier (Dyna Co., Dynakit 70-A) and from the amplifier to a speaker (University Sphericon T203). The signal was monitored with the d.c. oscilloscope between the filter and switch. Recordings on the Precision Instrument tape recorder were calibrated by employing an oscillator (Hewlett Packard 204B). By recording a sound of known frequency with the Precision Instrument tape recorder one could then play back the recorded sound through a filter into the oscilloscope for accurate calibration. Alternatively, the sound from the oscillator could be passed through an amplifier to a speaker and then recorded with the B and K microphone passing the sound through the microphone amplifier to the Precision Instrument tape recorder

and then displaying the recording through a filter on the oscilloscope screen.

Amplitude calibration during playback was checked accurately by playing back the recorded sound through the amplifier and speaker to the B and K microphone whereupon the exact amplitude could be read off the amplitude meter on the B and K amplifier. Rigid ring stands and clamps facilitated constant distances and positions between loudspeaker and microphone during calibration. Except where otherwise indicated, intensities were reproduced as close to the natural intensity as possible.

RECORDING TECHNIQUES FOR *TENREC ECAUDATUS*.—Juveniles were recorded in a box measuring 0.3 by 0.6 by 0.3 meters depth. The box was made of styrofoam and was lined with absorbent insulation. The animal could be released into this box and subjected to a variety of stimuli while the microphone was held in position directly over the stridulating organ. In addition, juveniles of *Tenrec ecaudatus* could be released in an open field arena measuring 2.7 by 1.1 by 0.7 meters with a leaf-mold covering the floor. By following the animal with a hand-held microphone, the stridulation could be monitored almost continuously. Playback to *Tenrec ecaudatus* families was accomplished in the 2.4 by 1.2 meter arena by placing the nest box of the animals in the arena and allowing them to become accustomed to it for several days prior to playback. Loudspeakers could be positioned anywhere within the arena and sound played back to the animals as they freely foraged and fed. Control sounds throughout the *Tenrec ecaudatus* tests consisted of the background noise of the tape raised to the same amplitude level as the stridulation recordings and alternatively the sound of rustling leaves. Equivalent intensities were obtained by using intensity of natural stridulation as a standard; the loudspeaker was placed 4 centimeters from the B and K microphone and calibrations for all signals were measured in the same way. The distance and position was determined by noting the arrangement that yielded the best response from the loudspeakers using a given signal intensity. This distance and position was then held constant for that loudspeaker.

RECORDING AND PLAYBACK TECHNIQUES FOR *HEMICENTETES*.—For our experiments with *Hemicentetes* the hookups were similar to those just described. Although stridulation by *Hemicentetes* is almost continu-

ous when the animal is active, it was rather difficult to make good recordings from this species by holding a microphone above the stridulating organ as it moved freely in an arena. We were forced therefore to resort to handholding techniques especially to obtain the loud stridulation produced by an aroused animal. In handholding *Hemicentetes*, the B and K microphone was clamped firmly on a work table and the animal was brought to it either in a small container or while held firmly in the observer's hands. The stridulating organ could then be brought very close to the microphone and loud rapid stridulation was easily recorded.

As described in the text, playback to *Hemicentetes* was undertaken in a variety of conditions: Loudspeakers were placed in large cages inhabited by family groups and stridulation was played back to them as they passed in the vicinity of the speaker. In this way the animals were subject to very little disturbance and their initial state of arousal could be recorded by an observer prior to the onset of the test signal. In a second series of experiments, the animals were placed in an arena and their behavior observed as stridulation or control sounds were played back to them. The arena experiment imposed some artificiality since the mood of the responding animal could not be controlled as easily as was the case when the playback apparatus was set up in the home cage.

#### Appendix I. Care and maintenance of captive Tenrecidae.

Tenrecs were maintained in cages of various sizes. The smaller species of tenrecids, such as *Echinops*, *Setifer*, *Microgale*, and *Hemicentetes*, were held in cages measuring 0.6 by 0.5 by 0.3 meters deep. These cages were made of plastic which served very well to insulate the tenrecs since they exhibit an unstable thermoregulation. It is important that the holding cages be of plastic or wood since metal cages are prone to conduct away too much body heat from the animal. Sawdust may be used as a substrate in the cages; however, newspapers are equally convenient. The animals were generally fed on newspaper since they have a tendency to scatter their food and the use of newspaper reduced the incidental ingestion of sawdust which would take place if the food were placed directly on a sawdust substrate. *Tenrec* was maintained in larger cages generally having some 0.9 to 1.3 square meters of floor area. An earth or peat moss substrate

proved useful although again newspapers provide an inexpensive floor covering. All tenrecs will build a nest from hay or paper strips. A nest box is highly desirable and permits the animal to maintain a reasonably high body temperature.

All genera of the Tenrecidae can be maintained on a basic meat ration: Raw ground horsemeat is mixed with powdered milk and Pervinal (manufactured by U.S. Vitamin and Pharmaceutical Corporation, Veterinary Products Division, New York, N.Y.). To this mixture is added a vitamin supplement (Abdec) and ground egg yolk. This basic meat mixture has been extremely useful with the following genera: *Microgale*, *Echinops*, *Setifer*, and *Tenrec*. However, *Hemicentetes* cannot be maintained on this meat mixture alone and, although it will take meat, it must be fed earthworms in supplement to the meat ration. As indicated in the text, *Hemicentetes* without meat supplement can eat up to 100 grams of earthworms per 24-hour period. *Microgales* do well if crickets or mealworms are added as a dietary supplement to the basic meat ration. *Setifer* takes earthworms readily but *Echinops* does well if crickets are given for a dietary supplement. Baby mice or adult skinned mice may be offered weekly to *Tenrec ecaudatus*.

Temperature is extremely critical in rearing and maintaining tenrecs. In general, the subfamily Tenrecinae exhibits greater thermal lability than does the subfamily Oryzoricinae. The tenrecines exhibit a 24-hour periodicity in thermoregulation and the cloacal temperature can fall over a range of 7° C during the resting phase of their cycle. In addition to the diel periodicity in thermoregulation, the tenrecines tend to show a period of seasonal torpor. The timing and duration of the torpid period is entirely a function of local conditions (see text). In the laboratories at Washington and Baltimore, the animals are permitted to hibernate at temperatures ranging from 16° to 22° C. During the breeding season the animals are maintained at 23° to 26° C.

BREEDING TECHNIQUES.—Prior to their entry into torpor, individual tenrecs show an increased appetite and rapid fat deposition. In order to promote the reduction in accumulated fat reserves and allow the specimens to complete their annual cycles in accordance with their periodic physiological rhythms, we now place all specimens of the subfamily Tenrecinae in rooms maintained at approximately 16° C for three or four months during the summer.

After emerging from torpor, the animals gain weight rapidly and will exhibit mating behavior in about 2 weeks. Females vary in their receptivity but, after several days with the male, mating is generally accomplished. Separation of the male from the female after mating appears essential for the successful breeding of *Setifer setosus* and *Tenrec ecaudatus*. Females of these species appear very sensitive to any disturbance prior to parturition and abortion or resorption of embryos is not uncommon in our colony. Although *Hemicentetes semispinosus* is quite tolerant and even forms extensive family groups in the same burrow system, there is nevertheless a marked tendency for the female to withdraw to a separate nest box at partus and for this reason we now separate all pregnant females.

The breeding of *Microgale dobsoni* and *M. talazaci* was accomplished with great difficulty. These animals are very subject to disturbance and the females appear to abort easily. Breeding could be accomplished only by pairing the male and female for about a month and then separating them, and leaving the female completely undisturbed with nesting material and a closed box. Since the nest box could not be examined during the initial rearing phase, much valuable data concerning the growth and development of the young was lost; however, we are convinced that further breeding can be successfully accomplished. This problem is still under study.

The nest boxes for *Tenrec ecaudatus* have a central chamber measuring 45×29×20 centimeters with a connecting tunnel 21×13×27½ centimeters long. The other species utilize a smaller nest box of similar construction having a chamber 30×15×10 centimeters with a 9×7½×10 centimeter tunnel. Since *Hemicentetes* and *Tenrec* in nature are prone to defecate at the entrance to their tunnel, we have experienced some difficulty with these tunnel boxes. In captivity the specimens frequently defecate and urinate in the wooden tunnels complicating problems of sanitation. We now recommend that the tunnel be eliminated for those females which defecate in the nest box. The nest chamber itself should be reduced to 25×20 centimeters of floor area for breeding tenrecs since the larger chamber permits the new born litter to become scattered and reduces the chance of successful rearing.

Gestation in tenrecoid insectivores is rather prolonged being 58 to 64 days for *Tenrec ecaudatus*, 58–62

days for *Hemicentetes semispinosus*, 65 to 69 days for *Setifer setosus*, and 62 to 65 days for *Echinops telfairi*.

Litter sizes in captivity compare favorably with data from the wild for *Hemicentetes*, *Setifer setosus*, and *Echinops telfairi*; however, litter size in *Tenrec ecaudatus* has been consistently lower than data obtained from the wild. The size of the litter in captivity for the four genera are as follows: *Tenrec ecaudatus* 1 to 4, *Hemicentetes semispinosus* 2 to 11, *Hemicentetes nigriceps* 2 to 4, *Setifer setosus* 1 to 4, *Echinops telfairi* 1 to 10 with a mode of 7, *Microgale dobsoni* 3, and *Microgale talazaci* 2.

**HAND-REARING TECHNIQUES.**—The susceptibility of *Setifer* and *Tenrec* females to disturbance resulted in poor rearing by the mothers. As a result hand-rearing techniques were attempted. Four common tenrecs, *Tenrec ecaudatus*, were born on 23 February 1967 to a female which had been unsuccessful in rearing a previous litter. Since one of the second litter did not survive the first day, two siblings were taken for hand rearing. The birth weights were 22.8 and 27.4 grams and total lengths were 84 and 88 millimeters. The average birth weights and lengths for the previous litters of this species were 25.2 grams and 85.2 millimeters, respectively. The two youngsters appeared to do well on 2-hour feedings of equal parts of Carnation evaporated milk and water but died two days after birth as a result of temperature stress.

The last one of the litter of four was found outside the nest box on the sixth day and weighed only 18.2 grams. This baby was successfully hand reared on a 2:5:1 mixture of Esbilac:water:Carnation evaporated milk. Lactinex (Hynson Wostcott and Dunnin, Inc., Baltimore, Maryland) was added as a dietary supplement for the natural bacteria removed in the process of milk sterilization.

This young tenrec was kept in an incubator at 82° F during the first month of its life. Feedings were given every 2 hours during the second week until the animal regained the birth weight of its siblings and then at 3-hour intervals until it ate solid food at 3½ weeks of age. Between ¼ and ½ ounce of milk was generally accepted from an eyedropper per feeding, totaling 2 to 4 ounces consumed daily. The tenrec eliminated spontaneously. The tenrec was weaned to a diet of chopped earthworms and horsemeat including supplemental vitamins (Vidaylin M. of Abbot Laboratories,

Chicago, Illinois; and a 2:1 Pervinal, U.S. Vitamin and Pharmaceutical Corp., New York; calcium carbonate mix).

A giant hedgehog tenrec, *Setifer setosus*, was also hand reared on a similar diet. It was removed from the mother on the fourth day after a gram-weight loss from 21.7 on the third day. Two modifications were introduced for rearing: (1) Since the animal was cool and inactive when incubated at 70° to 80° F, a higher incubator temperature of 85° F was employed; and

(2) a dietary supplement, Zymadrops (Upjohn and Company, Kalamazoo, Michigan) which has a higher vitamin D content, was substituted and dicalcium phosphate (D.C.P. 340, Parke-Davis and Company, Detroit, Michigan) at 0.1 to 0.2 grams per ounce of milk was added to the diet to curb rickets. The diet was also restricted to reduce obesity which developed in the animal during the first three weeks of rearing. It is suggested that the leanest possible meat be employed in the weaning process for this species.

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