The Natural History of the Central American Agouti (*Dasyprocta punctata*)

NICHOLAS SMYTHE

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 257

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 257

The Natural History of the Central American Agouti (*Dasyprocta punctata*)

Nicholas Smythe

SMITHSONIAN INSTITUTION PRESS
City of Washington
1978

ABSTRACT

Smythe, Nicholas. The Natural History of the Central American Agouti (*Dasyprocta punctata*). *Smithsonian Contributions to Zoology,* number 257, 52 pages, 25 figures, 2 tables, 1978.—In this report the behavioral ecology of the Central American agouti (*Dasyprocta punctata*), a large caviomorph rodent, living on Barro Colorado Island in the Panama Canal Zone is described. This two phase study includes social structure, activity patterns, maturation, courting, agonistic and comfort behavior, and acoustic, vocal, visual, and olfactory communication systems, as well as the interrelationship of the animals' behavior with the environment.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Smythe, Nicholas
The natural history of the Central American agouti (Dasyprocta punctata)
(Smithsonian contributions to zoology ; no. 257)
Bibliography: p.
Supt. of Docs. no.: SI 1.27:257
1. Central American agouti. 2. Mammals—Panama—Barro Colorado Island. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 257
QL1.S54 no. 257 [QL737.R644] 591'.08s [599'.3234] 77-608187

Contents

	Page
Introduction	1
Acknowledgments	3
Materials and Methods	3
Behavioral Ecology	3
The Trap-Mark-Release Program	6
Phase I: Results of Seasonal Changes on Behavior	6
Seasonality of the Food Supply	6
Effects of Seasonal Abundance of Food	7
Seasonal Changes in Aggressive Behavior	10
Phase II: Results of the Trap-Mark-Release Program	11
Species Trapped	11
Numbers and Age Classes	11
Trapping Locations	12
Life History Curves	13
The Ridgetop Traps	18
Adult Males	18
Life Expectancy of Juveniles	19
Mortality Differences between the Sexes	20
The Use of Space	20
Agouti Territories	20
Territories and Nonreproductive Animals	21
Activity Patterns	22
Feeding and Foraging Behavior	23
Types of Food	23
Foraging	24
Feeding Spots	24
Feeding Techniques	25
Scatterhoarding	25
Comfort Behavior	26
Allogrooming	26
Autogrooming	26
Protection against Biting Dipterans	27
Reaction to Rain	27
Sleeping	27
Courtship and Mating Behavior	28
Introductory Behavior of Captives	28
Courtship of Free-living Agoutis	29
Agonistic Behavior	30
Interspecific Agonistic Patterns	30
Intraspecific Agonistic Patterns	30
Maturation of Young Agoutis	32
Parturition and Nest Selection	32

	Page
Maternal Care of Nest-bound Young	33
Breakup of the Mother-Young Bond	36
Role of the Male	37
Survival of the Young	38
Communication and Displays	38
Visual Communication	38
Olfactory Communication	39
Marking with Anal Gland Secretions	39
Urine Marking	40
Mechanical Communication	41
Thumping	41
Derivation and Function of Thumping	42
Drumming with the Forefeet	42
Sounds Made with the Teeth	42
Vocalizations	42
The Alarm Bark	43
Reactions of Conspecifics to Alarm Barks	43
The Purr	44
The Creak-Squeak	44
Fight Grunts	44
Rumble	45
Growl	45
Distress Scream	45
Conclusions	45
Competition and Ecological Separation among Terrestrial Frugivores	45
Agoutis and Seed Dispersal	47
The Adaptive Value of Monogamous Pairs	48
Limitations Imposed by the Necessity of Hoarding	49
The Status and Future of the Agouti	49
Literature Cited	51

The Natural History of the Central American Agouti *(Dasyprocta punctata)*

Nicholas Smythe

Introduction

Since their appearance in the New World during the late Eocene, the caviomorph rodents have undergone an intensive adaptive radiation, so that today the group exhibits a diversity that is, in comparison with other groups of mammals at the same taxonomic level, extraordinary. The taxonomic affiliations of the agouti (based on Simpson, 1945) are illustrated in Figure 1.

The porcupine (*Erethizon dorsatum*) is the only caviomorph that occurs naturally north of the southern part of Mexico, the remainder being confined to Central and South America, where some are small arboreal animals, one almost entirely fossorial, and two semiaquatic. Some of the larger genera appear to occupy ecological niches similar to those of various Old World small ungulates. Thus, as Kirchshofer (1960a) points out, the mara (*Dolichotis patagonum*) bears many resemblances to some of the small, plains-dwelling antelopes. Indeed, the remarkable running gait known as "stotting," which is so characteristic of many ungulates, also occurs in the mara (Smythe, 1970a). Dubost (1968) considers some of the similarities between cavimorph rodents and West African mammals, and Eisenberg and McKay (1974) discuss convergences with Asiatic forms.

The agouti (*Dasyprocta punctata*) is similar in many respects to some of the small forest-dwelling antelopes (Dubost, 1968; Bourlière, 1973) and to the mouse deer *Tragulus* (Morris, 1965). Agoutis (Figure 2) are large, cursorial, diurnal, principally frugivorous rodents that occur in broadleafed forests from southern Mexico to northern Argentina. Their habit of "scatterhoarding" (Morris, 1962) food items makes them one of the most important dispersers of the propagules of their food plants. It appears, in fact, that many of the trees within their natural range have no other regular means of dispersal. The importance of the dispersed distribution of Neotropical forest trees, as an adaptive characteristic, has been discussed by various authors (Ridley, 1930; Janzen, 1969, 1970). If the dispersal agents are removed (for example, by indiscriminate hunting), then the natural distribution will not be maintained and the character of the forest will gradually change. Predation upon various parts of the trees and the pathogens affecting them will increase, recruitment will decline, and the species composition of the community will change.

Agoutis are an important food source for man throughout their range. The meat is not generally considered as desirable as that of their nocturnal relative the paca (*Cuniculus paca*), but agoutis are commoner and are more easily caught. Firearms are not necessary for a successful agouti hunt since, due to the unwillingness of the animals to leave their rather small home range, they can be run to ground with dogs and then killed with machetes. For many of the chronically protein-deficient poor people within the range of the agouti, it is one of the most important meats.

Nicholas Smythe, Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Canal Zone.

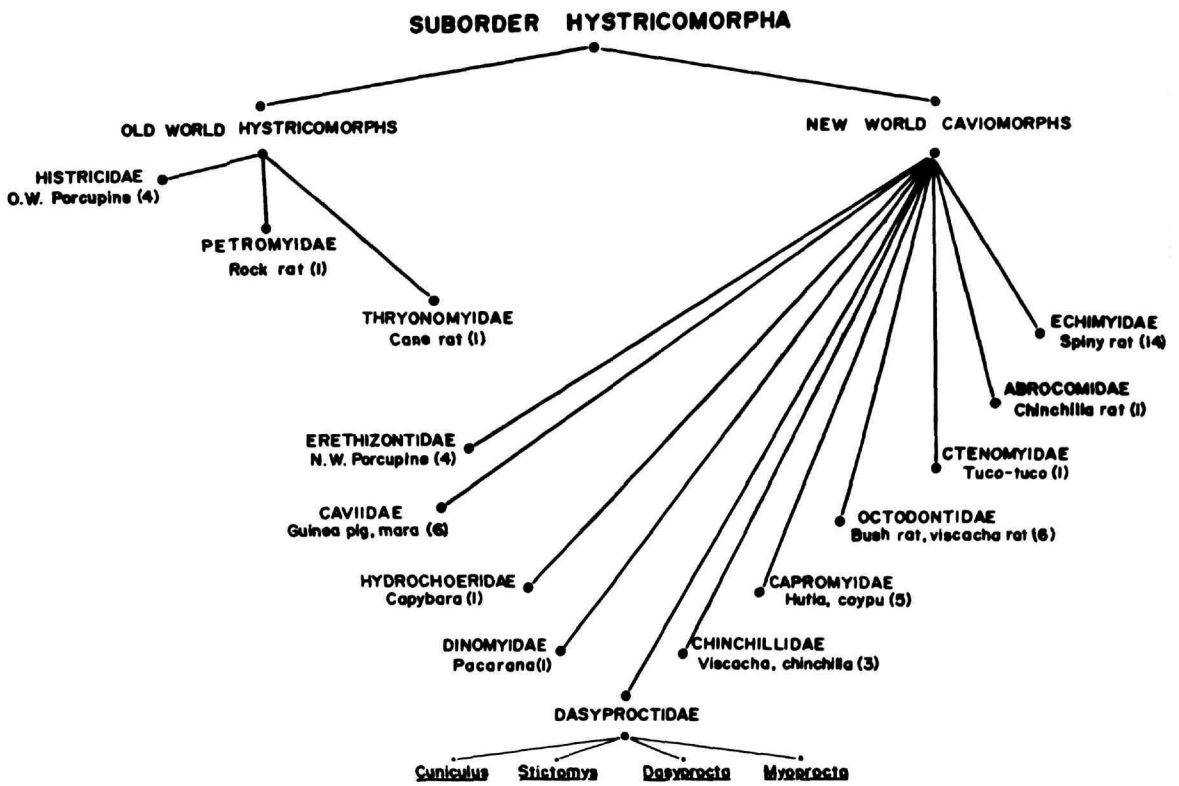


FIGURE 1.—Taxonomic relationships of the suborder Hystriocomorpha (after Simpson, 1945; numbers in parentheses indicate number of genera in each family).

In addition to constituting a food for man, agoutis are also important in the diets of several carnivorous animals. They are probably a principal food item for ocelots (*Felis pardalis*) and jaguarundis (*Felis yaguaroundi*), and an important occasional food for jaguars (*Panthera onca*) and pumas (*Felis concolor*), as well as tayras (*Eira barbera*) and coatis (*Nasua narica*). Many of the larger snakes undoubtedly eat an occasional agouti and M. Alvarez del Toro (pers. comm.) has found agouti remains in the nest of an ornate hawk-eagle (*Spizaetus ornatus*).

In the few remaining Neotropical lowland forests that have not been severely disturbed by man, agoutis are the most commonly observed diurnal terrestrial mammals (Eisenberg and Thorington, 1973:157; pers. obs.). It may thus seem surprising

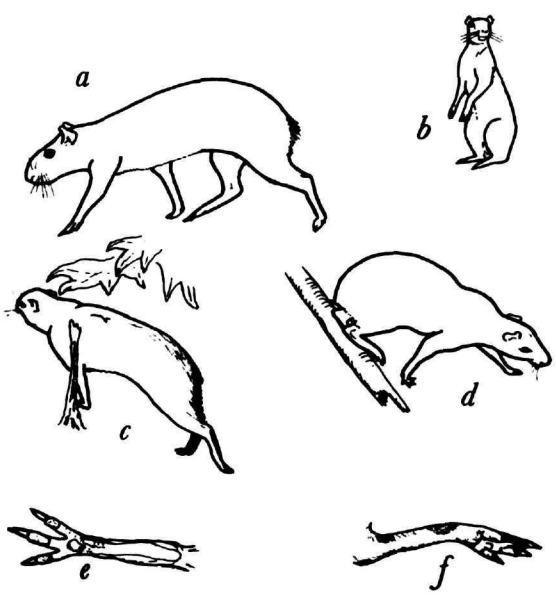


FIGURE 2.—*a-d*, Locomotion and general morphology of the agouti; *e*, hind foot; *f*, forefoot.

that so little is known of their habits. They are, however, shy animals and those generally noticed by a walker in the forest are already fleeing and have advertized their presence with alarm barks. A few studies have been made on captive agoutis (Weir, 1971; Roth-Kolar, 1957) and more detailed studies have been made of captive acouchys (*Myoprocta* sp.) (Morris, 1962; Kleiman, 1971, 1972). *Myoprocta* is very similar to *Dasyprocta* though it is considerably smaller. Practically nothing is known of *Myoprocta* in the wild, but in captivity many of the behavioral patterns are similar to those of *Dasyprocta*.

Enders (1935), in what is still the most informative work on the life histories of many Neotropical mammals, considers agoutis at some length, but he did not work with a known group of individuals nor did he study their interactions with such factors as the food supply.

ACKNOWLEDGMENTS.—John F. Eisenberg introduced me to the agouti, suggested it as a subject, and contributed much to the approach to, and interpretation of, the study. The Smithsonian Tropical Research Institute and my colleagues there have borne, and borne with, me during the protracted gestation of this paper. To them, and to others too numerous to mention who have also contributed, I offer my sincerest appreciation. I thank Michael H. Robinson, Ira Rubinoff, Martin H. Moynihan, A. Stanley Rand, and Donald M. Windsor for critically reading various parts of the manuscript, but apologize and accept full responsibility where I have not followed their suggestions.

I thank Arilla H. Kourany and Vielka Vergel for their considerable efforts in typing several drafts of the manuscript.

Sections of this paper were submitted as part of the requirements toward the degree of Doctor of Philosophy at the Department of Zoology of the University of Maryland.

Phase II of the study was supported by the Smithsonian Institution Environmental Sciences Program.

Materials and Methods

I studied agoutis at the Smithsonian Tropical Research Institute station on Barro Colorado Island in the Panama Canal Zone from August 1965 until December 1967, and again from late 1971 until May 1977. Descriptions of Barro Colorado Island may be found in Allee (1926), Kaufmann (1962), and in the literature cited in those papers. The first phase of my study (1965–1967) was concerned chiefly with field observations of a small, known population that lived to the north of the laboratory clearing.

The second phase is a trap-mark-release study (which is still going on) and is part of the Smithsonian Institution Environmental Sciences program. It is being conducted in a watershed basin to the south of the laboratory clearing (Figure 3). I have also watched wild agoutis in various parts of Costa Rica; in Chiapas, Mexico; in the Darien forest, and other parts of Panama. I have observed captive agoutis at the University of Maryland, Department of Zoology; at the U.S. National Zoological Park; at the Zoological Park in Tuxtla Gutierrez, Chiapas; and in cages on Barro Colorado Island.

Behavorial Ecology

During the first phase of the study agoutis were caught in Tomahawk (National), 23 × 23 × 81 cm, double-doored traps that were set in a large circle roughly following the 60-m contour line in the study area (Figure 3*a*). Animals were caught chiefly for the purpose of marking them for subsequent identification. I have found it impossible, so far, to regularly trap agoutis at any time of the year except when falling, ripe fruit is scarce. Even at that time adult animals will seldom enter traps. Thus the usefulness of traps in the determination of home ranges and population structures is rather limited.

During phase I, each captured animal was marked according to a coded pattern with a black fur dye (Durafur, I.C.I., U.K.) and, in addition, by means of a tattooed number in each pinna. The phase II animals are marked with the tattooed numbers only. Agoutis molt from mid-February through April, and the season of fruit shortage, during which most of them were captured, lasts from mid-August through January. The dye marks thus remained visible from two to eight months. The pinnae are very thin, so the 1-cm-high, tattooed numbers are easily readable at distances up to 20 m with the aid of good, tripod-mounted 7 × 35 binoculars.

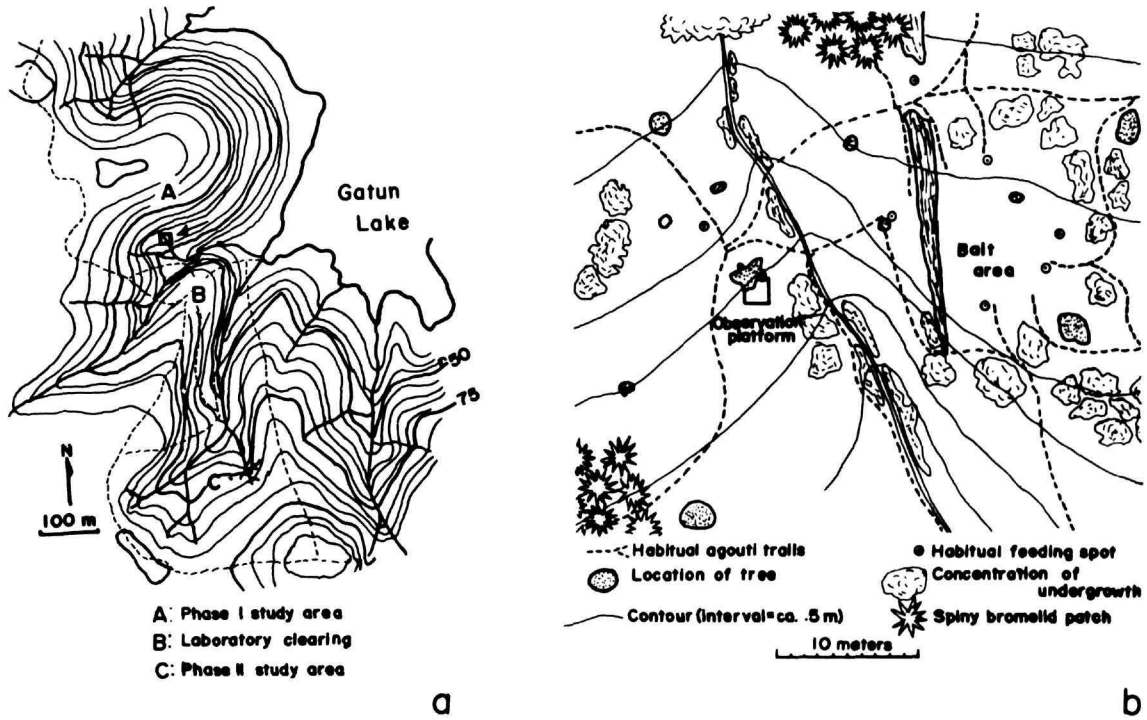


FIGURE 3.—Barro Colorado Island: *a*, locations of the study areas (arrow indicates the bait area and observation platform; watershed basin constitutes the phase II study area); *b*, phase I bait area.

Unmarked animals that frequently visited observation areas were initially identified by differences in the color pattern of the rhinarium, by the condition of the pinnae (which frequently become torn around the edges) and by whether they were of the darker or lighter of the two color phases present on Barro Colorado Island. After a few weeks of observation of the regular visitors it became surprisingly easy to recognize animals by general appearances or differences in behavior. They were assigned code names consisting of the initials of the description of an obvious characteristic. The numbers of the trapped animals, or the letter codes of the others, are preceded by single letters indicating sex. Mature animals are designated by upper-case letters, others by lower-case ones.

The sex designating letter was assigned to each phase I animal as soon as I was able to determine it. If the animal subsequently became mature its code name was not changed. Thus m22 was a subadult male, the 22nd phase I agouti that I trapped. He became mature and reproductively active before the end of phase I, but his sex designating letter was not changed.

The agoutis that regularly visited the bait area below the observation platform were:

Adults	*Young*	*Comments*
MSS (Scar Shoulder)	m14	MSS and FSP were a mated pair at the beginning of the study; m14 was their only offspring during phase I that survived to begin foraging independently
FSP (Spot Nose)		
MRE (Rim Eye)	mSN (Scar Nose)	MRE and F13 were mated at the beginning of phase I; three of their offspring survived to begin independent foraging
F13	m18 f29	
m22		m22 was subadult at the beginning of phase I, FSB was adult when first identified but they were not yet paired; they had two offspring during phase I, one of which, f27, survived to forage alone
FSB (Scar Back)	f27	

In addition, two other males, MSH (Sharp Ear) and MWS (White Shoulder) visited the bait area often enough that I learned to recognize them. Unmarked animals that did not regularly visit the bait area, but whose presence in the study area I knew of, were assigned the appellation DY. (This was to make the recording of notes easier. Any animal that I was unable to identify but whose behavior I noted was identified in the notes as DY. If its sex was apparent, then it was noted as MDY, mDY, etc.).

I studied captive agoutis in order to become familiar with the various components of their basic behavioral repertoire. In the field I would often see only a small portion of a behavioral sequence, and many times my knowledge of the captive animals helped in the understanding of its context. I used a 4 × 10 m observation cage that was built in the forest and had eight 1.2 × 2 m living cages attached to its outside. The doors of any combination of living cages could be opened and the occupants allowed into the main cage so that I could watch social encounters.

To supplement direct field observations, I modified four electrically advanced, single-frame (popularly known as "half-frame") 35-mm cameras so that they could be tripped by animals passing through their field of view. These, together with small electronic flash units in moisture-resistant boxes, were placed in different locations in the study area. A 24-hour clock was placed in the field of view and the area in front of each camera was baited twice a day with a handful of dried corn. Animals tripped the camera shutters by touching a wire connected to a microswitch or by breaking the beam of a photoelectric switch. Seventy-two frames could be exposed in each camera before the film was exhausted. In addition to aiding in the determination of activity periods, the cameras were useful in plotting home ranges and territories since those animals that were dye-marked were easily recognizable in the photographs.

Because of their shyness, it is difficult to approach wild agoutis in the forest without affecting their behavior. The best way to observe them (and most other local animals) is to sit still and wait for them to come into view. The probability of seeing them is greatly enhanced at some times of the year by putting out bait piles. Depending on the availability of naturally occurring ripe fruit, the animals in the study area came to such baited areas within a few minutes of the bait being set out, within one or two days, or not at all. Once they began coming it took them about a week to become habituated to my presence, although they still spent much of their time watching me unless I was separated from them by the valley of a creek, by a very steep slope, or by a tree. Five of these baited areas were set up in the study area in order to aid in the determination of home ranges. Most observations were made from a semipermanent observation post that was set up between the border of two home ranges. It consisted of a platform about 5 m up a tree. Bait could be thrown from this platform into a small natural clearing across a seasonally dry stream (Figure 3*b*). The fact that I was on a different level from the floor of the forest had several advantages: terrestrial animals were much less shy, their reactions toward me being much the same as toward monkeys foraging overhead. Also I could vary the quantities of fruit that I dropped at any one time, thus more nearly simulating a naturally fruiting tree. By varying the amount and position of the fruit thrown, I could manipulate, to some extent, the behavior of animals visiting the area.

I concentrated my observations on the group of agoutis that lived in the vicinity of the observation platform from December 1966 until November 1967. Whenever possible, I observed for two periods of three to four hours each day. In addition, I watched any animals that I saw while I was working on the equipment in the study area. I observed the behavior of female agoutis and their young by sitting as far away as possible from the nest while still maintaining a clear view.

Observational data were recorded on, and later transcribed from, a battery-powered tape recorder. Sounds made by the animals were also recorded on this machine by means of a microphone suspended over the bait area at the end of a length of shielded cable. Field recordings were generally of rather poor quality because of the high level of ambient noise made by insects, anurans, and birds, which precluded the making of sonograms. Some photographic records of the animals visiting the area were made using a 6 × 6 cm single-lens reflex camera with lenses of 80 to 500 mm focal lengths. The line drawings included in this paper were made from the photographs so obtained.

Agoutis are typically almost wholly frugivorous, living mostly on the soft parts of ripe falling fruit when this is available, and practically exclusively

on the seeds that they buried earlier, when it is not. (In the mora swamp of the Osa peninsula agoutis occasionally eat crabs; those living on Ancon hill in the Canal Zone, an area isolated from surrounding forest by houses and streets, eat grass when fruit is not available. The diet is thus not necessarily entirely of fruit, but this is preferred when it is available.) It is thus possible to measure the quantity of food available to the animals living within a certain area by setting out "traps" to catch a sample of falling fruit. I set out 75 polyethylene sheets totaling 175 m^2 in area in the phase I study area, and measured the weight of falling fruits and seeds over a period of 17 months (Smythe, 1970b).

The Trap-Mark-Release Program

In September 1971, 50 Tomahawk (National), 23 × 23 × 81 cm, double-doored traps were placed in a rough triangle more or less encompassing the bed of a creek that drains a 10.01–hectare watershed basin on the opposite side of the laboratory clearing from the phase I study area (Figure 3). During the summer (June–August) of 1972, an additional 50 traps were set out around the perimeter of the watershed basin.

The phase II trapping area is topographically well suited for occupation by agoutis in that there are many small creeks that supply potential nesting places for the young. The southeast slope is covered by older second-growth forest trees and there are patches of much older forest toward the south. During the early 1960s there were several extensive landslips on the northwest slope, so the forest there is generally much younger. There are fewer of those fruit trees that the agoutis most prefer in this area than there are in the phase I area, but I do not believe that the population density is significantly different.

Each trap is hooked open and baited almost every day with a handful of dried maize. Every second Thursday afternoon the hooks are released and the traps are baited and set. Captured animals are removed the following morning at about 0900–0930 hours. They are identified, weighed, marked, and released. It is difficult to find an accurate field scale to weigh animals in the 1–10 kg range. The one that I use is a compact beam balance purchased from a home wine-maker's supplier. Its capacity is 20 lb (9.1 kg) and, provided it is kept level, it is accurate to about 1 oz (28 gm). The animals are marked using the ear-tattooing method described earlier. This mark proved to be long-lasting although it was becoming diffuse and difficult to read in some animals still living in the area in 1975 that were trapped in late 1971. The phase II numbering system was started from "1" so that the numbers of the phase II animals bear no relationship to those of phase I. Errors were occasionally made in the phase II marking, two animals being tattooed with the same number or a number being skipped entirely. In the case of two animals being marked with the same number, they were subsequently identified in the field by their sex or by their weight. For record-keeping purposes they were identified as "a" and "b" and are shown as such in the weight-curve and range figures (Figures 10–15).

Phase I: Results of Seasonal Changes on Behavior

Seasonality of the Food Supply

Many aspects of the behavior and ecology of the agouti are affected by, and appear to have evolved in response to pressures caused by, seasonal variations in the amount of food available. The chief manifestations of periodic food shortages, with regard to the behavior of the agoutis that I studied, were the increased probability of their entering traps and the increased time that they spent in the baited areas during those months when food was scarcest. The time spent together by members of a pair and the general level of intraspecific tolerance vary partly as a function of food abundance. As the fruit fall increases, territory holders tolerate trespassers to a much greater degree than they do at other times and maturing individuals may wander away from their parental home ranges to strange areas. Wandering males may court any females that they meet and newly formed pairs may set up territories in occupied areas. These areas may be unsuitable because of the lack of seeds that will last as a hoard.

The seasonal abundance of fruit falling into the "traps" described earlier varied as in Figure 4. A total of 72 species of fruits and seeds fell into the traps, and the number falling into any individual trap varied from 3 to 14 species. The number of species fruiting in any given month varied from

11 to 26, while the combined weight of fruits and seeds varied from a monthly average of 0.061 to 1.93 gm/m²/day. Large-seeded fruits, the preferred food of agoutis, tended to be more seasonal than those with small seeds (Smythe, 1970b).

There is thus a season of the year, from mid-April until mid-August when ripe falling fruit is very abundant. During the remainder of the year it is very scarce. Observations over subsequent years have indicated that the times of abundance and scarcity are fairly predictable. Evidence from several sources confirms this. For example, about the middle of each August, coatis (*Nasua narica*), tapirs (*Tapirus bairdii*), and pacas (*Cuniculus paca*) begin to frequent the laboratory clearing, especially the kitchen area, in search of "handouts." On the other hand the degree of shortage during the lean season appears to vary considerably from one year to another. During one year only a few beggars will appear, and they will stay for a short time. Whereas during another year many will appear and will not leave without having obtained something to eat.

Effects of Seasonal Abundance of Food

Figure 4 shows the relationship between the amount of time spent in the bait area by all the phase I agoutis using it and the quantity of fruit falling into the fruit traps. The time spent by the agoutis in the area was measured as the number of minutes each animal was present, expressed as a percentage of the total time I spent observing. Thus, if, for example, I observed for 100 minutes, during which time one agouti was present in the bait area for 75 minutes and another for 50 minutes, then the total agouti minutes spent in the bait area would be equal to 125. This would be expressed on the left ordinate as 125 percent of my watching minutes.

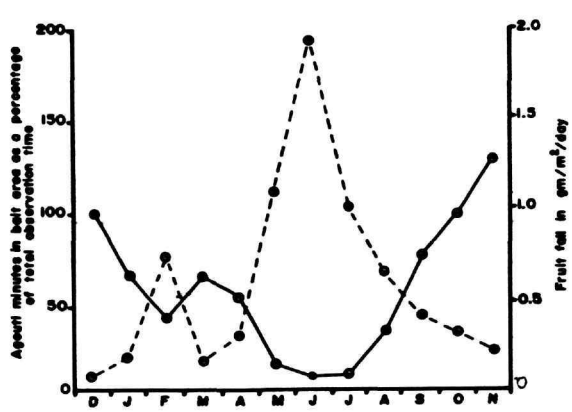


Figure 4.—Time spent per month by all phase I agoutis in the bait area (solid line) related to the abundance of fruit fall (broken line).

Figure 5 indicates the time spent in the bait area by the individual phase I agoutis that regularly visited it. The observation platform and the bait area were originally set up near the edge of the territory held by MSS and FSP. The neighboring territory holders were MRE and F13, who frequently foraged in the bait area.

The adjacent males, MRE and MSS, spent less total time in the bait area than did their mates, F13 and FSP, which were there approximately in proportion to the abundance of falling fruit. This is principally due to two factors. First, males spend more of their time within their own territories than do females, and secondly, when a male follows his mate as she goes foraging he usually only eats a few pieces of fruit before leaving to patrol in a circle around her. So when FSP and MSS arrived together, MSS would usually stay only briefly before leaving to patrol in a circle around her. During December and January, MRE did not follow F13 very often when she came to the bait area.

As fruit became more abundant, the time spent together by the members of a pair increased (Figure 6), so that both MSS and MRE appeared in the bait area more often with their mates. Then, when fruit was at its maximum abundance, both males started to spend less time with their mates in the bait area. This was partly a reflection of the general increase in attendance by all animals, but was also probably because both of the females gave birth at that time, so that, when they visited the bait area it was only to eat a little and then take some food back to their youngsters. As fruit became more abundant both members of the pairs spent more time deeper within their territories, foraging and scatterhoarding.

The subadult male m22 was living in an area to the southeast of the bait area in September of 1966 (Figure 7). I believe that he was the offspring of F20 and that his parents had recently driven him out of their territory. In December, he became paired with FSB who came from somewhere to

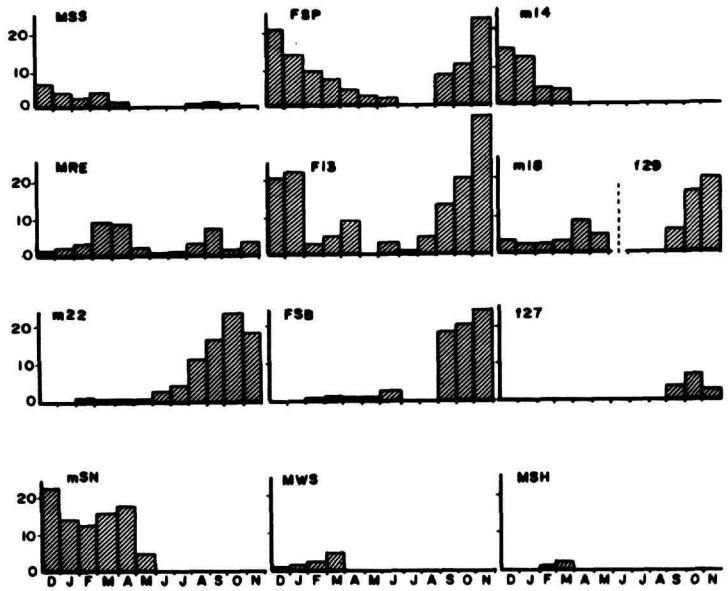


FIGURE 5.—Time spent per month by individual phase I agoutis in the bait area (ordinate values are percentages of total observation time).

the south or west of where he was living. FSB was already an adult female when she first appeared and could have lost a previous mate before joining with m22. They occasionally visited the bait area as individuals until April (Figure 5) when all agoutis were generally visiting it less often (Figure 4). From June onward m22 and FSB began defending the bait area as part of their territory and, when fruit again became scarce, were the dominant animals there (Figure 7).

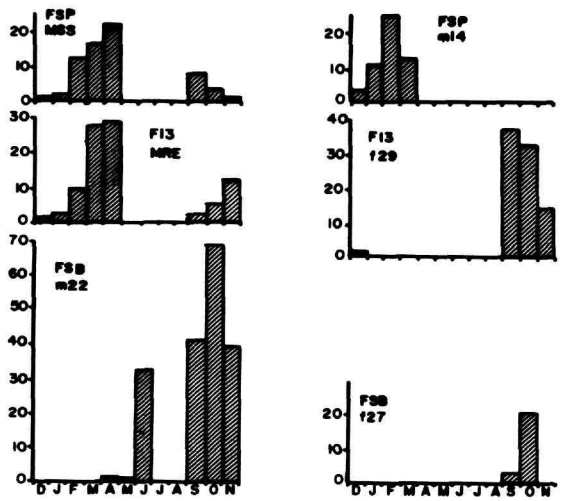


FIGURE 6.—Percentage per month of time spent in the bait area by phase I adult females with their mates or offspring (ordinate values are percentages of total observation time).

The area around my observation platform, especially to the south, where m22 originally spent most of his time (Figure 7), was used very little by adult agoutis and thus appeared to be suboptimal habitat. The fact that I supplied fruit during the season when none was available in the forest, even though the quantities that I put out were small, made my bait area temporarily more favorable than the surrounding area. As fruit became generally abundant in the forest, the more central areas of the surrounding territories became more favorable to their occupants, who moved there to feed on the greater quantities and greater varieties of fruits, as well as to scatterhoard the seeds.

One of the main reasons why the area where m22 and FSB were living was suboptimal was probably that it contains few agouti food-fruit trees. So my bait area would still have represented their best source of food, and it became the focus of their activities. They hoarded food there, deposited scent marks, and made more trails, and eventually

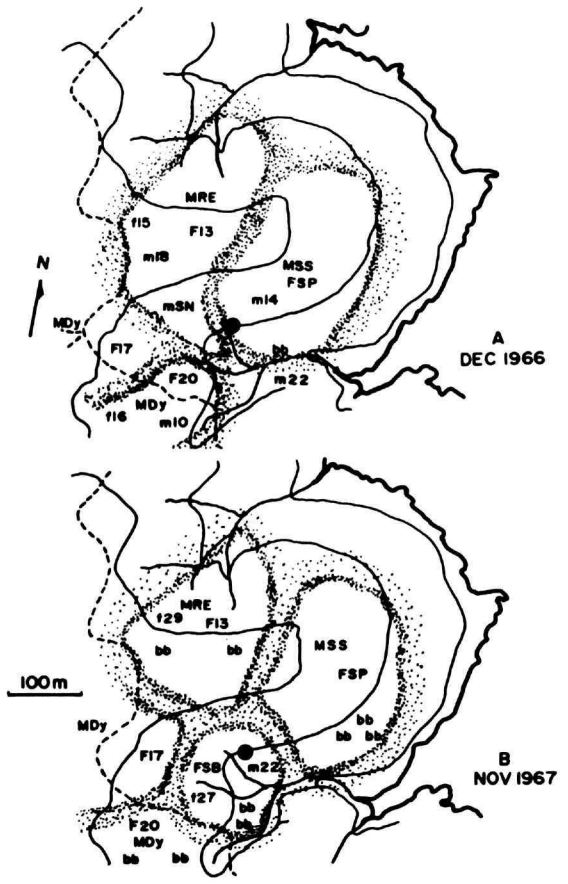


FIGURE 7.—Phase I territories surrounding the bait area (large dot) and the changes undergone between the end of 1966 and the end of 1967 (bb = infants that did not survive to leave the nest).

set up a territory that they were able to defend when fruit in the forest again became scarce and the surrounding territory holders attempted to return. I do not know what happened to m22 and FSB after I terminated the study and stopped putting out bait, but since this consisted of pieces of banana it would not have lasted as a hoard. I suspect that they had some trouble surviving the remainder of the season of fruit scarcity.

A similar situation could have existed for the older subadult males that disappeared. They could have moved into adjacent suboptimal habitats when fruit became generally abundant and attempted to set up hoards there. One of the factors that probably contributes to a habitat being suboptimal is a lack of food plants bearing seeds that, once scatterhoarded, remain available and edible until they are needed as a food source. The subadult agoutis could have moved into such areas and then, when fruit once again became scarce, died of starvation or other causes related to lack of food.

Any males that survived the season of scarcity would be fully adult by its end and perhaps would challenge the surrounding territory holders for mates. MWS and MSH could thus have been the surviving males from the year before, unsuccessfully challenging the territory-holding males for their mates. Also FSB could have been a subadult female that survived the season of scarcity in a suboptimal habitat, joining with m22 in December.

The attendance in the bait area of juveniles and subadults is represented in Figure 5. Juvenile male 14 and mSN utilized the area in inverse proportion to the amount of fresh falling fruit, until the time when it became abundant, and then they suddenly disappeared. Although the time he spent in the bait area was more irregular, m18 also disappeared during the time when fruit was abundant. I saw none of these animals again, and can only speculate on their fate. Data from phase II indicate that such animals probably die (Figure 17).

Two strange adult males, MWS and MSH, came to the bait area early in 1967, were there occasionally until sometime in March, and then disappeared. They both appeared to be in reproductive condition, for they courted and attempted to enurinate both F13 and FSP.

During both phases of the study the probability of agoutis (and the other species of animals that were trapped) entering traps varied approximately inversely with fruit abundance. During each year of the phase II trapping program the incidence of trapped animals has risen sharply about the middle of August.

In order to further verify the existence of a seasonal shortage of food I put out small (about 200 gm) conical piles of dried maize at various points in the study area. During those months when the fruit sampling data indicated that large quantities of fruit were falling, these piles would remain completely undisturbed, except by falling rain, and the seeds would germinate. This resulted in a small clump of seedlings that withered and

died, probably for lack of light. During those months when very little fruit fell, the piles of maize would be totally consumed within one to four hours of their being put out, and the ground in a 2-m circle around each pile would be rooted up (by collared peccaries, *Tayassu tajacu*) to a depth of 25 cm or more.

I conclude that all animals in this habitat that depend heavily on fruit for food experience a season when it is in short supply, and so must either store food in some way or change their diet in order to survive the season of deprivation. The fruits with larger seeds (> 1.5 cm in their largest dimension) undergo the greatest seasonal variation in abundance, so the animals depending heavily upon them for food must undergo the greatest seasonal adjustment.

Frugivores that can climb or fly have the advantage of being able to obtain fruit that is ripe enough to eat but not yet ripe enough to fall. They may thus be able to obtain ample food some months before the purely terrestrial frugivores. Many trees have protective devices such as spines on their trunks, apparently to protect the immature fruits from these attacks, but the protection is often subverted and the early food supply is utilized by monkeys, coatis, bats, and others.

Seasonal Changes in Aggressive Behavior

Figure 8 illustrates the ratio between the amount of aggressive behavior initiated and the amount sustained by each individual in phase I and the seasonal changes in this behavior. A monthly index of aggression for each agouti is derived by taking the number of attacks initiated against any conspecific by the particular animal per unit time spent in the bait area and multiplying this by the number of different conspecifics attacked. Subtracted from the result is the number of attacks sustained by the same animal per unit time spent in the bait area multiplied by the number of agoutis initiating these attacks. The resulting numbers are positive, negative, or zero, and correlate well with my subjective impressions of which animals were dominant.

In December 1966 the animal with the highest index of aggression was MSS, who is dominant in the area upon which the bait area was situated. MRE, the nearest territory-holding male, initiated

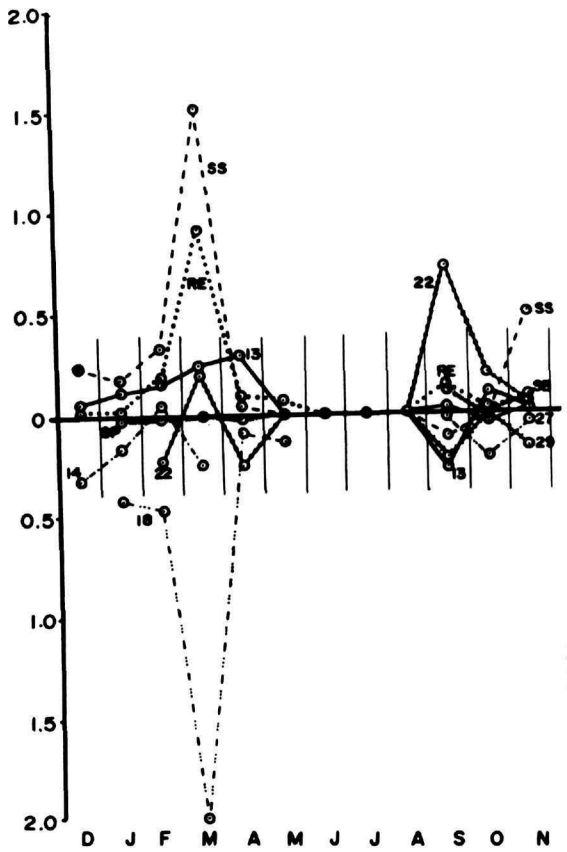


Figure 8.—Aggressive indices for phase I agoutis.

only slightly more attacks than he sustained; but, since falling fruit was scarce in the forest, he continued to exploit the bait that I had put out (Figure 5). In March there was a decided increase in the total amount of agonistic behavior exhibited by the group. MSS was still the dominant animal but MRE was also initiating a considerable number of aggressive encounters. The subadult males m18 and m14 were both sustaining a large number of attacks (m22 was in the bait area for only 10 minutes, so the index for him is misleading). Females generally neither initiate nor sustain much aggression. F13 was more aggressive than either FSB or FSP, which I believe is due to her greater age and the possibility that she is a local "matriarch."

The number of agonistic encounters fell sharply in April and remained very low throughout the rest

of the time that fruit was abundant. Agoutis, when they met, were more tolerant of one another at this time. In addition, since many more trees were dropping fruit and the animals were moving from one food source to another they met less often and thus had less opportunity to fight.

In September, however, as fruit became scarce, the surrounding agoutis began to return to the bait area for food. During the months when fruit had been generally abundant, m22 and FSP had been utilizing the bait area and the area around it as the center of their activities. In September, however, there was an increase in the number of agonistic encounters as m22 defended what had now become his territory. In October and November, the neighboring males attempted to utilize the bait area less, but the females came there approximately in proportion to the decrease in the amount of available wild fruit (Figures 4, 5).

Phase II: Results of the Trap-Mark-Release Program

Species Trapped

In addition to agoutis, six other species of mammals regularly enter the traps. These are, in approximately descending order of trapping frequency, *Cuniculus paca,* the paca; *Proechimys semispinosus,* the spiny rat; *Nasua narica,* the coati; *Didelphis marsupialis,* the common oppossum; *Philander opposum,* the four-eyed oppossum; and *Sciurus granatensis,* a red squirrel. In addition, *Tayassu tajacu,* the collared peccary, and *Diplomys darlingii,* an arboreal rat, have occasionally been caught, as have several common iguanas (*Iguana iguana*). Doves (*Leptotila cassini*) were frequently caught.

Numbers and Age Classes

For the sake of meaningful analysis, it is necessary to divide the population of agoutis into reproductive and nonreproductive animals. Among the animals that I observed during phase I were several that had achieved the weight of breeding animals but were not mated, were more nomadic, and were the recipients of more aggression than they initiated. So weight alone cannot be a true indicator of the status of an agouti. Moreover their reproductive condition is not necessarily immediately evident even when the animal is in the hand. I therefore decided to label all animals whose weight was below 2300 gm as "juveniles" and all those whose weight was greater "adults." As I shall show, it is often possible to identify nonreproductive "adults" from characteristics that appear in their trap records.

The results of the trapping program are illustrated in Figures 9–17 and in Tables 1 and 2. (The apparent discrepancy in Table 1 between the total number trapped and the highest number marked is due to some numbers being omitted in the tattooing process.) A grand total of 87 agoutis had been trapped as of 19 December 1975. Of these, 48 were male and 39 female. According to the age criterion given above, 34 of the males were juvenile when first caught, and 14 were adult. Twenty-five of the females were juvenile and 14 were adult.

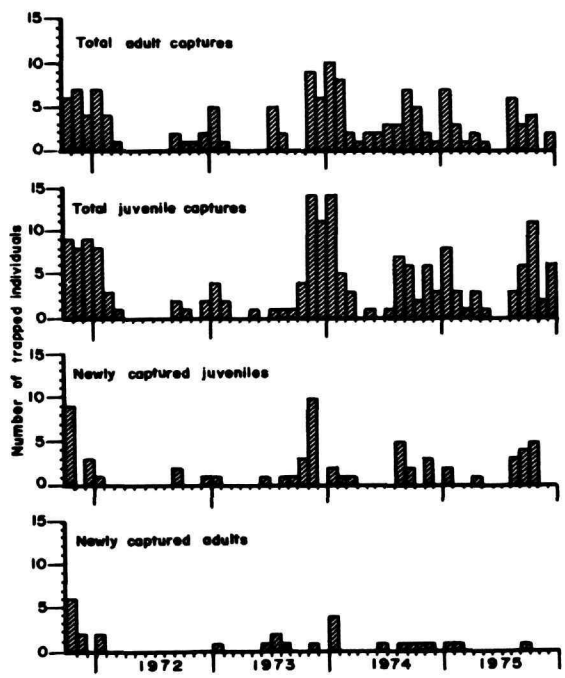


Figure 9.—Numbers of phase II agoutis trapped during each month.

Trapping Locations

Figures 10–12 show the locations at which each animal was caught during the "winter" (August-February) of each year. Each figure is a map of the study area, the narrow lines representing the creeks that drain it and the dots representing the locations of the traps. The thick lines join the trap locations at which individuals were caught, but no attempt is made to indicate the sequence of captures, nor to signify multiple captures at a given point.

For those animals that were captured at more than one location, I measured the maximum distance between their capture points (Table 1).

Reference to the trapping maps of the juveniles (Figure 11) shows that they tend to occur in groups, and that there is surprisingly little overlap between the groups. The data from the observational phase of the study indicate that there should be a pair of adults with each group of juveniles. But I also learned at that time that adults, especially males, seldom enter traps, so it is not surprising that it is not possible to identify a pair of adults for each group of juveniles. There is, however, an adult female that occurs in the same area as some of the groups and usually in the same small area year after year.

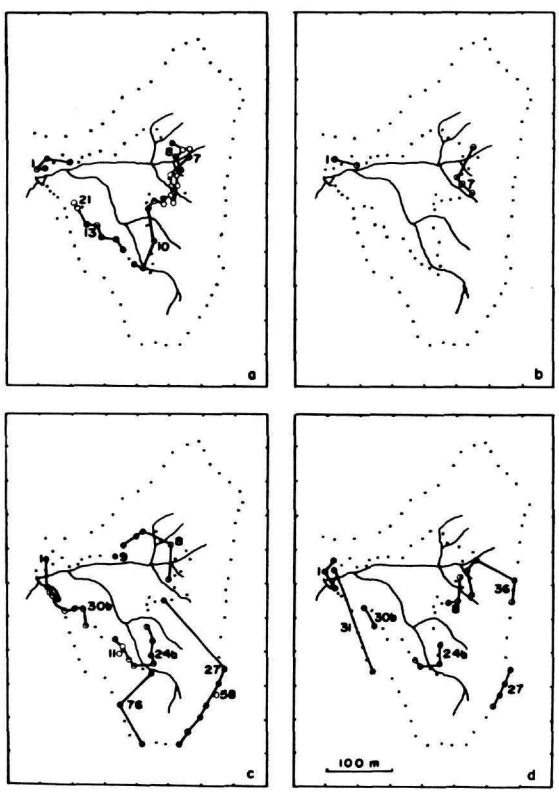


Figure 10.—Winter (Aug–Feb) trapping locations of phase II adult female agoutis: *a*, 1971; *b*, 1972; *c*, 1973; *d*, 1974.

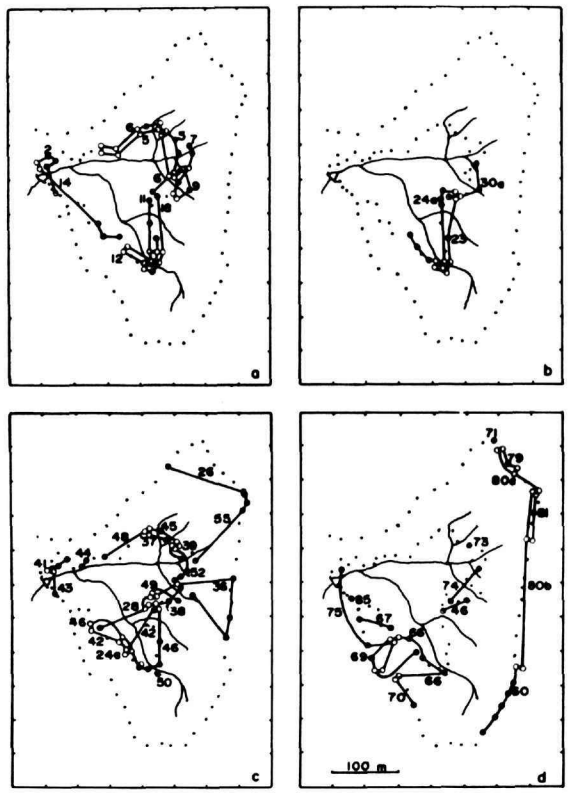


Figure 11.—Winter (Aug–Feb) trapping locations of phase II juvenile agoutis: *a*, 1971; *b*, 1972; *c*, 1973; *d*, 1974.

The groups of juveniles were most clearly delineated in 1971 and 1973 (Figure 11). If we compare Figure 11*a* with data for adult females for 1971, (Figure 10*a*), we see that female 1 is in the same area as juvenile male 2 and that adult females 7 and 8 are in the same area as juveniles 5, 6, and 9.* Female 10 is the adult whose area corresponds with that of juveniles 11, 12, and 18, while female

* f1 was below 2300 gm only the first time she was caught, gaining weight very quickly thereafter. She is more likely to be a sibling than a parent of m2. She subsequently became established as a dominant female in the same area. Female 7 started the season as a juvenile, probably the twin of f9 (Figure 15), so F8 is the locally dominant female.

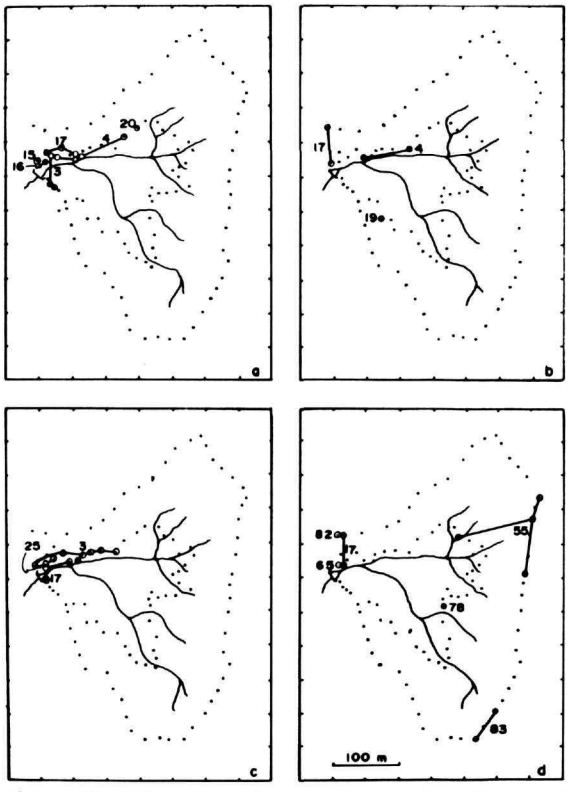


FIGURE 12.—Winter (Aug–Feb) trapping locations of phase II adult male agoutis: *a*, 1971; *b*, 1972; *c*, 1973; *d*, 1974.

13 (with F21 as a brief visitor) occupies the same area as juvenile 14.

LIFE HISTORY CURVES

Figures 13–15 represent the weights of each animal each time it was caught, and thus form a graphical history of each animal's participation in the study. If an animal was caught more than once during any given month, its weights during that month were averaged. In each of the weight-curve figures for juvenile animals (Figures 15, 16) I have marked a broken line which represents the average rate at which three captive-born agoutis grew (with as great a food supply as they would eat). Those wild animals that were born during the seasons of fruit abundance could reasonably be expected to grow at approximately the same rate as the captives since, in both cases, a superabundance of food was available. In fact, wild animals probably grow somewhat more slowly since they must devote some of their time and energy to the avoidance of predators and they must move further than across a cage to collect their food. During the season when food becomes scarce, the growth rate of the wild animals will be considerably lower, and some may even lose weight. If, however, the captive growth curve is fitted to meet the first capture point of those juveniles that were initially caught during, or shortly after, the season of abundance then an approximate date of their birth may be derived. (In early versions of these graphs I calculated the probable growth rate for those animals that were caught for the first time outside of the period of fruit abundance on the basis of the average growth rate of others that were repeatedly trapped. The curves thus derived indicate that practically all of the juveniles caught in the entire study were born during or very close to the season of fruit abundance. I have not included the additional curves here since the figures are already cluttered.)

If the estimated dates of birth derived from the captive weight curves are taken literally, it is obvious that f11, m12, and f18 were born at too nearly the same time to have had the same mother (assuming litters no bigger than two and a three-month gestation period). There are a number of possible explanations for this (and similar cases): the locally dominant female could have had a litter of more than two. I think that this is very unlikely; one is the usual number successfully raised to the point of foraging without parental accompaniment, although litters of two, especially during the season of fruit abundance, do occur. I have never seen larger litters. A second possibility is that there is more than one breeding female to an area. This is quite possible. In the phase I population there was an older female (F13) who was able to wander through the surrounding territories with relatively little chance of being chased (p. 21). I believe that she was the mother of several of the surrounding dominants and, while she held an area of her own (a task chiefly relegated to her mate), she was able to move freely through those of her offspring. Her newer young would tend to stick much more to her home area and not to wander with her. So I do not think that the discrete groups of juveniles in phase II had more than one set of parents involved. The remaining possibility is that the estimated birth

TABLE 1.—Statistics on each phase II agouti (asterisk indicates that the animal was caught for the first time during the winter of 1975, which was not over at the time of this analysis)

Animal	No. of times trapped	Months betw. 1st and last capture	Maximum distance betw. trap-sites (m)	Animal	No. of times trapped	Months betw. 1st and last capture	Maximum distance betw. trap-sites (m)
			ADOLESCENT MALES				
m2	5	4	56	m66	8	17	94
m5	16	18	121	m67	4	5	53
m6	7	4	121	m68	2	6	0
m12	5	4	55	m70	3	2	53
m19	2	10	25	m71	1	-	-
m23	6	7	102	m74	3	14	62
m24a	18	17	117	m75	4	5	123
m26	4	17	121	m80a	5	6	98
m30a	3	12	62	m80b	3	2	249
m34	1	-	-	m81	4	4	87
m41	4	3	45	m82	1	-	-
m42	5	4	91	m84*	2	3	-
m44	3	2	11	m87*	3	5	-
m49	2	2	128	m88*	2	2	-
m50	1	-	-	m89*	4	4	-
m55	11	20	153	m90	2	4	-
m59	1	-	-	m92	2	1	-
			ADOLESCENT FEMALES				
f1	10	28	62	f46	6	11	100
f7	15	39	77	f48	2	3	76
f9	11	28	51	f51	1	-	-
f11	11	4	93	f52	4	21	49
f14	4	29	151	f60	7	18	147
f18	6	3	109	f69	5	4	47
f28	14	28	83	f73	1	-	-
f36	14	29	136	f79	3	3	41
f37	5	3	60	f85	1	-	-
f38	1	1	25	f86*	3	3	-
f39	1	-	-	f97*	1	-	-
f43	3	1	30	f98*	1	-	-
f45	3	4	47				
			ADULT MALES				
M3	8	29	121	M53	1	-	-
M4	4	22	89	M54	2	-	0
M15	1	-	-	M57	1	-	-
M16	1	-	-	M65	1	-	-
M17	17	50	93	M78	1	-	-
M20	1	-	-	M83	2	4	37
M25	2	5	0	M93*	2	-	-
			ADULT FEMALES				
F8	15	50	109	F31	2	7	164
F10	8	44	108	F40	1	-	-
F13	8	26	96	F47	3	3	-
F21	1	-	-	F58	1	-	-
F24b	11	23	70	F76	4	14	106
F27	12	17	213	F77	1	-	-
F30b	7	14	76	F91*	1	-	-

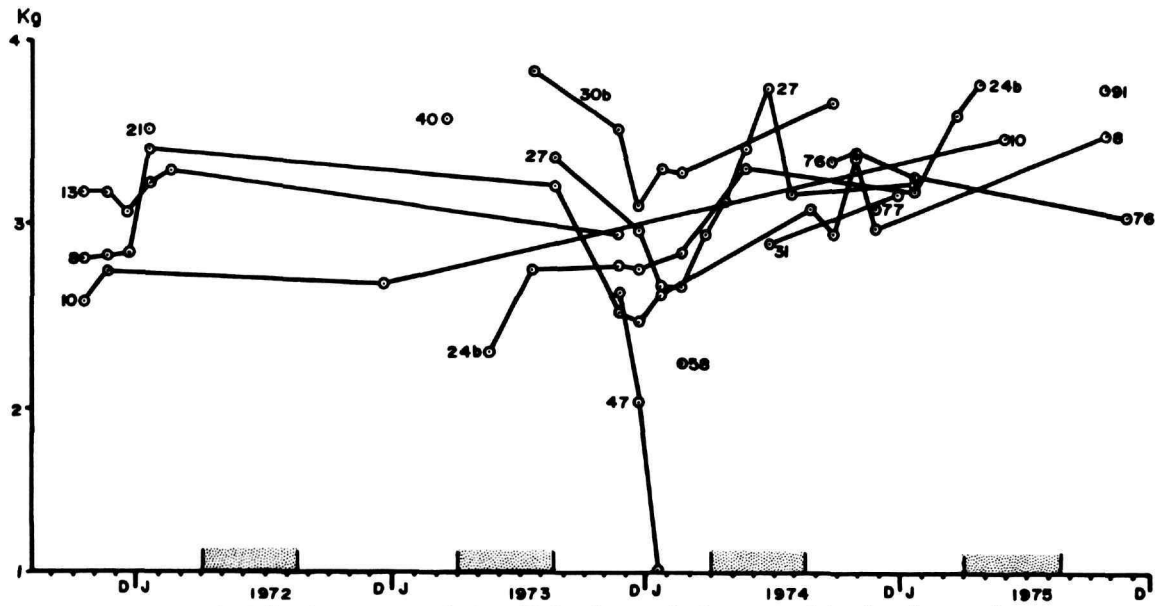


FIGURE 13.—Life history curves of phase II female agoutis that were adult when first caught (stippled areas = seasons of fruit abundance).

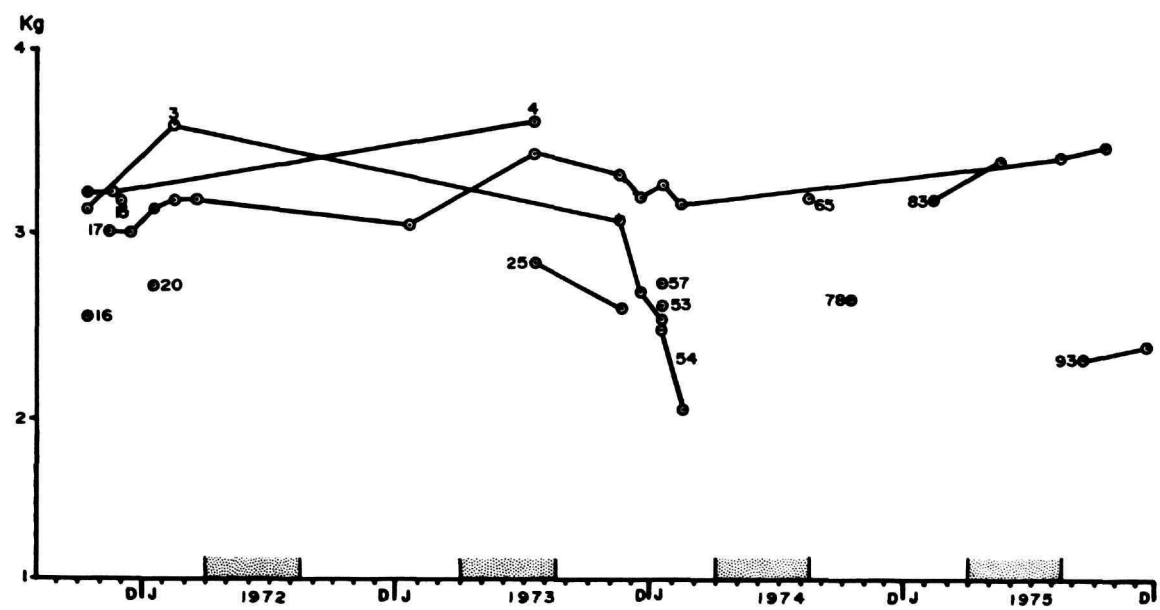


FIGURE 14.—Life history curves of phase II male agoutis that were adult when first caught (stippled areas = seasons of fruit abundance).

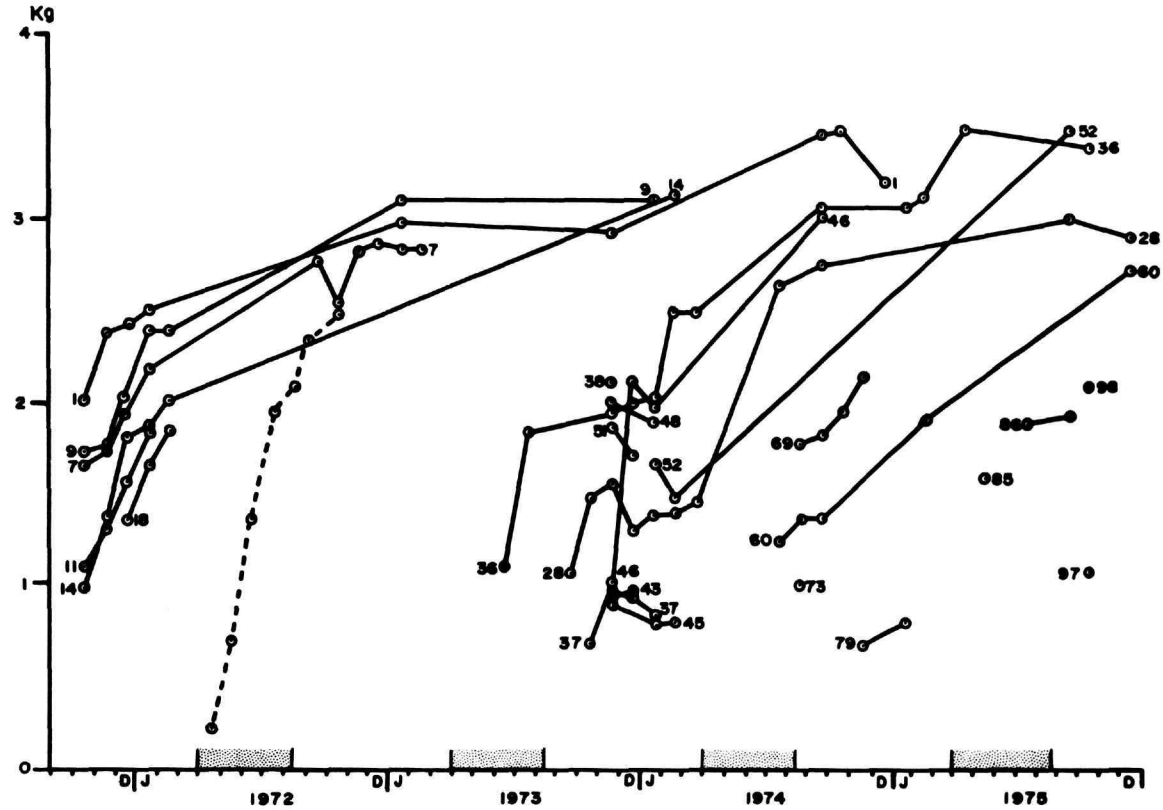


FIGURE 15.—Life history curves of phase II female agoutis that were juvenile when first caught (broken line = average growth rate of 3 captive-born agoutis; stippled areas = seasons of fruit abundance; no weight data for f39).

dates are wrong. This is the most likely explanation, although I believe that the error occurs in a predictable fashion: very young agoutis, while under the care of their mothers, may grow at the same rate as captives that have access to superabundant food supply, but as they become older and must spend more time guarding against attack by conspecific aggressors and predators, their rate of growth falls below that of captives of the same age. Thus the estimated dates of birth should be displaced more to the left (i.e., earlier in the year) the older an animal was when it was first captured. So f11 and f18 were probably twins born in August, and m12, who weighed about 300 gm more when first captured, was born 3 months earlier.

In 1973 (Figures 10*c*, 11*c*, 12*c*), the groups are not as clearly delineated, but there have been some interesting developments since 1971 (Figures 10*a*, 11*a*, 12*a*). Now adult f1 still occupies the same area and juveniles m41 and f43 appear there (Figure 11*c*) Now adult f7 has reached adult weight; she and f1 were the only adult females trapped in 1972 (Figure 10*b*), but F8 was almost certainly still present for she appears in precisely the same area again in 1973 (Figure 10*c*). In fact, F8 is probably the oldest female in the study, since she was fully adult when first trapped in November 1971 (Figure 13). Now adult f9 appears in the same area as F8 in 1973, but looking back to Figure 15 we see that f9 has a similar history to that of f7; she was born during the season of abundance of 1971, and was first captured during October of that year. She grew to adult weight at approximately the same rate as the captive animals, remained in the area for a while and

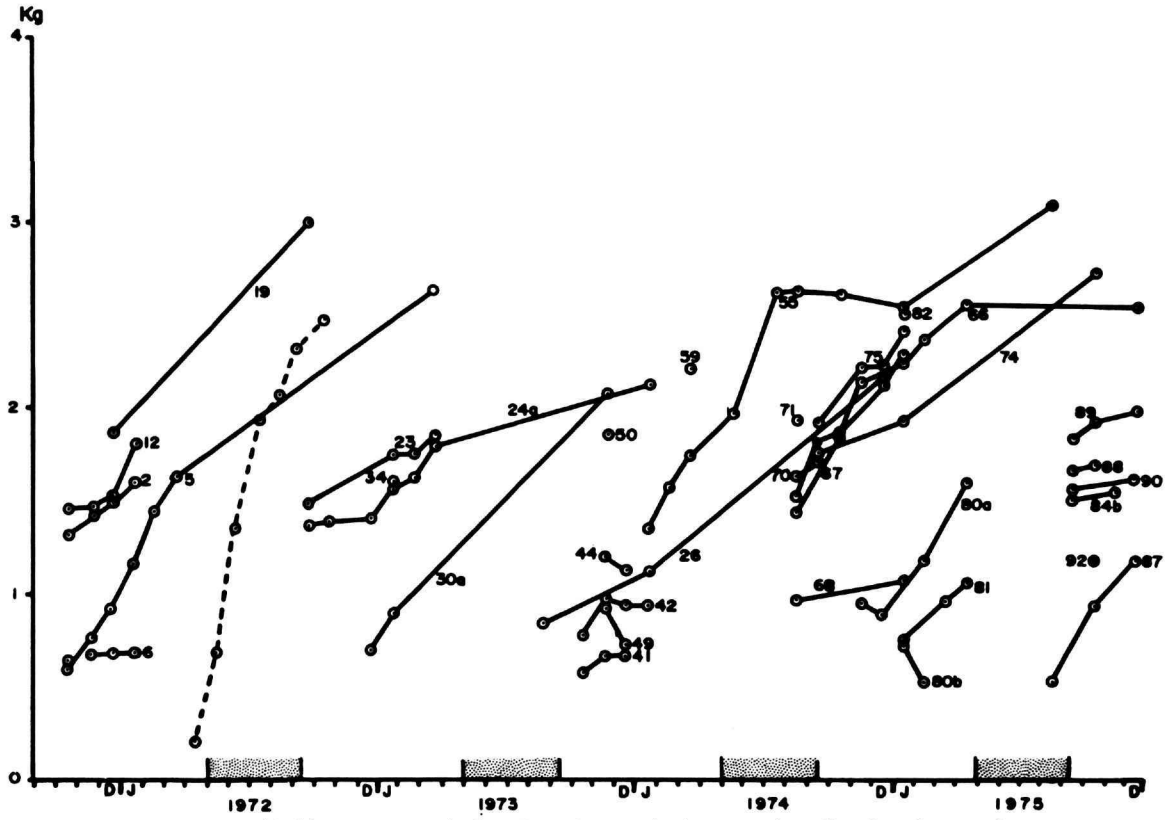


FIGURE 16.—Life history curves of phase II male agoutis that were juvenile when first caught (broken line = average growth rate of 3 captive-born agoutis; stippled areas = season of fruit abundance).

then was suddenly absent from the traps. The juveniles appearing in F8's area in 1973 are f37 and f45 (possibly twins born in September) and f48 and f52 (twins born in June or early July). F24b appears early in 1973 (Figure 13) and achieves adult weight. It appears that she is the locally dominant female, but then we see (Figure 13) that F10 was retrapped in May 1975. A range map has not yet been prepared for the 1975–1976 period of deprivation, but F10 was caught in the same trap that she entered in November 1971. She was limping rather badly in May 1975 and did not appear very healthy, although her weight did not indicate this. During the first part of 1975, F24b gained weight steadily; probably partly as the result of pregnancy. Her apparent thriving condition, as opposed to the poor condition of F10 the last time she was caught, may have indicated that F24b was in the process of displacing F10 as the locally dominant female.

Some general conclusions can be drawn from the weight-curve figures. It is evident, for instance, that not all seasons of abundance or deprivation are equal in their effects on the animals. During the winter (August through February) of 1971, most animals showed some increase in weight. Food could not have been actually abundant at this time or the animals would not have entered the traps; nor, I believe, could the food used in the prebaiting program have contributed substantially to the general weight increases. The same quantities of bait were used during the winter of 1973 and during that time there was a general loss of weight throughout the population; a loss that was fatal to some animals. This indicates that there was probably a

general lack of hoardable food items during the summer of 1973.

The Ridgetop Traps

The outer ring of traps, which follows the ridgetops that form the boundaries of the study area basin, has always been less productive than the inner ring. This is what I would have expected from my earlier observations, which indicated that agouti activity is generally concentrated toward the beds of creeks rather than toward the ridgetops. Nevertheless, analysis of the few captures in the outer ring is informative. In 1973 (Figure 10*c*), F27 appeared and was fairly regularly trapped there. F58, who was barely heavy enough to be designated an adult, was also trapped there once. But no young juveniles (who were not first caught lower in the creekbed areas) appeared there. Then, in 1974, F27 reappeared (Figure 10*d*) in the same area and so did two juveniles, f60 and m80b (Figure 11*d*), but they were not trapped in the lower area. Reference to the weight curve of F27 (Figure 13) indicates that her weight was high when she was first caught (in August 1973, at the end of that period of fruit abundance). Then her weight fell sharply in the ensuing lean period. She gained weight again as food became more abundant and almost certainly gave birth around the end of June, for at that time her weight again dropped sharply.

Since F27's weight loss in late 1973 was too great to be caused by parturition alone (many other agoutis lost significant weight at the same time), and since it occurred at the time of minimum food abundance, I believe that the following conclusions are warranted. When first trapped in August 1973, F27 was a nonreproductive young adult, probably born during the period of fruit abundance of 1972. Her parents lived in the creek drainage area that runs in the opposite direction from the study area creek (i.e., on the other side of the ridge on which she first appeared). She survived the winter of 1972 living on and around her parents' territory, and reached adult weight in the spring of 1973. When she achieved potential breeding size she was harrassed by her parents and, taking refuge in the less desirable ridgetop area of their range, discovered the trap line. The prebaiting program assisted her survival, in spite of a severe weight loss, through the winter of 1973. She then mated and settled somewhere on her home slope (either by replacing or, more probably, living near her parents). During the winter of 1974, she continued to exploit the traps, having become familiar with the area. At the same time her offspring, f60 and m80b, as well as an adult male, M83, who could well be her mate (Figures 10*d*, 11*d*, 12*d*), followed her there.

Adult Males

As I had discovered during the first phase of the study, adult males will seldom enter traps. The data concerning them are thus rather sparse; however, some interesting information can nevertheless be gathered about them. Only one, M17, has been trapped regularly since the inception of phase II, and he was already a full-grown adult at the time. His area almost exactly coincides with that of f1 throughout the study and it is very probable that they are a mated pair. At the beginning of the study another adult male, M3, lived in the same area, and was somewhat heavier than M17. It is thus possible that M17 was one of those animals that had achieved adult weight but was not yet reproducing at the time that M3 was reaching the end of his life. As f1 became old enough, she and M17 mated and began to take the area over from M3 and his mate, who remains unidentified. M3 was not trapped again until the end of 1973, at which time his weight went into steep and almost certainly fatal decline.

Adult male 55 may have been born in August or September 1973 and is probably the offspring of F8. He weighed only 1300 gm when first trapped in January 1974 (Figure 16). This means that he was born very late in the season of food abundance of 1973, and would still have been small when food began to grow scarce. Difficulty in competing with larger juveniles (at a time when, judging by the number of animals that lost weight, food must have been very scarce indeed) probably drove him to explore further afield than would normally have been the case for one of his age. Thus he found the outer ring of traps and exploited the food that was available there. He, m26, f36, f46 were the only animals caught during the lean period of 1973 who showed any significant gain in weight each time that they were caught. Most of the rest of the agoutis caught during that period lost some weight. Juvenile female 36 was first caught in June of 1973. She was

caught again just over a month later and had gained weight at approximately the same rate as captive animals. She was not trapped again until November and at that time weighed very little more than she had in July. Actually she had probably gained weight through July and early August and had then lost some of it before the next time she was trapped. In February 1974, she was caught in the outer ring of traps for the first time. She was caught again in March and showed a slight loss of weight. Thereafter she gained weight to become a large adult (3670 gm) by April 1975. The weight increases that she showed in early 1975 may well have indicated pregnancy and it is probable that she has successfully established residence as a reproductive dominant in the area. Whether she, and the other animals that have been moved apparently as the result of my prebaiting program to less favorable areas, can continue to survive there is difficult to say. It would seem that their reproductive success will probably be lower on account of there being fewer nesting refuges for the young. The adults, however, may continue to live there for some time.

Life Expectancy of Juveniles

Figure 17 shows the length of time over which individual agoutis that were juveniles when first caught were trapped. The left axis shows the number of survivors, divided according to their sex, and the right shows the cumulative precentage that dropped out of the study after a given period of time. Table 2 shows the number of months spent by the members of each class in the study.

Figure 17 can also be interpreted as a curve of probability of survival for those young agoutis that leave the nest to begin foraging on their own. If it is accepted as such, we see that the times of greatest mortality in the population of growing animals occurs at those times when food is scarcest and that few young survive to become reproductively active animals. We have seen from Figures 15 and 16 that most of the young that survive to leave the nest and begin foraging on their own are born during the time when food is most abundant. As the season of abundance ends and food becomes more difficult to find, agoutis (especially the younger ones) begin to enter the traps. At the same time there is heavy

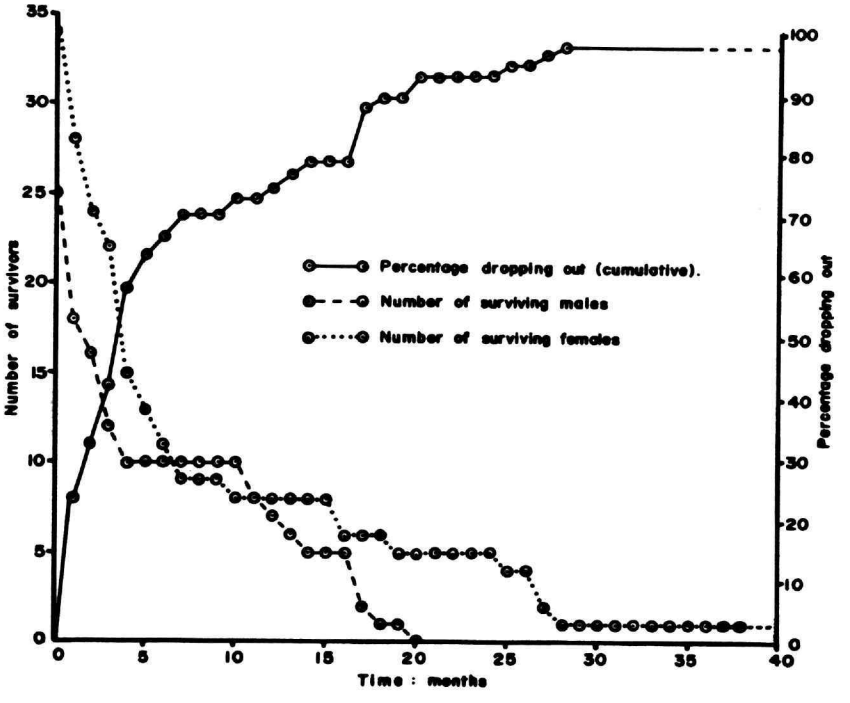


FIGURE 17.—The time between first and last entrapment for phase II agoutis that were juveniles when first caught.

TABLE 2.—Average number of months between first and last capture for each age class of phase II animals (the last two entries show the average for adults caught more often than in only one month)

Age class	Average number of months
Juvenile males	6.53
Adult males	8.00
Juvenile females	8.83
Adult females	15.50
All adults	11.75
All juveniles	7.68
Adult males caught more than once during phase II	18.50
Adult females caught more than once during phase II	24.20

mortality so that about seven months after food begins to grow scarce, more than 70 percent of the original population of subadult agoutis has died. Food becomes scarce about the middle of August (Figure 4). If August is taken as the hypothetical point of initiation of the time axis in Figure 17, it can be seen that this first seven months represents the first season of deprivation for a growing young agouti and the subsequent increases in mortality occur predictably at roughly those times when food would be expected to be growing scarce.

In terms of probability of mortality, an animal suffers a 70 percent chance of dying during its first period of deprivation (months 1 through 7), but a less than 5 percent chance of succumbing during the succeeding season of plenty (months 8 or 10 through 13 to 15). By the end of that season any surviving agoutis will be potentially sexually mature and thus subject to increasing aggression from locally dominant animals. As food becomes scarce again there is another increase in mortality with the males suffering more than the females. (In Figure 17, the curve for males drops to zero surviving in month 20. This, of course, would not happen for the entire population. It is an artifact of the number of animals participating in the study.)

MORTALITY DIFFERENCES BETWEEN THE SEXES

In the population making up the study group there were nine more males than females when they began entering traps. But, by the end of the first lean season, the numbers of the sexes were equal. The number of males and females remains equal through the following period of food abundance and then the number of males drops to zero. Sixteen to 20 months after their first becoming old enough to forage from the nests, all the animals would be potentially sexually active. The more rapid extinction of the young males could possibly be caused by their receiving a greater amount of aggression from the adult population.

The Use of Space

AGOUTI TERRITORIES

Among the agoutis that I have watched, the social units for reproductive adults consists of a mated pair. The amount of time that the members of the pair spend in one another's company may vary seasonally, being greatest when falling fruit is least abundant (Figure 6), but the pairs seem to be permanent and to last until one of the members dies. Each pair occupies an area of approximately one to two hectares (Figures 7, 10–12), within which they are aggressive against and normally dominant over conspecifics, and in which they spend most of their time.

I speak of agoutis as being territorial many times in this paper. It is not my intention to cause confusion in the minds of those who reserve the term to describe the defense of an area from which all conspecifics of the same sex are excluded. In order for that situation to pertain it is necessary for the defender to maintain better communications with the limits or boundaries of the defended area than is possible for forest-dwelling, terrestrial animals. Other agoutis can, and regularly do, enter adjacent defended areas. If a tree comes into fruit on a given territority it is regularly visited by the agoutis living in the surrounding areas. Both reproductive and nonreproductive animals trespass. When the resident animals detect the presence of intruders they may attempt to drive them away. The rigor with which they do this varies seasonally; being most pronounced when falling fruit is scarce, and greatly reduced when it is abundant.

At times when food is scarce the male will usually drive away any strange agoutis that he detects, but he is more aggressive toward other males. Females are less active in the defense of their territory but they will usually drive away other females. Both sexes harass any subadults that they meet and will attack the juvenile offspring of adjacent territory

holders, even when they meet them on their parents' territory.

The defensive activites of the residents are more concentrated within the territories than around the edges, and the deeper into a territory that an intruder goes, the more likely he is to be attacked. The boundaries of the territories are not absolutely defined and, moreover, they may vary seasonally, the areas of heaviest use shifting as trees in different parts come into fruit. As marked in Figure 7 the boundary lines connect points from which I saw residents successfully drive off adult conspecifics, or they represent paths along which patrolling residents moved or did not cross (or they join each of these types of indicators).

There is considerable individual variation in the behavior of adult dominant animals as far as their defenses of a home area is concerned. Female 13, who I believe was the oldest animal in the phase I study group, was able to wander through the surrounding territories at any time of the year, with far less probability of suffering an attack than was any other agouti. In this respect she was similar to the founding female of the group of agoutis in the 900 m^2 enclosure in the zoological park at Tuxtla, Mexico. This female could closely approach, and successfully compete for food with, any other group member and received practically no aggression in return.

The young animals are continually harassed by reproductive adults but they (especially the young females) nonetheless seldom move very far away from their parents' territory. Unless they are able to set up a breeding territory of their own their chance of survival much past the age of normal sexual maturity is slight (Figure 17) and the likelihood of a maturing animal being able to set up a territory is also slight unless a local territory holder dies at the appropriate time. It thus seems probable that the territory of an old animal will be surrounded by those of its offspring, and that, even though territories are maintained, there will be interterritorial dominance heirarchies set up as well. Female 13 was probably the mother of several of the surrounding territory holders and may have maintained her earlier dominance over them and thus have been able to move with relative impunity through territories that they rigorously defended against others.

The "territories" are thus not, in the strictest sense, territories. But they are much more than merely home ranges. It might be more accurate to speak of "local, long-term dominance hierarchies amongst reproductively active animals" but repetition of such terminology becomes tedious. In subsequent discussion I therefore refer to areas that are occupied for long periods, and defended (with seasonally varying vigor) by reproductive agoutis against some or all conspecifics, and upon which food is hoarded (not necessarily only by the dominant resident) but upon which conspecifics regularly trespass, as "territories"!

Territories and Nonreproductive Animals

Agouti territories usually include a length of creekbed, and it is here that the nests of their young are generally situated. Most of the scatterhoarding done by reproductive agoutis is done within their own territories, though they may occasionally bury a piece of food on a neighboring territory when they are foraging there. Each territory also includes a number of agouti food trees. The subadults (after they leave the care of the mother) generally live and sleep outside of the areas most heavily used by the adults, even though they must do most of their foraging there.

As they grow older and gradually move further from their nests, young agoutis remain within the territory of their parents, exploring by themselves if the mother is raising a second litter, or in her company if she is not. When the level of aggression of the parents and other adults increases, the young animal must spend much of its time avoiding them, and so is forced into the peripheral regions of the surrounding territories or into areas that get little use from reproductive dominants. The result is that the home ranges of the subadults are less well defined than are the territories of the adults, and they overlap the edges of the surrounding territories. Subadults do not defend a specific area, but if approached by a smaller agouti when feeding, especially during the season when food is scarce, will attack and drive it away.

Agoutis become potentially sexually mature at the age of about six months (Roth-Kolar, 1957:369). This appears to depend upon the sufficiency of the diet, for many animals in the phase II study passed the age of six months and were obviously not big enough to be sexually mature. On the other hand,

some of the animals that I observed in both phases passed the age and weight necessary for sexual maturity and still retained many of the behavioral characteristics of juvenile animals: fleeing at the approach of the territorial adults and living largely in the areas between territories. Such animals remain unmated, but those of the same sex establish a loose dominance hierarchy among themselves. Thus, in December of 1966, the oldest phase I subadult agouti regularly visiting the bait area, mSN, was dominant over m14, who in turn was dominant over m18. This relationship held no matter where these animals met one another in the surrounding territories. The juvenile m22 was about the same age as mSN, but the former did not begin to visit the bait area until February of 1967, at which time his status was changing to that of an adult territory holder, and he was forming, or already had formed, a liaison with FSB. I do not know where FSB came from, but it was somewhere to the south of the study area, so that when the opportunity arose, she was more available to m22 than to mSN.

Those animals older than six months are apparently able to change their status very quickly should a local reproductive adult die or become unable to maintain its dominance. The consistent harassment the subadults suffer from the dominant animals and their resulting inability to maximally utilize marked trails and food resources places them under increased selective pressures, so that mortality is high. But when the opportunity arises to acquire territory-holding status it is practically guaranteed that an animal of potentially high fitness will be available to fill the gap.

Activity Patterns

Agoutis begin to move about shortly before dawn, when light levels in the forest are still too low to permit observation (Figure 18). The activity period becomes extended when food becomes scarce, and they may even forage until shortly after dark. Younger, nonbreeding animals are often active at times when the territory holders are sleeping or resting. On very cloudy days, or on mornings when it is raining, the beginning of the activity period is postponed. Leaving the sleeping spot is preceded by a lengthy bout of stretching and grooming. In the wild, the members of a pair of agoutis usually sleep within a few meters of one another, and when the female has finished grooming, she leaves her sleeping spot to begin foraging. The male follows her, often circling her at a distance of 5–20 meters, apparently attempting to detect the pres-

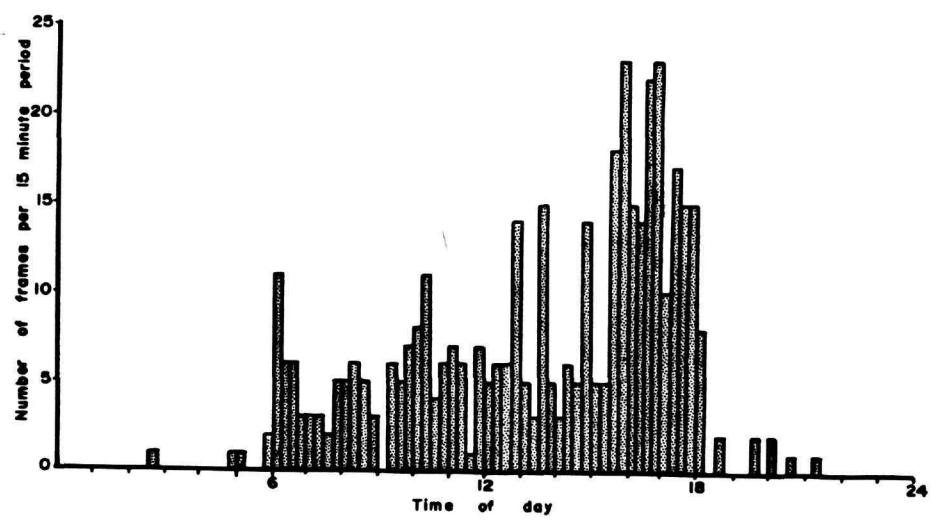


FIGURE 18.—Activity periods (the number of times an automatic camera was tripped by agoutis during each hour).

ence of any other agoutis that may be in the area. The male also occasionally approaches the female and attempts to enurinate her (see p. 28).

After a period of foraging, the length of which depends upon the abundance of available food, the female follows one of three patterns: (1) if she has an infant, she picks up a piece of food and goes to the nest; (2) if she has none, she sits or lies in a feeding spot and rests, often appearing to doze; or (3) she may set out on "patrol." If she goes to the nest, the male either approaches as close to the nest as she will allow him, and then he sits and rests, or continues patrolling the territory, forages, or rests elsewhere. If the female rests near the foraging area, the male may rest near her or he may continue to patrol in a circle around her. If she sets out on patrol, he follows, usually within a meter of her, occasionally sniffing at her rump.

The action of patrolling appears to enable the animals to maintain familiarity with the territory. Patrolling agoutis follow habitual trails, biting small vines and other vegetation that have recently fallen nearby. They may stop and eat, but they generally walk more quickly and along more regular trails than do normally foraging animals. They may patrol for an hour or more, often moving from one side of the territory to the other, or circling it, several times. But they usually stop and rest before starting to forage again sometime between 1030 and 1200 hours.

A female with a nest-bound infant leaves it around 1030–1100 hours and goes to forage. If her mate has been waiting, he usually joins and follows behind her. From about 1200 or 1230 hours until 1300 or 1330 hours agoutis usually rest and then begin actively foraging until dusk. They continue foraging until darkness falls in the forest, gradually moving toward a sleeping spot. Having reached a sleeping spot, they sit and groom for some time before lying down and sleeping. If they are disturbed during the night they quietly leave and generally move to a point that is higher than the surrounding area, such as upon a large log, where they sit quietly. If approached, they flee in much the same manner that they do in the daytime. (This behavior may partly account for descriptions of agoutis as being nocturnal, since the dull red glow of the eyes is easily spotted in the light of a headlamp.) I heard only one alarm bark during hours of darkness and this was too far away for me to find out what circumstances elicited it.

Young animals and unmated adults spend much of their time in cautious exploration of the area, for they are in constant danger of attack from the resident pair. They were usually the first to enter the bait area in the morning but they seldom fed for more than a few minutes before they were interrupted and driven off by the residents.

The activity pattern described here may undergo considerable variation, depending on the availability of food or the presence of various disturbances, such as snakes, which may cause agoutis to spend several hours in alarm reactions. Figure 18 shows the times when agoutis visited baited cameras, and indicates that they were active throughout the day. But this figure represents the activities of about 20 individuals at a time of the year when falling fruit was very scarce (they were not attracted to the baited cameras except when food was scarce). The frequency and duration of resting periods depends upon the abundance of falling fruit, and much of the time spent by agoutis in the bait area when fruit was abundant was devoted to resting or sleeping. As fruit becomes more abundant, an increasing amount of time is also spent scatter-hoarding (see p. 25).

Feeding and Foraging Behavior

Types of Food

I tested captive agoutis with the object of finding out what types of food they would eat, and found that they react to any approximately spheroidal object, within a wide range of sizes, as though it was food. They prefer objects of greater than approximately 1.5 cm in the largest dimension, but they will eat, or attempt to eat, objects as small as 5 mm, and often eat fruits as large as 10–15 cm in diameter. The agoutis that I tested would eat apples and pears upon first encountering them. They also treated such things as drawing pins (thumb tacks) and glass marbles as though they might be food items. They reacted to such objects by picking them up with the mouth (with considerable difficulty in the case of the marbles), manipulating them and going through the motions used in peeling fruit, and then burying them.

Although fruit and seeds form the vast majority

of the food of the agoutis that I studied, they did browse occasionally. I saw agoutis eating leaves only three times, all during the period when falling fruit was scarce. They are reputed to eat roots and sugar cane (Cabrera and Yepes, 1960:44,45; Walker, 1968:1027). The only roots that I saw them eat in the wild were those projecting from germinating seedlings, although captive animals eat carrots, potatoes, and cassava (locally called, "yucca"). I think it entirely possible that they eat such things in areas where the forest has been cut to such an extent that there is not enough fruit to hoard against times of deprivation. None of the captive animals that I tested would eat sugar cane. They occasionally ate a little ground beef and, like the animals studied by Roth–Kolar (1957), preferred cooked to raw meat. On one occasion, an adult male *Liomys pictus* escaped from its cage in the same room as a group of captive agoutis. It wandered into the agouti cage, where it was killed and almost entirely eaten.

Foraging

Agoutis are attracted to the sound of fruits falling to the forest floor, and will travel 50 meters or more to pick up one that they have heard. Native hunters drop stones from trees to attract agoutis within the range of their weapons (Goldman, 1920:130). Agoutis also follow bands of monkeys for short distances, picking up fruits that the monkeys drop. This may be an important source of food at some times of the year since the monkeys, particularly spiders (*Ateles paniscus "geoffroyi"*) and howlers (*Allouatta palliata*) are able to reach many fruits that are not yet ripe enough to fall but are ripe enough to eat. The monkeys typically take only one or two bites from a fruit before letting it fall.

The sound of falling fruit also appears to act as a stimulus to feed. On several occasions when an agouti had fed in the bait area and then had laid down to rest, I threw a piece of banana so that it landed 3–5 meters away from the animal. Upon hearing the falling fruit, the agouti would usually get up, walk past or over other pieces to the one that had just fallen, and eat it.

The sound of another agouti eating will also attract agoutis to a food source, and they also find fruit by its odor. I set up temporary observation stations at several points in the study area. Each was baited with a pile of banana (about 2 kg) cut into short pieces. I sat 20 or 30 meters away and was able to watch approaching animals from before they had apparently detected the bait. On several occasions an animal walking tangentially to the baited area would suddenly pause, sniff the air, and turn and walk directly to the bait pile.

An agouti approaching a food source that is within another territory, or in an area of disputed territory in the season when fruit is scarce, usually circles the food area before approaching it. It will often pause about 10 meters from the food, thump a few times (see p. 41), get up and make a complete circle of the food area, returning to the spot where it first thumped, sit and thump again for a few minutes, and finally get up and enter the area. The first piece of fruit that is encountered is usually carried out of the immediate vicinity, often to the place where the agouti sat and thumped before entering the area, and is eaten there. Subsequent pieces may also be carried out of the area and eaten, but after carrying away the first two or three, the agouti usually starts to eat them nearer to where they fell.

Feeding Spots

When agoutis find a fairly steady source of falling fruit, such as my bait area or a fruiting tree, they habitually carry fruit to regular spots to eat it (Figure 3*b*). Whether by active removal, or from normal wear, these spots become smooth and devoid of litter, so that they are easy to identify. They are similar to, and may double as, sleeping spots (see p. 27). The feeding spots may be on small elevations in the open, giving the animal a view of the surrounding area, or they may be under vegetation such as large leaves.

A feeding agouti seldom eats more than two or three pieces of food in a single feeding spot, but moves from one to another after picking up a piece of food. The spots apparently become marked with agouti odors, for not only will other agoutis from the immediate area make mutual use of them, but those passing through the area will eat and mark on them the first time they visit the food source.

Feeding Techniques

Agoutis sit on their haunches to eat (Figure 19), in the same manner common to many other rodents (Eibl-Eibesfeldt, 1958). The forepaws are used to manipulate fruits and seeds. Fruits are generally systematically peeled and the peel either chewed to extract the juice (e.g., as in the case of *Astrocaryum*), or discarded. Seeds may be held so that the animal can gnaw a very tough seed coat at the same point consistently.

Scatterhoarding

When an agouti encounters a concentrated food source, it usually eats a few of the fruits or seeds and then starts to bury them. If the fruit consists of a hard seed surrounded by a fleshy pulp, the animal usually eats or peels off the pulp before burying the seed. Seeds are occasionally buried near to where they fall, but more often are carried individually for distances up to about 50 meters, in various directions from the source, and placed in carefully dug holes from 2 to 8 cm deep. They are then covered with soil, which is smoothed with the forepaws, and a leaf or twig is usually placed on top. This is very similar to the behavior described in the green acouchi (*Myoprocta pratti*) by Morris (1962).

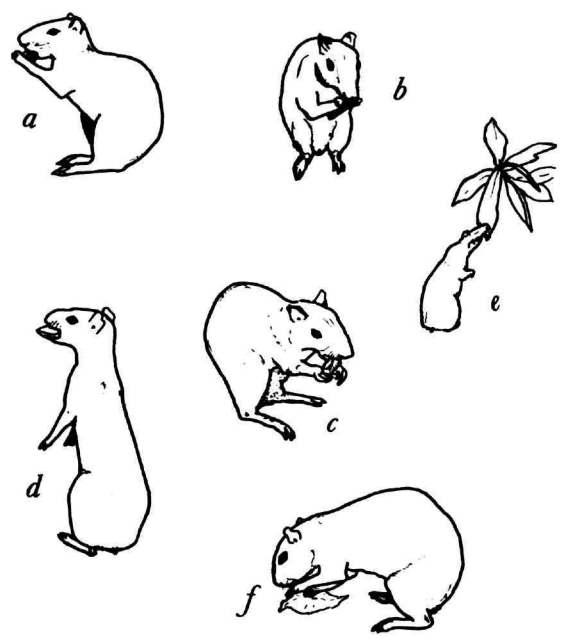


Figure 19.—Feeding behavior: *a, b, c,* typical feeding postures; *d,* food held in mouth while animal sits up to observe surroundings; *e,* agouti browsing; *f,* placing a leaf over a buried food item.

The buried seeds may be dug up again almost immediately or not until up to about eight months later. An agouti other than the one that buried the seed will often come along and dig it up within a day or so, take it away, and then rebury it. In this way a single seed may be transported and buried as much as 150 meters away from the parent tree. When falling fruit becomes scarce, agoutis live almost entirely on scatterhoarded seeds, though not necessarily on ones that they themselves buried. Most of the seeds that a territory holder digs up are from within its own territory, but many of them were buried there during times of abundance by young animals, not necessarily from the same territory, that have since died or moved elsewhere. I do not have data to show the percentage of the scatterhoard that is retrieved; but, during times of abundance, all agoutis hoard considerably more than they eat. When a large, multiseeded fruit such as *Gustavia* or *Tontalea* is encountered, the animals may bury from one to five seeds for each one that they eat. They may also partly eat some of the seeds before burying them, which could prevent germination. When single-seeded fruits with a hard exocarp and a surrounding sweet pulp are found, the pulp is removed and the remainder usually buried.

Since the population, all of whom are hoarding more than they are eating, is highest during the latter part of the six-month period when fruit is most abundant and since many members of that population do not survive to exploit the seeds that they have hoarded, it seems logical to assume that many of the seeds are never disinterred. Moreover, it seems highly probable that many of them will be under excellent conditions for germination. Thus many agouti food plants have their seeds efficiently dispersed.

The question arises as to how agoutis find seeds that they have buried when they need them. It is possible that the slight disturbance of the soil that remains after the seed is buried acts as a clue. But it seems unlikely that such a disturbance could remain visible for several months, since all that would appear necessary to obliterate it would be

a heavy rainshower. The perineal region of an agouti usually contacts the ground at some time when burying is in progress. Hoards are thus marked, whether intentionally or inadvertently, but the odor mark could not last for very much longer than the signs of disturbance.

Howard, March, and Cole (1968) showed that *Peromyscus* can smell buried seeds and Murie (1977), working in my phase I study area, has recently shown that agoutis can find buried seeds, apparently using predominantly olfactory cues. They usually bury seeds near fallen trees or at the bases of small clumps of palms or other undergrowth, and it is near such structures that they tend to search in later months when fruit is scarce. Therefore, it may be that they find buried seeds at this time by searching in similar situations and detecting the odor once they are over the spot where the seed is buried.

Comfort Behavior

Allogrooming

Like acouchies (*Myoprocta pratti*) (Kleiman, 1972), female agoutis frequently groom their young (p. 33). Some allogrooming also occurs between members of a pair, but agoutis would generally be classed as "distance animals" in the sense of Hediger (1955:66).

Autogrooming

Murray (1961) demonstrated the importance of autogrooming in rodents. As might be expected in a tropical, terrestrial animal, agoutis devote considerable time to grooming and apparently remove many ectoparasites. Trapped animals that appear to be in poor physcial condition are usually infested with ectoparasites whereas those in good condition are generally almost entirely free of them. A heavily infested animal may be host to more than 100 ticks of various sizes, have small areas of the body covered with orange mites, and have upwards of a hundred fleas.

When grooming themselves, agoutis sit on their haunches and use the forelimbs and incisors to manipulate the hair of the ventrum and flanks (Figure 20). The forefeet are used to rake the hair and to draw it within reach of the incisors, which

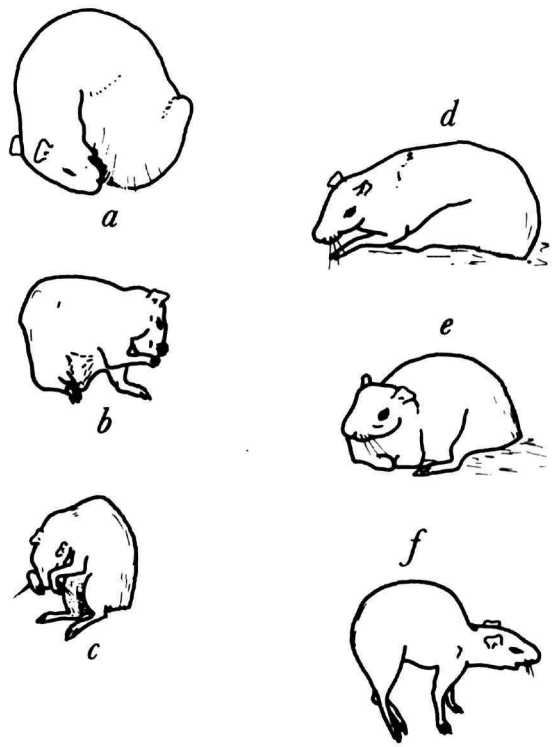


FIGURE 20.—Comfort behavior: *a*, combing rump hair with incisors; *b*, grooming face with surface of forefeet; *c*, grooming face with "parasite combs"; *d*, *e*, sleeping posture or position assumed for protection of ventral parts from biting dipterans; *f*, stretching.

are then used as a comb. The top, the sides, and the back of the head are groomed with the forelimbs, which are used either singly or together. Between each sweep of the forelimbs, the animal may lick the inside surface of the wrists, where there is a small oval patch of skin, bearing short fine bristles (Figure 2). At certain times of the year small ticks and ectoparasitic mites are very abundant in the forest and may attach themselves to any animal that moves through the undergrowth. The short bristles on the wrist patches would appear to function as combs to remove these pests. Agoutis may have so many small orange mites on them that they have been described as having a "bright orange, fungus-like growth" (Enders, 1930: 287). These mites and the many small ticks that the agoutis sometimes have, however, are usually

situated in regions that the "parasite combs" cannot reach, such as the soft skin in the cleft below the cheek bones.

Agoutis often scratch themselves with the hind claws. This is usually done while the animal is in a sitting position, but occasionally also while it is standing. Each claw is carefully cleaned with the incisors after a bout of scratching.

Protection against Biting Dipterans

Mosquitoes and tabanid flies often cause agoutis a great deal of apparent discomfort. The most vulnerable areas seem to be the pinnae, the rhinarium, the perineal region, and the extremities of the hind limbs. In response to biting insects, agoutis twitch their pinnae rapidly back and forth. They will do this even when in the freeze position after having been alarmed, often giving away their positions to an observer. When bitten on the rhinarium, agoutis wipe at it with either forepaw, and often do this while walking along, hardly breaking stride.

Insects biting their perineal region seem to cause much discomfort. When the insects are abundant, agoutis will sit in such a way that the perineum is pressed close to the ground (Figure 20*d, e*). When insects are biting their hind legs, agoutis will lift the foot off the ground and give it a quick flick. If the biting persists, they will sit down and attempt to bite the insect or the spot where it is biting.

Reaction to Rain

The approach of heavy rain showers is usually signalled by a noticeable darkening within the forest, the roaring of howler monkeys (*Alouatta palliata*), the noise of the rain on the vegetation and occasionally by thunder. Agoutis generally left the bait area at these times before the rain actually arrived and went out of my sight. On those occasions when they stayed in view, they moved under large leaves and lay down, or sat and groomed, until the rain was over. They paid little attention to lighter showers, the water from which takes some time to penetrate the canopy if it comes through at all. One subadult went into a mild frenzy dance (p. 28) when it was raining lightly and animals foraging under such conditions often wipe their faces with their forepaws and wrists.

Sleeping

Each agouti has several habitual sleeping spots on its home range. These are usually in hollow logs, shelters formed by buttress roots or under vegetation such as large leaves or tangles of vines. They are recognizable as circular patches from which the ground litter has been removed, either purposefully or as a result of continued use. Some sleeping spots are not in sheltered places but are small bare areas similar to the feeding spots; these may be utilized by the animals for both feeding and sleeping. Agoutis often use one sleeping spot for a few days and then move to another. Territory-holding animals may sleep anywhere within the territory; nonterritory-holding younger animals tend to sleep near to the area of the holes that they inhabited as infants.

I did not observe any adult agoutis sleeping in burrows, but since most of the burrows in the study area were in the banks of the creeks, they were difficult to observe. I set up an automatic camera outside four different burrows in an area where I knew that a pair of agoutis was sleeping, but the only animals entering the burrow were an armadillo (*Dasypus novemcinctus*), a pair of motmots (*Electron platyrynchum*), and an iguana (*Iguana iguana*).

Sleeping agoutis commonly lie on the ventrum, with the forelegs folded so that the feet are under the chest (Figure 20*d, e*). This posture exposes a minimum amount of the areas commonly bitten by insects and may be adopted for that reason. Agoutis in captivity, housed in insect-proof cages, usually lie flat or curled on one side to sleep.

When they awaken, agoutis stretch in a similar manner to many other mammals, first arching the back while stretching the legs, then stretching the forelegs alternately forward, often while yawning, and finally taking a step forward while extending a hind leg stiffly to the rear. Stretching is often followed by a bout of grooming before the animal leaves the sleeping spot.

Agoutis rest often while they are foraging, but territory holders rest more than nonterritory holders. They generally rest on one of the feeding

spots in the area or may leave a foraging area and go to a sleeping spot on their territories. The female of a territorial pair rests more than the male. He often lies down near her when she rests, but he seldom remains resting for more than a few minutes, and continually gets up and makes short patrols around her. The postures adopted for resting are the same as those used for sleeping. Resting agoutis often fall asleep, but usually awaken, raise the head, and look around every few minutes.

Courtship and Mating Behavior

Introductory Behavior of Captives

In mature, captive agoutis that have not been previously introduced to one another, contact, courtship, and attempted mating behavior follow a usual pattern (Figure 21): (1) brief naso-nasal contact; (2) urine spray or enurination (Southern, 1948:177) attempt by the male, followed by front foot trembling; (3) following or driving of the female by the male; (4) enurination and foot trembling; (5) attempted mount; (6) mount with thrusting; and (7) intromission and ejaculation. Steps 3 and 4 are commonly repeated whether or not they are followed by steps 5, 6, and 7.

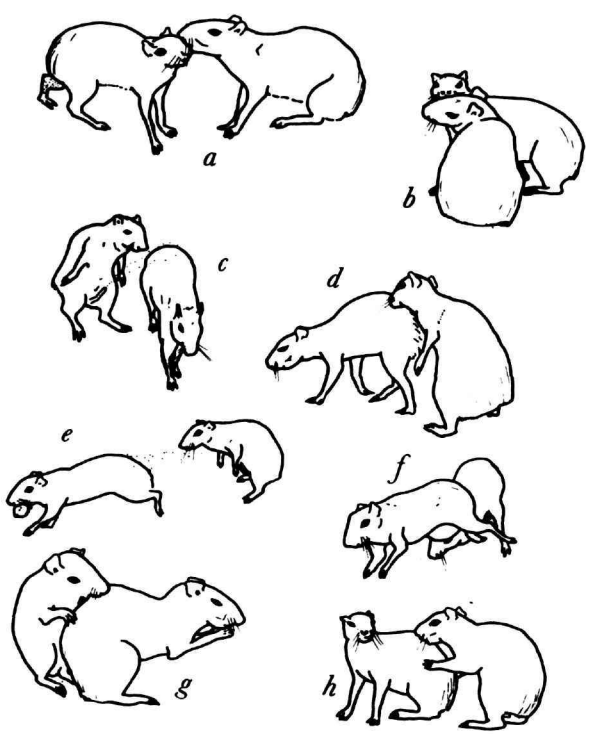


FIGURE 21.—Courtship behavior: *a*, *b*, naso-nasal contact; *c*, *d*, *e*, enurination; *f*, frenzy dance; *g*, *h*, dorsal grooming of female by male.

The naso-nasal contact may be initiated by either the male or the female, and it is often accompanied by "purr" vocalizations by either. It usually lasts for no more than a second; then the female breaks off contact and avoids the male. It is interesting to compare this behavior with that of *Myoprocta*. Nothing is known about this "miniature agouti" in the wild, but it is said (Morris, 1962; Kleinman, 1971:261) to be considerably more socially tolerant than its larger cousin. Kleiman (1971) has studied the sexual behavior of captive *Myoprocta* and report that females tolerate and indeed intitiate contact with males to a much greater degree than occurs in agoutis.

In his attempts to approach her, the male agouti walks obliquely toward the female, rears up on his hind legs, pivots toward her, erects his penis and squirts urine at her from a distance of up to about 1.5 m (Figure 21*a-c*). As he rears up the female usually jumps out of his way, so that his initial spray seldom hits her. The male then starts to follow the female as she walks about. He may make squeaking noises (p. 44) at this time and, when he pauses, his front feet may be vibrated in a rapid trembling motion. Every time the female pauses to eat, to rest, or to groom he attempts to get in position to enurinate her. He usually succeeds on the second or third try.

Being sprayed with the urine of the male has an interesting effect on young females, causing them to go into what I call the "frenzy dance." At first the female appears to ignore its occurrence; then, after 15 or 20 seconds, she begins to toss her head and to prance around. She sometimes; leaps into the air, twisting as she does so, and lands on her side or on her back. Then she jumps up and starts to run in circles, apparently aimlessly, for she crashes into any object in her way. At first the male merely watches her, then her behavior appears to infect him for he starts to act in the same manner and the two animals rush about together.

After a minute or so of this behavior the female suddenly stops and begins to eat or to groom. The

male also stops and attempts to get into position for another enurination. After receiving the first few sprays, the female gradually allows the male to approach more closely until he is eventually able to crouch over her in the mounting position, but without actually touching her. He also grooms her back with his incisors when approaching her closely (Figure 21*g*). Subsequent to each enurination the male sits and trembles his forefeet. During the process his scrotum becomes enlarged and there is a noticeable increase in his odor.

Of the four captive females that I observed, none would tolerate contact by the male during the day of their introduction. On the fourth successive day, one of the females allowed the male to mount briefly, although I do not believe he gained intromission, and another engaged in some mutual grooming with the male. Since my major concern was with the behavior of wild animals and it appeared that copulation would not occur in the captives for some time. I did not persist in observation beyond this stage. Copulation in captive agoutis is described in Roth-Kolar (1957:369) and in *Myoprocta* by Kleiman (1971:268).

Courtship of Free-living Agoutis

In the group of wild animals that I watched, two pairs were already established at the beginning of phase I and remained so throughout, although the animals spent varying amounts of time in one another's company (Figure 6). One phase I pair (m22 and FSB) formed during the study, but I did not see the initial behavior involved in its formation. The remaining animals, with few exceptions, engaged in no sexual behavior. One exception was m14, who, when he was about 5–6 months old, attempted repeatedly to copulate with his mother, FSP. It is interesting that, at the time, FSP had recently given birth and m14 would meet her when she left the nest area to forage. Her mate, MSS, would also meet her and, if he encountered m14, would drive him away. But m14 was often able to remain with FSP for some time before MSS detected him. Sometimes he would nudge his mother over onto her side and would nurse; at other times he would attempt to copulate with her. On three occasions I saw her stand still while he mounted, made a few rapid pelvic thrusts and then dismounted or slid off when she moved. I do not know whether any of these attempts represented complete copulations.

The most commonly seen courtship behavior in wild agoutis consists of the male "driving" the female. Wherever she goes, he follows at a distance of a meter or less, occasionally coming close enough to sniff her anal region. Except on rare occasions, even in established pairs, the female avoids all but the briefest contact with the male and will generally not allow him closer than about 0.5 m. The only physical contact that I observed between the paired animals in the study area consisted of mutual grooming of the ear region and of the male occasionally attempting to take food from the female in the same way that juvenile agoutis do. Males frequently attempt to get into position to enurinate their mates, but succeed only about 20 percent of the time. After each attempt they usually sit with their front feet trembling.

I did not observe the frenzy dance in enurinated females in the wild, probably because the pairs that I watched were well established by the time I was aware of their existence. A milder form occurs under the following conditions:

1. In young animals (about 3–8 weeks of age) when they are engaged in practice and exploration behavior. Both single young and members of a pair of twins occasionally engage in abandoned rushing about in response to no apparent external stimulus.

2. In response to light rain. I was observing phase I f27 when a light rain began. She began to prance in a manner very similar to that seen in the frenzy dance.

3. As an after effect of submissive behavior when confronted by an obviously stronger animal. On separate occasions during phase I MRE and m14 were feeding in the bait area when a group of collared peccaries arrived. Each started toward a piece of banana at the same time as a peccary, which made a short rush at the agouti, frightening it away. In both cases the agouti sat for a few seconds outside the bait area, and then jumped up and performed a mild version of the frenzy dance. On another occasion, when m14 was driven away from his mother by MSS, m14 sat for a few seconds and then started to leap and prance around in a manner similar to that seen in the frenzy dance.

In all cases where this behavior occurred it was in response to a situation that probably involved

an inability to follow through on an aggressive impulse either because the object arousing the aggression was absent (in the case of the rain shower) or because it was inappropriate (in the case of meeting an obviously stronger competitor for food, or a conspecific that transmitted a sexual rather than an agonistic signal).

Between the time that young agoutis leave their parent and the time that they become territory holders, all their encounters with conspecifics involve some aggression. Young animals are either harried by territory holders or are involved in competitive situations with other nonterritory holders. Each agouti spends several months learning to avoid contact with all conspecifics regardless of their gender. As the age of potential sexual maturity is attained the situation becomes aggravated and territory holders expend considerable energy seeking out and driving away potential usurpers of the same sex. The maturing animal must now learn to be prepared to fight, but to flee before suffering significant damage from a stronger animal. It seems unreasonable to expect that the initial exchange of sexual signals between potential partners could suddenly abolish months of learning that the prospective mate is a potential threat. It seems more likely that, by the male's transferring his odor onto the female through enurination, both members of the pair come to recognize one another as nonthreatening, but, during the initial period when this is being accomplished, each recognizes the other as simultaneously threatening and attractive. The sexual overtures serve to decrease the threat but not entirely to negate it. This would also help to explain why the male periodically enurinates the female throughout the year even when not actually engaged in mating behavior; it is a means of maintaining the pair-bond.

The frenzy dance thus consists of *in vacuo* fighting during which both aggressive and defensive behavior patterns appear in each animal. The abandoned running is accompanied by jumping and head flinging which are similar to the movements of an animal trying to jump over and to bite another, and also by kicking backwards with the hind feet, avoidance jumps and rolling on the back while kicking upwards, which are defensive movements.

Kleiman (1974:177) in a general review of Hystricomorph behavioral patterns states that the frenzy dance (termed by Kleiman "frisky hops" after Rood, 1972) is a play pattern with practice predator-escape as its major component. In agoutis, components of flight behavior are certainly present, but flight behavior is an important part of intraspecific hostility. Of course, many aspects of fighting between conspecifics and of predator avoidance of behavior will be similar; but, because of the factors mentioned above, I believe the frenzy dance to be principally a manifestation of frustrated intraspecific aggression.

Agonistic Behavior

Interspecific Agonistic Patterns

Except in the defense of their young against coatis and what is possibly redirected aggression when they are driven away from food by peccaries, I saw very little interspecific aggressive behavior on the part of agoutis. In a foraging situation, they reacted to the direct approach of practically any other animal as they would have to the direct approach of a conspecific, i.e., by retreating. One reason for this is probably that most of the animals that agoutis come into contact with are larger than themselves. I saw only one encounter between an agouti and a smaller mammal. This occurred when two agoutis were feeding on some maize that I had put out and a squirrel (*Sciurus granatensis*) came down a nearby tree and began to eat some of it. One of the agoutis made a brief lunge toward the squirrel, which retreated up a liana but quickly returned and began eating again. The agouti drove it off several times, each time in a less energetic manner, and finally the squirrel was tolerated at a distance of about 2 meters.

I found that wild-trapped agoutis never attempted to bite. On one occasion, when a subadult male escaped from my handling net, I caught him in such a way that my index finger was in his mouth, and he still did not attempt to bite. The chief means of fighting back against predators is with the hind feet, with which agoutis can exert a powerful and damaging kick. Agoutis also "mob" potential predators of particular types (p. 41). This behavior might be considered to have some aggressive components.

Intraspecific Agonistic Patterns

When one agouti walks toward another, this

constitutes a simple act of aggression and, if the aggressor is an adult male, such behavior will elicit appeasement squeaks from females, juveniles, or subordinate males as they get out of its way. Under situations of higher apparent aggressive motivation the aggressor may rush at the other with the rump hair erected and/or the anal glands everted. An attack against a conspecific of the same sex and approximately the same age consists of a rush and an attempt to bite, or, at a higher intensity, of rushing and jumping over the other animal and lashing out at it with the hind feet when directly overhead (Figure 22).

A type of aggressive behavior that is initiated by all age classes in captivity, but which I saw used in the wild only by adult females against younger agoutis, consists of the aggressor running at the other and drubbing it with the forefeet. This is the first overtly hostile act performed by a mother against her maturing offspring as it attempts to take food away from her. A young animal sustaining this type of attack usually crouches and remains stationary, which probably inhibits a more damaging attack since, if the young animal flees when the female first threatens, she is liable to attack it more vigorously, chasing and biting it.

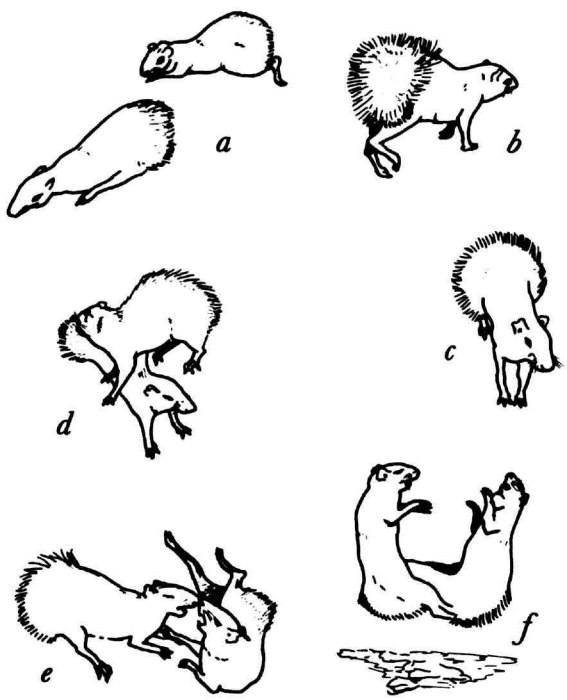


FIGURE 22.—Agonistic behavior: *a*, chasing; *b*, *c*, rump hair fully erected; *d*, jumping over and striking with hind claws; *e*, biting attempt; *f*, jousting.

If an agouti, when approached by another, turns and flees, the one approaching is liable to attack. On several occasions subadult males were feeding in the bait area at the same time as, and obviously within sight of, territory-holding adults. A sudden movement made by the adult (or a sudden, quite unrelated noise) would cause the subadult to flee, and only after it had started to run away would the territory holder pursue it. An agouti, chasing another that is fleeing, attempts to bite it on the rump, usually uttering a series of grunts similar to those that precede the alarm barks (p. 43). The fleeing animal often receives superficial wounds from the biting of the pursuer. On one occasion a large adult male (but obviously not territory holding) escaped from his cage and went into the forest early one morning. I left the cage open and, in the evening, he returned and was cowering inside, bearing many wounds of the type received by an agouti that is bitten while fleeing from another.

Either the animal attacking, or the one fleeing, or both, may have the rump hair erected during an aggressive encounter (Figure 22). When both are in the same age class and/or reproductive state, both will raise the hair to the maximum level. In such a case, the one that is furthest from the center of its territory will usually flee; but if it does not, an elaborate form of fighting, similar to the "jousting" that has been described in rabbits (Southern, 1948:181), may take place. The following excerpt from my notes describes an encounter during phase I between MSS and MRE, both reproductive males. MSS was normally dominant over MRE at this time in this area, but MRE had just succeeded in driving off m14, which apparently raised his fear threshold and lowered his aggressive threshold, and MSS had just driven off mSN, which had a similar effect on him:

16 March 1706 hrs: F13 appears 5 m north of the north end of the log [Figure 3*b*] and goes straight into the bait area. Her mate MRE returns to the bait area after a lengthy chase of m14, sees F13, raises his rump-hair and chases her out of the bait area. MSS is sitting just south of the bait area, after chasing mSN into the creekbed 30 m to the south. MSS turns when MRE makes fight grunts as he chases F13,

and runs into the bait area. MRE apparently hears him coming and turns to meet him. MSS stops about 1.5 m from MRE and they circle one another, stepping sideways, both with the rump hair fully erected. They suddenly rush together, leaping into the air just before meeting and lashing out with the hind feet. MSS is thrown off balance by this and lands on his side. MRE jumps on him and tries to bite him, but MSS jumps up and flees with MRE chasing him and trying to bite his rump. MSS turns and attacks MRE about 20 m north of the bait area. They chase one another in large circles for nearly 10 minutes, to the north and east of the bait area. F13 has meanwhile returned and eats in the bait area. MSS returns alone and attempts to enurinate F13, but she jumps out of the way. MSS goes off south.

1721 hrs. MRE returns to the bait area. His fur is tufted out on the flanks and he has a bleeding spot on the top of his nose. He enurinates F13, and sits with his front feet trembling.

This was the only time that I saw this type of fighting behavior in the wild. It did occur in my observation cage, either between adult males or between adult females. Severe wounds are liable to result from the fighting use of the claws of the hind feet. One of the females hit the other on the haunch, leaving a wound nearly 5 cm long and more than a centimeter deep. I found a dead adult male, outside my study area, that had been disemboweled. The body was still fresh and undamaged (apart from the long gashes in its ventrum) by either predators or scavengers, and I suspect that the animal died as the result of a fight with another agouti.

Maturation of Young Agoutis

I did not witness actual parturition in the group of agoutis that I studied. The process has been described by Enders (1931) for a semitame animal that lived in the laboratory clearing on Barro Colorado Island. I observed the development of three captive-born agoutis from shortly after they were born until they reached maturity, and watched the early development of six wild ones (two pairs of twins and two singles), four of which were killed or disappeared before reaching potential maturity.

Parturition and Nest Selection

I believe that parturition in wild agoutis occurs in one of the habitual sleeping spots of the mother. Three of the six infants that I saw shortly after birth were born sometime during the night, and the mother and young were resting when I first observed them in the morning. Single births seem to be more common than twins in the Barro Colorado Island population. Of the 12 litters that I saw, six consisted of single young, three others probably were single but I did not observe them for long enough to be certain, and three were twins. As in most other caviomorph rodents (Kleiman, 1974:190), the young are extremely precocial at birth. They are fully furred, with their eyes open, and are able to run, though somewhat unsteadily, within the hour of their birth. At first they have some difficulty finding the nipples of the mother, but suck a little by the end of the first day and by the beginning of the second day they are attempting to eat solids.

The two phase I mothers that I observed on the morning after they had given birth followed a slightly different pattern. The one (FSB) with the single youngster (f27) got up from her sleeping place under a dense clump of bamboo at 0645 hours on 14 March 1967, stretched in the usual manner, then started walking straight toward what would become the nest of the young animal: a small hole under an abandoned water tank in the forest bordering the laboratory clearing, about 15 m from her sleeping place. The infant followed, running close beside her front feet and continually attempting to nuzzle her in the side of her mouth as she walked. She went straight to the hole and put her nose near it. The young one went into the hole and did not reappear. The female lay down outside the hole (which was far too small for her to enter) and rested until 0950 when she got up and put her nose near the hole again. At the time, the ambient noise level was too high for me to hear any noise she might have made but later, under the same conditions, I could hear a short purr. The baby came out of the hole and, when the mother lay down on her side, nuzzled in her fur, obviously attempting to find a nipple.

One of the workers on Barro Colorado Island told me that the hole that this baby used had been used by agoutis repeatedly in the past and it has been used by others since. I think it likely that FSB used it as an infant and that there may be a traditional use of such nesting places in agouti populations.

The other case during phase I was further from

the laboratory clearing, and I observed it from the tree platform. I had been aware for some days that F13 was about to deliver, for the movements of the fetus are clearly visible within the female for about two weeks before parturition. One evening F13 was very restless and had spent some time lying on her side with one hind leg elevated, which is an unusual position for an agouti. She had also been licking her perineal region.

The next morning, as it became light enough for observation at 0630 hours, I saw her lying in one of her sleeping spots just east of the bait area, with two newborn young. At 0645 she got up and started walking north, up the hill. Both young followed her and showed the same nuzzling of the side of her mouth that was shown by FSB's baby. They turned west across the hill about 25 m north of me, and she put her nose into a small hole. Both young animals went into it, but they came out again almost immediately. The female continued west across the hill, followed by the two babies, and they went out of my sight. Only three minutes later a large band of female and young coatis came down the hill from the direction that the three agoutis had taken. The next day F13 came to the bait area and ate there, but did not take any food away with her. Females that were suckling new young visited the bait area for only brief periods, and almost always took a piece of food with them when they left. F13 did not appear to be lactating in the weeks that followed. Nor was she provisioning young. So I concluded that both of her young ones died in some manner, and that it is quite possible that they fell prey to members of the band of coatis.

When the young agouti is three to five weeks old it becomes too large for its first nest entrance and moves to another burrow. In the three cases where I observed this, the young animals moved to burrows that were already in existence. I presume they would dig their own if none was available, although I believe that nest sites are largely traditional, females eventually using the ones they were born in, and there is seldom a need for digging fresh burrows. The only digging I saw in agoutis (wild or captive) occurred in the burying or digging up of food. On several occasions I kept wild-trapped individuals for a few days for observation in cages with soil floors. None ever attempted to dig out.

Maternal Care of Nest-bound Young

Female agoutis do not sleep with their young, but instead go to one of their habitual sleeping spots. They go to the nest after a brief period of early morning foraging, usually carrying a piece of food, remain with the young most of the rest of the morning, feeding and grooming it or merely resting, and then usually go foraging again at 1030 or 1100. Sometimes they wait until early afternoon before going off on the second foraging trip. I was not able to watch agouti nests with young occupants during the time when fruit was scarce, but observations of mothers who bore young during this period indicated that they spent more time foraging and less time resting near the nest. The behavior of individual females differed in this respect too. FSB would visit the nest, feed and groom the young, rest, and then return to foraging. She would eat food where she found it and would occasionally rest while foraging; then she would return to the nest, usually carrying a piece of food. FSP generally spent less total time near the nest but visited it more frequently. She would go foraging, eat one or two pieces of food where she found them, and then carry one back to the nest. Then she would eat the piece of food, let the baby eat it or bury it near the nest entrance, and go foraging again. She would rest both near the nest and while she was foraging. The females generally left their nests about 1300–1400 and foraged from that time until about 1730, shortly before dark. Then they would return to the nest, and feed and groom the baby before going to one of their sleeping spots to spend the night.

When female agoutis arrive at the nest, they call the infant with a sharp purring noise (Figure 23) and then sit and wait for it to come out, which it usually does within a few seconds. It may then attempt to eat some of the food that the mother brought with her or, if she has eaten some of it while waiting, may eat pieces she dropped. The first thing she does is to start grooming it. Sometimes she begins by grooming it around the ears, but wherever she starts she works quickly back to its perineal region which she begins to lick very energetically, often lifting the baby off the ground if it is standing, or rolling it over on its back (Figure 23). When licked on the perineum, the baby urinates and defecates and the female ingests

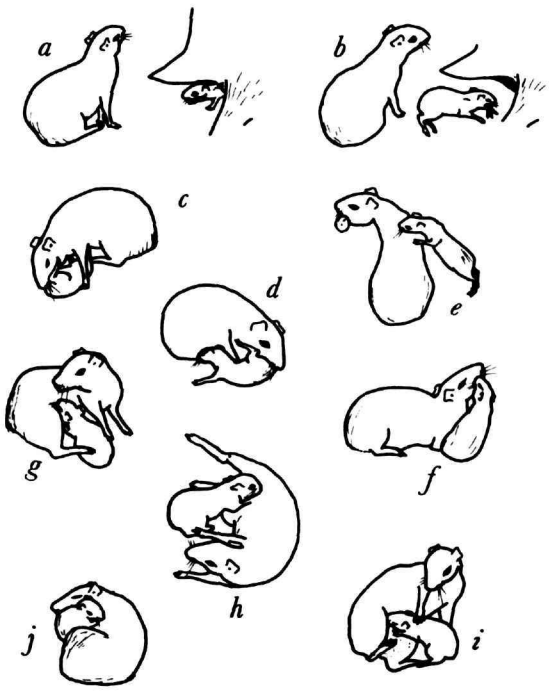


FIGURE 23.—Parental care: *a*, female waits for infant outside nest; *b*, nest building by infant; *c*, *d*, perineal grooming by mother; *e*, *f*, infant seeking solid food brought by mother; *g*, *h*, *i*, nursing; *j*, infant autogrooming.

all the products, then nudges the baby out of the way and licks the ground underneath it. After it is a few days old, the young agouti seems to try to avoid the perineal grooming, running in small circles, jumping out of the way, sometimes even kicking its mother in the face as she tries to lick its perineum. But sooner or later the baby comes close to suck and she will not permit it to do so until she has groomed it, and has ingested the urine and feces. On several occasions the baby was very slow to defecate, taking 15 minutes or more and several grooming sessions to do so. As soon as it begins to defecate it is allowed to suck (Figure 23). The pattern of grooming the perineum of the baby is repeated shortly before the female goes away to forage again. The morning sessions of sucking are often very short, lasting no more than a minute or so, and there may be two or three of them. When the female returns to the nest before dark there is usually a longer session, lasting 20 to 30 minutes.

During the first week the baby never comes out of the hole unless the mother is there. After the first week it begins to look out when the mother is not there, and then to come out for longer and longer periods. At the age of about two weeks the infant begins to follow the female as she leaves the nest. At first it merely follows her to her resting spots, but then attempts to follow her as she leaves to go foraging. She often turns and lunges briefly at it as it tries to follow her and, initially, this is enough to chase it back into the nest. Eventually the infant retreats into the nest only when it is frightened by something other than the mother, and at this time (when it is 5–7 weeks old) will sometimes venture with her all the way to a foraging area. During the initial exploration of the area the young animal finds, enters, and occasionally plays in, the progessively larger holes that will become its subsequent nest sites as it grows out of the smaller ones.

In spite of this exploratory activity, during the first three weeks of its life, most of the time of an infant agouti is spent around the mother as she rests outside of the nest. It carries nesting material into the hole, leaps or climbs onto or over her (Figure 24), or merely runs around in short, rapid bursts. She pays little attention to this, but sometimes turns and grooms the baby with her tongue and incisors, mostly around the head and ears, but occasionally over the rest of its body surface. The baby also grooms her around the back of her head and on the sides of her face, and usually follows this by grooming itself. Mutual grooming occurs between mother and young up until the time that they become separated.

Two other important behavioral patterns that appear during the second week are sitting up on the haunches to eat and food burying. Up until this time baby agoutis eat small pieces of solid food from the ground, neither picking it up nor resting on their haunches to eat. Week-old babies also begin to bury small pieces of the food items that the mother brings to the nest. At first they dig holes that are much too shallow to conceal the food, but by about the third week they are efficiently burying seeds.

Adult male coatis (*Nasua narica*) often attempt to get into nests housing young agoutis (Smythe, 1970*c*). If the female is present when they arrive she gets up and moves a short distance away,

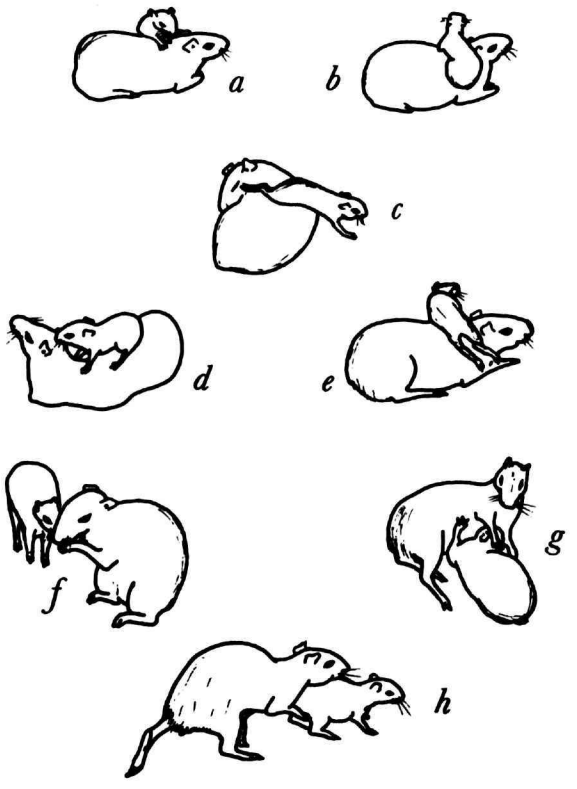


FIGURE 24.—Parental care: *a-e*, rubbing over; *f*, four-month-old juvenile stealing food from its mother; *g*, six-month-old agouti nursing; *h*, male adult, having enurinated infant, attempts to mount it.

erects her rump hair, and growls. She also may make short rushes at the coati, and sometimes succeeds in driving it away. Sometimes the coati will charge the adult agouti, and the frequency of such attacks increases as fruit becomes scarcer.

Occasionally, when the infant is sitting with its hind end near the female's face, it will suddenly leap up, lashing out with its hind legs as it does so and kicking her in the face, before dashing away a meter or so. In adults a similar behavior is sometimes seen in one agouti that is being chased either by another agouti or by a running, potential predator, but an interesting difference is that the hair on the rump of the animal that is being pursued is always erected, whereas in young animals it is not. A similar case is seen when a litter consists of twins. When they play they sometimes go through the complete fighting sequence, including the mutual leaping into the air and lashing out with the hind feet (p. 31); but, whereas adults always have the rump hair fully erected during such an encounter, juveniles do not.

One advantage of the infant's selecting a nest the entrance of which will only just admit it is that potential pedators of any greater size are excluded. As the young animal grows, however, it begins to have difficulty entering the nest itself; finally reaching the point when it must crawl in, holding the hind legs straight out astern. The age at which this occurs is not the same for all animals, since the size of the initial nest hole varies from one to another. As the young animal begins to experience difficulty entering its nest, or somewhat before this happens, it begins to spend more and more time in a nearby (5–30 m away) larger burrow. Finally it abandons the original nest altogether, although it may still occasionally return and play outside it. As with other aspects of the ecology of agoutis, there is considerable individual variation in the number of times the growing animal moves and the amount of time it spends in each of the burrows. One that I watched lived in four successive burrows, while another moved directly from its first to a considerably larger one, which it occupied until it was subadult and was living most of the time above ground.

Any time after the young one is about 15 weeks old, its mother may have another litter. When this happens the older offspring begins to spend more time foraging alone, gradually moving farther away from its nest, but returning to it if frightened. Much of its time is now spent exploring the edges of the area with which it is familiar, apparently learning the system of trails used by the other agoutis in the area. It will often walk along one of these trails, moving away from the familiar area, and then will turn suddenly and run very rapidly back to the familiar area; then, as often as not, it will turn around and run back along the trail again. This type of erratic running is strongly reminiscent of that seen during initial sexual encounters. An exploring juvenile sometimes misses the trail and runs into the undergrowth. I saw one get its front feet momentarily entangled in a small vine and fall down. Had there been a predator nearby it could easily have reached the agouti before it was able to recover, which illustrates the

adaptive value of what otherwise seems like aimless behavior.

Exploring juveniles also cut small branches with their incisors in much the same way that adults do, but the adults only cut them when they are across one of their trails, whereas the juveniles may cut them anywhere. They also scent-mark frequently as they are exploring, though this behavior does not appear until they are four or five weeks old (cf., Roth–Kolar, 1957).

Breakup of the Mother-Young Bond

A young agouti may forage with its mother until it is four or five months old. If she has not had a subsequent litter, the young animal remains with her constantly from the time it is 3.5–4 months old, sleeping with her in one of her sleeping spots and following close behind when she goes foraging. Females with small, nest-bound young are often joined by their older offspring as the females leave the nest area to go foraging, and they allow the older young to nurse occasionally when they are away from the nest (Figure 24).

Nest-bound young agoutis take food out of their mother's mouth whenever she brings some to the nest. This behavior persists as they follow her on foraging trips. Each time a foraging female picks up a piece of food she utters a single, loud "purr" similar to the noise made when she calls the younger animal out of its nest. When the adult makes this noise, the young animal immediately runs over and takes the food out of her mouth. Even if it has already found a piece of food and is eating, the juvenile will drop its own and take whatever the mother is holding. At first the female willingly gives up her food to the young animal; but, as it grows older, she seems progressively less inclined to do so, eventually mixing a high-pitched whine with the purr and holding onto the food so that the youngster has to pull quite hard to get it away from her. The juvenile persists in taking her food and, after some time, she begins to attack it whenever it approaches her when she is feeding, drubbing it with her front feet and not allowing it to take the food. Even at this stage she makes the purr whenever she picks up a piece of food, as though she cannot help doing so. Finally, she attacks the young animal whenever she sees it and, since it persists in attempting to approach her, there is a period when she shows more aggressive behavior toward her own offspring than toward any other animal from the immediate area.

At this time a young animal is chased by almost all the other agoutis that it meets, and spends much of its time avoiding them. It is also in more danger than usual of predation at this time because of unfamiliarity with escape routes and because of the possibility of blundering into a predator during one of the frequent flights from a conspecific. My data, both observational and from trapping, indicate that of the agoutis that survive infancy, few survive the period between leaving their mother and obtaining a territory of their own (Figure 17). On the other hand, several animals in the second-phase trapping area were trapped as adults four years earlier. Therefore, the probability of mortality falls sharply as an agouti achieves reproductive status.

The disintegration of the mother-young bond is accelerated by two factors: the female giving birth to subsequent young and/or the food supply decreasing. If a second infant is born at the time when fruit is abundant, the first has a better chance of surviving since, during the time when it is learning the characteristics of the environment, the territories are less assiduously guarded and the predators are not as hungry (some agouti predators, such as coati and tayra, are also frugivorous). All four mother-young pairs that I watched extensively through the process of disintegration broke up at a time when the food supply was beginning to dwindle. The two young animals that attempted to join foraging mothers when the period of deprivation was further advanced appeared to suffer more than the two who were already foraging with their mothers when it began.

I observed the phase I group of agoutis through 1966 but did not begin intensive observations until December of that year. Only three juveniles survived the 1966 period of fruit scarcity, and all were males. The oldest, mSN, was foraging by himself by the time fruit began to grow scarce, but the other two, m14 and m18, were still with their mothers. In 1967 two juveniles survived and both were females. I was able to observe some of the behavior involved in the breakup with their mothers of the two youngest males and the two females. A brief synopsis of my observations in each case follows.

About the middle of May 1966, FSP had a male baby, m14. She had a subsequent litter (which I did not see, but the existence of which I inferred from her behavior) in August, but it did not survive for more than two weeks. Thus, m14 remained with her as he grew up, sleeping and foraging with her from late July until fruit began to grow scarce in October. They spent less time together through the time when fruit was in lowest supply. By January 1967, m14 was potentially sexually mature and began to attempt to copulate with his mother, even though he still showed occasional nursing behavior. By the end of January and in February, his father, MSS, began to show serious aggressive behavior toward m14 and would actively seek him out and chase him. MSS's aggressive behavior toward m14 became still more pronounced in March, although FSB still tolerated him, and then he suddenly disappeared.

In late July 1966, F13 also had a male baby, m18, which was not ready to leave the nest and forage with her until the end of September, by which time fruit was becoming very scarce. Both F13 and her mate, MRE, showed considerable aggression toward m18 the first time he came to the bait area. During the months of January, February, and March, m18 sustained more attacks than any other animal that I had under observation. He survived until the end of May, when he disappeared. But he was always easily recognizable up until that time because of his small size. He did not gain significant weight through the three most severe months of food scarcity. The last time I trapped him was toward the end of December, but before he disappeared he did not look much larger. It seems reasonable to attribute his puniness to lack of food when he was young, and this, in turn, to parental aggression.

In early June 1967, F13 had another baby, and this time it was a female, f29. I was away in July and August, but by the first of September the two were foraging together and f29 was regularly taking food from her mother's mouth. F13 tolerated this until the middle of October, when she began showing signs of aggression. By the end of the first week in November she would attack f29 on sight.

During the third or fourth week of June 1967, FSB had twins, of which one (a female, f27) survived to leave the nest and start foraging with its mother in late September. I saw very little aggression between these two animals, but f27 spent considerably less time in the bait area with her mother than did f29 with F13 (Figure 6), and by late October came to the bait area alone.

It thus appears that a juvenile that joins its mother while fruit is still relatively abundant will be tolerated by both parents for a longer time than one that attempts to do so later. Aggression toward male young seems to be initiated by their fathers and toward female young by their mothers. The onset of parent-young aggression appears to occur earlier if fruit is scarce and, if it is scarce enough, either parent may become aggressive toward a youngster of either sex.

The first phase of the study terminated in November of 1967, so I do not know what became of f27 and f29.

Role of the Male

During the first three weeks that the baby is in the nest, the female will not permit another agouti to come close, even keeping her mate and any previous offspring at a minimum distance of about 5 meters. During the third week the male sometimes comes to the nest when the female is off foraging, and the young one will come out of the nest and attempt to interact with him. The male apparently recognizes the smell of his mate on the juvenile and he treats it as he would her. Each time the young animal runs toward the male he rears up and enurinates it, so that by the end of a few minutes it is thoroughly soaked with his urine. He also attempts to mount the juvenile, but it runs out from underneath him, and he stands and trembles with his front feet in the same way he does when frustrated in his attempts to get nearer to his mate.

There is apparently a postpartum estrus in agoutis, for the male is in almost constant attendance just before parturition, in spite of the increasing aggressiveness of the female, and he shows a greater amount of sexual excitability than usual whenever he is with the female immediately after parturition. In addition, subsequent litters are usually born about three and one-half months later, which is approximately the length of the gestation period (Roth-Kolar, 1957:369) Roth-Kolar (1957) found similar behavior in her captive animals, and

says that subsequent litters generally followed parturition by from 110–190 days.

Survival of the Young

Although there is a definite increase in the number born from March through July, I observed young agoutis during almost every month of the year on Barro Colorado Island. But, of those born outside of the March–July period in the phase I study area, none survived to leave the nest. The chief factor involved in their mortality was that, in the absence of falling fruit, adult male coatis turned from being primarily frugivorous to a primarily carnivorous way of life and spent much of their time hunting juvenile agoutis (Smythe, 1970c). The fact that the coatis experience considerable success in this pursuit is attested to by my witnessing three actual captures by them from the observation platform.

I believe that the time of survival of those agoutis that do leave the nests to begin foraging is also rather short, although they merely disappeared from the bait area and I am not sure of their fate. They suffer a very high level of aggression from the older animals which, together with the seasonal shortage of fruit, contributes to their undergoing considerable hardship from September through December. These conclusions are substantiated by the data gathered in phase II (Figure 17).

It would seem likely, therefore, that unless maturing agoutis find an unexploited area where they can establish a territory and accumulate a food hoard, which they would have to do by emigrating unless a local territory holder died, their chances of survival are not good.

Communication and Displays

Visual Communication

The act of walking toward another agouti is regarded by the one being approached as an agresive gesture. The animal being approached almost always avoids the other by walking or running out of the way. (As might be expected, this leads to difficulties when a male is attempting to get close enough to a female for copulation.) Occasionally a juvenile is frightened by something or will inadvertently run toward an adult male. In this case the adult runs out of the way of the approaching juvenile, as it would if attacked by another adult, but it then generally circles and attacks.

There seems to be little or no recognition of mates or other individuals by visual means. An excerpt from my notes during phase I serves to illustrate this:

> 24 April, 1730 hrs: An unidentified agouti chases F13 toward the bait area itself. MRE (the mate of F13 and a high-ranking male) is eating in the bait area and, as she passes him, she suddenly turns and rushes at him. He runs away for about 3 m, with his rump-hair fully erected, then turns around and rushes at F13. She wheels and flees, making appeasement squeaks. He slows down, so does she. He approaches and tries to enurinate her, but she avoids him. He sits with his front feet trembling (a sign of sexual arousal).

Such cases are common. An agouti would be aggressively aroused and would attack the next one it encountered, which would often be its mate. Then recognition would suddenly occur when the animals were close together, I believe, by one recognizing the odor of the other.

Exaggerated piloerection of the rump hair (Figure 22*b*, *c*) occurs as a manifestation of readiness to flee, even though it invariably appears in both animals engaged in aggressive encounters. It is a graded response, in its lowest intensity consisting merely of raising the long rump hairs to an angle of about 30° from the body. At the highest intensity the hairs are raised to nearly 90° so that they form a fan of hair on the rear end of the animal, and the display may be accompanied by eversion of the anal scent glands.

The fullest degree of piloerection is seen when one animal flees from another. It also occurs in the pursuer, but in such cases the one fleeing will usually turn and attack the one pursuing, i.e., their dominance relationship is uncertain. In such cases, both animals keep the hair raised during the entire encounter. Full piloerection also occurs in an agouti that is being chased by a potential predator. I saw it in several chases by coatis (*Nasua narica*) and peccaries (*Tayassu tajacu*), in one by a tayra (*Eira barbara*), and one by a jaguaroundi (*Felis jaguaroundi*). The first time I saw MRE enter the bait area, FSP was sitting there eating. MRE walked slowly into the area in the investigative posture, with the neck outstretched and held low, ears forward, and hindquarters slightly crouched.

FSP paused and looked at him with her ears forward, and both animals were still, about 2 m from one another. A large branch suddenly fell off a tree about 50–60 m away, and both animals fled in opposite directions with their rump hair fully erected.

A lesser degree of piloerection is liable to occur in situations of mild alarm. For instance, an agouti eating in the bait area would occasionally hear a noise made by another animal, such as a bird, moving in the foliage nearby but out of sight, and would raise the rump hair to an angle of about 60° from the body surface. A similar response occurred when F13 came upon an infant of FSP's that had just been killed by a coati; she raised her hair to about 60° and thumped her hind feet on the ground, while sniffing at the carcass. (I had inadvertently driven the coati off while looking for it after hearing the distress squeals.) Hair erection also occurs when an agouti smells a spot where a stranger has marked. The further the marker had come, and thus the less familiar it is, the higher the hair is raised. The lowest intensity of the hair-raising response occurs when an unfamiliar but distant noise, such as a gunshot, is heard or when a familiar but loud noise, such as a thunderclap or the sudden crashing of monkeys in the overhead foliage, occurs.

The function of the exaggerated piloerection is uncertain. It may have some signal value, but if so I believe that this is secondarily derived from a more probable function: that of protecting the rear end of a fleeing animal from the teeth of a conspecific, or making the target less definite for the teeth or claws of a predator. (Similar behavior is obviously advantageous to other caviomorph rodents: the porcupines).

A certain amount of visual communication must also occur during fighting behavior in agoutis, especially in the highly synchronized "jousting" (p. 31), since this requires the cooperation of both animals. I am not sure what signals are exchanged, because the whole bout is over very quickly.

Olfactory Communication

Marking with Anal Gland Secretions

Odors play an important role in the communication system of agoutis. Both sexes possess eversible anal glands that are used to mark various structures in the environment (Figure 25) and secrete a substance that, to the human nose, has a powerful and long-lasting odor. After I had handled an agouti, especially a male, it would take repeated scrubbing with soap and water to remove the odor from my hands.

Males mark more frequently than females, but the frequency of marking by both sexes increases with the unfamiliarity of the situation. Thus a totally foreign object, such as a freshly placed trap, will elicit more marking than will a newly fallen branch. Even though the animals will not go near the trap, they will mark frequently at a distance of a few meters while looking at it. The smelling of the mark of an unfamiliar animal causes an agouti to increase the frequency of its marking, the increase being most pronounced when one adult male smells the mark of another. In such a case the perineal drag is often accompanied by

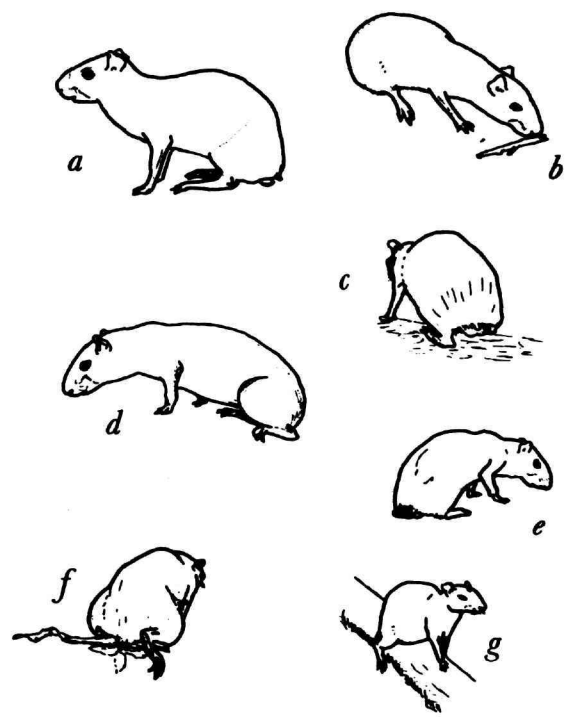


Figure 25.—Marking behavior: *a*, perineal drag; *b*, *e*, marking while sniffing unfamiliar odor, *c*, marking while thumping; *d*, *f*, marking with rearward scratching; g, marking on newly fallen tree trunk.

alternate rearward scratching of the hind feet, and also by thumping (Figure 25*c*). The same behavior pattern is sometimes seen during lulls between bouts of fighting or aggressive chasing, when the participants are out of visual contact but are about to seek one another out to continue the fight. Also during fighting the anal glands may be everted and, at such times, I was able to smell agouti odor from a distance of 10 m or more.

The only other times that I was able to smell agouti odor while watching wild animals was when a feeding animal was suddenly and violently surprised. On one such occasion, MSS was feeding in the bait area when a large male coati came within 5 m of him without his apparently being aware of its presence. (Coatis occasionally move slowly along, snuffling at the ground, apparently ignoring their surroundings. In this way they are often able to get quite close to feeding agoutis, who sit and watch them, probably relying on their much superior speed to escape if necessary. If able to approach within 5 m or so of a feeding agouti, the coati may make a sudden lunging rush at it. In most cases the agouti escapes, but at least one phase II male (m19), who was of "adult" weight and healthy, was caught and killed.) In the case of MSS on this particular occasion, the coati suddenly rushed at him and he fled making full alarm calls. A strong smell of agouti scent reached me within a few seconds. Similarly, an unidentified feeding agouti that was surprised by a jaguaroundi left a noticeable odor when it fled.

Scent marking of a home range by an animal that is potential prey for many predators might seem maladaptive, since the odor could provide clues to the prey animal's whereabouts. It is also possible, however, that the sudden release of a cloud of scent could have a confusing, "smoke-screen" effect on the predator by masking the specific location of the animal that released it. Scent marking is always performed by an animal that is thumping (Figure 25*c*), but it may be done without involving a perineal drag. An agouti that buries food probably also marks, but this is rather difficult to ascertain since the anal region is in contact with the ground anyway when the animal is digging. Feeding spots seldom seem to be intentionally marked, but if a strange agouti comes to one it will sniff at it and then mark, so it apparently recognizes the odor of the resident.

The rubbing-over behavior of young agoutis is probably a form of marking, in that there is a mutual exchange of odors. The behavior of its father toward a juvenile indicates that the odor of the mother is on it, and the male reacts as though the infant actually was the female. Later, when the juvenile no longer rubs over its mother, the male recognizes it as a different animal and reacts toward it aggressively rather than sexually.

Urine Marking

Besides the secretion of the anal glands, urine is also an important agent of communication. In sexual behavior (p. 28), urine is sprayed onto the female by the male from a distance of up to 1.5 meters. Males enurinate other males in aggressive encounters in captivity; but, although I have seen wild males briefly erect the penis after an aggressive encounter, I have never seen male-male enurination in the wild. Captive females, apparently in a high state of sexual arousal, will assume the crouching position typical of an enurinated male, and may urinate copiously on the ground. However, they are apparently not able to aim a stream of urine either forward or backwards, as are some other female caviomorph rodents (Kirchshofer, 1960b; Kleiman, 1974:186). In male agoutis the penis points backwards in its relaxed position, but males do not spray urine backwards.

Females with nest-bound young urinate repeatedly (at intervals of one or two days) on a spot outside the nest, and the baby lies on this spot when it comes out of the nest and the female is not there. In a sense it looks as if the spot is being treated as a surrogate mother. Adult males will perform a full ventral rub on the ground on the spot where their mate has urinated, and will sometimes sit and look at this spot and tremble their front feet. A male performing a ventral rub first smells the spot on the ground, then places his chin on it and, pushing himself forward with the hind legs, slides on the ventrum over the spot until the hind legs are almost straight out behind him. Then he pulls himself forward and into a standing position with the front legs. The whole pattern is strongly reminiscent of an agouti infant rubbing over its mother. All of these behavior patterns reinforce the contention that odor plays an important part in individual recognition by agoutis.

A mother agouti, before she permits her infant to nurse, licks the perineum and stimulates it to eliminate its metabolic wastes, which she then ingests. The infant, when the mother is not present, seeks out the place where she has urinated and lies there. Thus, from birth on, odors are of primary importance in an agouti's social gratification and communication. The rubbing over by a young animal probably functions in the establishment and maintenance of an odor bond between mother and young. The function of enurination during courtship is a means of overcoming the female's natural tendency to avoid the approach of her prospective mate. By spraying his urine onto her, the male transfers his own odor to the female. When he subsequently attempts to approach her, she has become accustomed to his odor and her fear of him is reduced. The original function (from the point of view of selection pressures) of a female's removing of the infant's metabolic wastes was probably to make the search more difficult for a potential predator. Later, urine becomes important in sexual bonding.

The constant marking of conspicuous objects within the animal's home range probably serves several functions. One is to give the animal a sense of security as it moves from one patch of its own identity to another. Roth-Kolar (1957:363) says that one of her captive females froze to death (in winter, in Germany) rather than enter a nest box in which the bedding material had been changed and so no longer smelled familiar. The facts that recognition of one member of the pair by the other is by means of odors, and that both male and female frequently mark in the home area, show that mutual use of the area is facilitated by the scent marking. The male marks more often than does the female, and he is also more active in driving off strangers. Anywhere that he has marked can be treated by her as being open for exploitation of food and living space. Because of his defense activities, she is less likely to be attacked by another agouti while she is within the marked area. At the same time, a strange agouti coming into the marked area may recognize the "ownership" of the residents and be ready to assume a submissive attitude during, or retreat from, an aggressive encounter. The smelling of a strange agouti's odor induces rump-hair erection (an indication of fear, hence of readiness to retreat) and an increase in scent marking by a potential trespasser, This results in each agouti's creating a border zone around each territory in which the adjoining residents have marked and within which each is prepared to be submissive. This may also result in reducing potentially damaging aggressive encounters. As either animal trespasses further into the territory of the other, he smells less and less of his own odor, and his readiness to flee probably increases proportionately. The resident, smelling more of his own familiar odor (or, if olfactory accommodation occurs, less unfamiliar odor) is more confidently aggressive.

Mechanical Communication

Thumping

Agoutis exhibit thumping behavior in response to an unfamiliar stimulus that is not moving toward them or that they are are unable to locate. In certain situations an agouti will lift both hind feet and rap them more or less simultaneously on the ground. This is usually done while the animal is sitting or crouching but occasionally occurs in a standing animal, in which case the front legs may also be thumped, so that the agouti actually jumps clear of the ground and makes the thumping noise as it lands.

Thumping is a graded response. A mildly disturbed animal sits and thumps with both hind legs, raising the legs from the ground, but not appreciably raising the rump. A more highly aroused animal, or one stimulated to thump by the thumping of another, will raise the rump slightly as it thumps, will evert the anal glands to some extent, and may exhibit some perineal dragging. At its maximum intensity, thumping of both hind feet (rarely both front feet as well) is accompanied by: (1) marking with full eversion of the anal glands, and (2) alternate rearward scratching of the hind feet.

Thumping occurs when an unfamiliar stimulus cannot be localized; for example, when a resident detects the odor of a fresh scent-mark of an unfamiliar animal. It also occurs when a presumably unfamiliar or potentially dangerous animal such as a snake, or a man, is detected but does not move. In this situation, it may be socially contagious and develop into mobbing behavior. When one agouti

detects a snake it begins to thump, to mark, and to erect its rump hair. Apparently in response to the thumping noise, other agoutis (often individuals that would otherwise be aggressive toward one another) join together and mob the snake. They come close (about 1.5–2 m) to the snake, not necesarily facing it, but never facing directly away, and thump on the ground. On one occasion I placed a 2.2 m boa constrictor (*Constrictor constrictor*) in a net in the bait area. Agoutis mobbed it continuously for five hours, after which I removed it. The same agoutis continued to show mobbing behavior toward roots and branches near the area where the snake had been (presumably because they have a similar shape to the snake) for a further two hours, at which time I discontinued observation.

An agouti going into an unfamiliar area will thump. This is usually seen when one comes into an area where another is dominant. The thumping acts to attract the attention of the resident, who usually goes and tries to drive away the interloper. Occasionally a juvenile animal (recipients of aggression from almost all adults) will be frightened into fleeing upon hearing another agouti thumping. Subadult males, who are beginning to show some aggression to other agoutis, will sometimes thump after they have been driven off by a dominant animal. This often has the effect of re-arousing the aggression of the dominant and results in further chasing of the subadult.

Derivation and Function of Thumping

An animal moving into an unfamiliar area, or an area where a conspecific is dominant, is usually in a state of readiness to flee. Agoutis achieve most of their running thrust from their hind legs; presumably using many of the same muscles involved in thumping, which may thus have been derived from flight-intention movements (Daanje, 1950).

Thumping is usually a response to a stationary or slow-moving stimulus that is potentially threatening but which is not actually attacking. If this is a predator or a conspecific that is preparing to attack, then there will probably be a state of psychological tension. The sudden thump may serve to startle the attacker into attempting its attack at a time when the thumper is maximally prepared to escape. It would be advantageous for other agoutis hearing the thumping to gather around the thumper in order to determine the whereabouts and intentions of the potential attacker. They, in turn, will begin to thump, which results in the predator being mobbed. Since some confusion would result if the predator did attack, the probability of one of a group of prey animals being captured would be less than for one alone. Also, in this respect, it is interesting to note that mobbing most often occurs in response to snakes, which are more sensitive to substrate-borne vibrations than to airborne sounds (Oliver, 1962:163). By thumping on the ground, agoutis are able to transmit a stronger signal to the snake than they would by vocalizations.

Drumming with the Forefeet

A sexually aroused male agouti will often tread rapidly with his forefeet (Kleiman, 1974:184). Occasionally this is done so rapidly that a pattering noise can be heard.

Sounds Made with the Teeth

Noises made by an animal moving its mandible so that the teeth rub or click together are hard to identify precisely. Agoutis make a chattering noise with their teeth; I believe that it is made with the incisors. It is often made after a soft fruit is eaten. Is is also made during agonistic encounters, usually between bouts of fighting.

When gnawing a hard seed, agoutis make a loud rasping noise that can be heard for 50 m or more. This acts as both an intra- and an interspecific signal. Conspecifics upon hearing this noise often move closer to the animal making it, either to chase it away or to partake of other food that may be in the area. On one occasion a jaguaroundi (*Felis jaguaroundi*) heard this noise and immediately began to stalk the animal making it. The tame jaguaroundis of Dr. R. F. Ewer on Barro Colorado Island regularly listened for the sound of agoutis rasping nuts and began to stalk as soon as they heard it (pers. comm.).

Vocalizations

Eisenberg (1974) summarizes the sounds produced by agoutis, compares their vocal repertory

with that of other caviomorph rodents, and discusses various ecological correlates.

The Alarm Bark

The best known vocalization of the agouti is the alarm bark. As usually heard by a person walking through the forest it sounds much like a repeated, rather high-pitched, bark of a small dog. If the observer is closer to the animal, however, he will hear that each bark, or pair of barks, is preceded by several deep grunts, "uh-uh-uh . . . ," which are usually made as the hind legs thrust forward at each bound. The alarm bark is always made by an animal running at a full gallop, never by one sitting still (and never by one in an enclosure too small to permit full-speed running). It is also made under particular circumstances. When an agouti detects the approach of an unfamiliar animal it will usually freeze. (If the animal is approaching directly, the agouti will sneak silently off into the underbrush.) If the angle of approach is such that the unfamiliar animal does not come within a critical distance (which varies from agouti to agouti, being longer in younger animals), then the agouti will remain still until after it has passed. If, however, the angle of approach is such that the critical distance is broached, the agouti will make alarm barks as it runs off on one of its habitual trails. The alarm bark is also given if the agouti is suddenly surprised, as by the rush of a predator.

Agouti alarm vocalizations are graded. At the lowest intensity only the preliminary grunts are uttered. This occurs when the agouti is frightened or surprised by a peccary or a feeding coati (i.e., one that does not attack, but is eating fruit); these are animals with which the agouti is familiar but which exert an interspecific dominance in a feeding situation and are potentially dangerous. The second intensity consists of the preliminary grunts along with one not very loud bark. This occurs when an agouti is chased by a potential predator (e.g., a coati or a peccary), but is not surprised and is easily able to outdistance the attacker. The third intensity is the loudest bark, repeated several times, singly or in pairs and preceded each time by the grunts.

Reactions of Conspecifics to Alarm Barks

If an alarm call was sounded while agoutis were in the bait area their reaction was generally not very pronounced. They would usually pause for one or two seconds, listen in the direction of the calling animal, and then return to what they were doing. Occasionally the rump hair might be erected to about 30°, which indicates a low state of arousal. If the alarm bark was sounded by one of the agoutis actually in they area, they might react to it a little more strongly. The following excerpt from my phase I notes is illustrative of this and other aspects of agouti behavior.

1 March, 1712 hrs: A male coati comes up the dry creek below the observation platform. An unidentified agouti starts thumping out of sight, east of the bait area, and m14 sits beside the north end of the large fallen log that is on the west edge of the bait area (Figure 3*b*). Then m14 sniffs in the direction of the coati, which is making a wide circle of the bait area. The coati reaches the north end of the log, jumps onto it and walks down it to the center of the bait area.

1717 hrs: The coati eats in the bait area, m14 goes east and then north. The unidentified animal still thumps out of sight.

1718 hrs: m14 stops at the north end of the log, thumps, and then goes east. He thumps again, then remains sitting about 3 m northeast of the log.

1720 hrs: mSN appears just south of m14 and walks toward the bait area. He stops and eats something on the way and then goes west to the path leading from the northern end of the log to the bait area. He goes down the path into the bait area, sees the coati and raises his rump-hair to about 45°. Then he picks up a piece of banana and moves to the east side of the bait area to eat it. (The coati eats on the west side of the bait area, on the other side of the log from mSN.)

1722 hrs: MSS and his mate FSP enter the bait area from the northeast. mSN thumps, and then thumps again.

1723 hrs: FSP goes toward mSN and then turns toward the center of the bait area. MSS suddenly chases mSN, who runs in a small circle. MSS makes a high-pitched grunt as he chases mSN, who goes up to the feeding spot at the north end of the fallen log and sits just on the east side of the log. MSS returns to the bait area, FSP has seen the coati and sits looking at it.

1724 hrs: MSS marks with a perineal drag. The coati walks toward MSS who moves a few steps out of its path. mSN has begun to gnaw a hard seed and the sound is clearly audible to me. m14 is walking slowly toward mSN. The coati goes north on the west side of the log, and jumps up onto it less than 2 m from mSN. This startles mSN and he leaps up and runs northeast, almost colliding with m14, then dodging out of the way and continuing northeast. m14 runs west directly at the coati, apparently only seeing it when about 1 m away. He veers southeast, in-

creases his speed and makes full alarm barks. The coati jumps away and freezes with his tail vertical. MSS and FSP freeze for about 30 seconds.

1729 hrs: MSS has walked in a circle under brush cover. He returns to the spot where m14 veered upon seeing the coati, and thumps and marks over the spot.

1730 hrs: MSS comes south into the bait area. He thumps, then thumps again, then marks. He walks straight through the bait area and goes east, out of sight.

Animals making alarm noises usually run for about 30–40 m, then stop, sit down and remain quite still for 15 to 40 minutes. They will then start to groom for a few minutes before getting up and walking back along the path they followed when making the alarm noises.

The Purr

Another sound in the vocabulary of the agouti is the purr. This resembles one "syllable" of the purring of a domestic cat but is usually rather louder. It may also contain some louder vocal interjection, the volume depending upon the context. The purr is essentially a contact noise and occurs in the following contexts: (1) by a nursing mother when arriving at the nest, while being groomed by the juvenile, upon picking up a piece of food when foraging with the juvenile, or when the juvenile takes food out of her mouth; (2) by the juvenile when being groomed by the mother, or during naso-nasal greeting of the returning mother; and (3) by adults when being closely approached by their mate, when being groomed by their mate, or when picking up a piece of food after searching some time for it.

When a nursing mother visits the nest, she puts her nose into the nest entrance, makes a single purr, and then sits down nearby. The juvenile usually comes out within five seconds, although I have seen a mother wait for as long as two minutes. All agoutis, in response to contact with their mate, their mother, or their young offspring, make the purr. Tame agoutis will make the same sound in response to the contact of a human.

The Creak-Squeak

A juvenile that is temporarily out of contact with its mother, or is following her as she walks along, makes a noise that I call the "creak-squeak." Upon first hearing this noise I thought that it was made by the animal grinding its teeth together. Later (when a tame agouti made the same noise) I could see that, while the sound is not accompanied by any movement of the mandible, there is some thoracic movement, and so I conclude that it is a vocalization. It is a difficult noise to describe, sounding rather like a very squeaky door that is moved rapidly at first and then more slowly, the resulting noise having two definite components: a high-pitched squeak followed by a definite staccato creak. This vocalization is repeated at very short intervals by a young animal following its mother, so that it is almost staccato in form.

The longer a juvenile has been separated from its mother, the louder the initial squeak is made. On two occasions I thought that I heard an adult female make the same noise when she was separated from her young; but because of the high level of insect noises in the forest, I could not be absolutely sure. The noise is made by adults in potentially aggressive situations and appears to have an appeasement function. If an agouti is attacked by another that does not have its rump hair fully erected and is not making "fight grunts," it will make the creak-squeak. It is typically made by subadults that fail to move out of the way of an approaching adult until it rushes at them. It is also made by adult females whose mates attack them "by mistake." In each of these cases the sound appears to decrease the aggression of the attacker. An adult male approaching a female to enurinate her may make creak-squeaks. The frequency of the sound appears to increase with the number of times she avoids him. Occasionally, if a male has been attempting to enurinate a female and she leaves the area without his knowledge, he will sit in one spot and make creak-squeaks with his front feet undergoing violent trembling. The same behavior sometimes results when an adult male attacks his mate. She may flee, making appeasement squeaks, while he sits and trembles his front feet.

Fight Grunts

The fight grunt is a short grunt that is repeatedly uttered by one agouti when pursuing another, usually while attempting to bite the fleeing animal's

rump. Animals making fight grunts usually have the rump hair raised to its maximum height.

Rumble

A trapped, wild agouti sometimes makes a very deep rumbling sound when approached. This sound is of a very low frequency, and must be near the lower limit of human audition. I have not heard the rumble in natural circumstances in the wild.

Growl

Between bouts of an aggressive encounter agoutis will utter a noise that sounds like the growling of a very small dog but is rather smoother. The same sound is uttered by a female when a coati is attempting to dig her young out of the nest.

Distress Scream

Agoutis of all ages make a distress scream, similar to that of a rabbit, when a predator has actually caught them. I use a nylon net to handle trapped agoutis. When in the net, none of them made distress screams. On two occasions animals escaped from the net while being marked, and I caught them by one hind leg. Both of these animals made distress screams. I have seen three infants and one adult agouti captured by male coatis but have seen no other actual case of predation. In each case of coati predation the agouti made loud distress screams that lasted five to ten seconds. In one case a nearby band of cebus (*Cebus capucinus*) monkeys appeared to become very agitated by the agouti vocalizations and in another a pair of creasted guans (*Penelope purpurascens*) called loudly for some minutes after the agouti screamed. The uttering of distress screams by agoutis that have been caught by any predator probably has been selected for because other animals are attracted to the scene and occasionally interfere with the predator, permitting the agouti to escape. Hunters throughout the range of the agouti fashion a simple whistle out of wood, plastic, or sometimes the caps of soft-drink bottles, with which they are able to render the distress scream with startling fidelity. I have been assured by a number of independent sources that a wide variety of animals can be lured within very close range by use of these whistles.

I was recently watching an apparent dominance contest between two agoutis outside both of the study areas. One of them eventually chased the other under a rather dense pile of fallen foliage—palm fronds and other material. There was apparently no easy exit from the space underneath since, when the aggressor entered, the aggressee remained inside. I could see nothing of what went on there but I could hear the animals scuffling about. Suddenly, one of them started to make distress screams. A male coati that I had not previously noticed trotted up to the pile of foliage and climbed partly onto it. The distress screams stopped and both agoutis erupted out of their cover and ran off in different directions. The coati remained motionless where it was until both agoutis had disappeared. This is the only occasion that I have heard distress squeals given in an intraspecific encounter.

Conclusions

Competition and Ecological Separation among Terrestrial Frugivores

During that part of the year when fruit is most abundant, a surprising array of mammals, including some that are generally considered to be carnivorous (e.g., tayra and coati) or browsers (e.g., tapir and deer) subsist on it. There is a period during most years when fallen ripe fruit is superabundant, so that much of it rots where it falls. During this period the frugivores cannot be considered to be competitors in the strictest sense.

As fruit becomes seasonally less abundant many of the facultative frugivores turn to other food sources but, since fruit is comparatively nutrient rich in terms of the effort expended to procure it, they will eat fallen fruit when they can obtain it. Thus, during the season when fruit is scarce it may be a factor in limiting the numbers of the animals exploiting it, and they must therefore be considered as at least in potential competition with one another.

The largest biomass of primarily ground-dwelling or terrestrial mammals of the forest of Barro Colorado Island consists of the following species: the common opossum, the coati, the agouti, the

paca, the spiny rat, the collared peccary, and the tapir. All of these mammals are either primarily or faculatively frugivorous and, in fact, during the period of fruit abundance they are all probably primarily frugivorous.

Of the above species, the agouti, collared peccary, and coati are diurnal, whereas the opossum, paca, spiny rat, and tapir are nocturnal. If we assume (and I believe it is reasonable to do so) that ripe fruit falls from a tree without regard to the time of the day, then at least during the time when fruit is abundant, the diurnal and nocturnal animals can be considered to be ecologically separated by the fact that they are active at different times. When fruit is the principal diet, the major potential feeding competitors of the agouti would be the collared peccary and the coati. (In recent years on Barro Colorado Island the local forest squirrel, *Sciurus granatensis,* has increased markedly in number. It can eat most of the same food items as the agouti and is thus a potential competitor. But the total biomass of squirrels is low enough that their effect is small.)

Coatis are unable to break through the seed coats of many of the agouti food plants (Kaufman, 1962:101) and so are excluded from these as a food source. I have seen peccaries, however, breaking *Astrocaryum* seeds with their powerful molars; therefore, they must be able to eat almost any seed that agoutis can and are their most serious food competitors.

The principal way in which agoutis contend with competition by peccaries, and to some extent by coatis, is by cleaning off any soft, odoriferous exocarp, and dispersing and burying the seeds as they fall. During the season of abundance, peccaries move from one fruiting tree to another, generally eating whatever fruit is on the ground when they arrive and then moving on. A band of peccaries has a home range that covers many times the area occupied by a pair of agoutis; so, if a pair of agoutis scatterhoards the fruits as they fall, it will be uneconomical for the peccaries to search for each item in the dispersed food source. The same holds true for a band of coatis.

During the season when falling fruit is scarce the situation is quite different. Since the supply of fruit is now inadequate to feed all of the animals that it supported through the season of plenty, the probability of there being competition between diurnal and nocturnal animals is increased. The feeding habits of the terrestrial frugivores become more diverse and each adopts different methods of compensating for the lack of available fruit.

There are four major ways of coping with seasonal shortage of food: (1) entering torpor and slowing the metabolic processes, (2) broadening the activity period and increasing the time spent foraging, (3) changing the diet and eating something that is more abundant, and (4) storing food in some way while it is abundant and then utilizing it when the supply diminishes. None of the animals under consideration appears to go into torpor.

The agouti and probably the spiny rats store food at times when it is abundant. Agoutis scatterhoard food items and spiny rats larderhoard in their burrows (pers. obs.). When fruit becomes scarce, agoutis spend less time resting and more foraging, and depend heavily upon the seeds that they buried earlier. I do not have enough data regarding the spiny rat to be able to state whether it alters its activity pattern or how much it depends upon its hoard.

Pacas neither scatterhoard nor larderhoard. They do store some food in the form of fatty tissue, which is a course presumably not open to agoutis since they rely upon their acceleration, speed, and stamina to escape predators. Pacas also change their diet and browse more, especially on seedlings, many of which probably grow from the seeds that agoutis have buried.

Peccaries do not store food. During times when fruit is scarce they browse and root more, and they also extend their normally diurnal activity period into the night. Any time that they find a concentrated food source during this period they "camp out" on it, exploiting it day and night, and making it essentially unavailable to agoutis or pacas. Male coatis also extend their activity period and change their diet, becoming more carnivorous (Smythe, 1970c). They also tend to camp out on a supply of fruit if they find one at this time (Kaufman, 1962:175). Female coatis seem to change their activity period very little, but they tend to eat more small litter animals, and they travel further for food than at other times of the year (Kaufman, 1962:174). The common opossum appears to keep to its normal activity period, but it may spend more time foraging. It also broadens

its diet and eats small, moderately hard, seeds that it rejects at the time of abundance.

Coatis and opossum (as well as other arboreal mammals) are able to climb and reach fruit at a time when it is ripe enough to eat but not yet ripe enough to fall; that is, while it is still unavailable to the strictly terrestrial species. The extent to which this benefits the climbing and arboreal species is not known; but the potential advantage is great; for example, coatis and other animals can eat the unripe fruits of the palm *Astrocaryum standleyanum* in January, when ripe, falling fruit is very scarce indeed.

The relationship between the terrestrial and the arboreal or aerial frugivores is complex. I will not discuss it further, beyond pointing out that there may be some mutual benefits involved. Agoutis often follow bands of monkeys as they move through the trees, picking up fruits that they drop. *Cebus*, spider, and, to a lesser extent, howler monkeys eat many of the agouti preferred fruits and might thus be considered to be potential competitors. Monkeys habitually drop many food items after taking only a single bite from them. Agoutis benefit from such behavior at times when falling ripe fruit is in short supply Similarly, I have watched peccaries (and, in darkness, pacas) going to the fruits dropped by arboreal feeders. Scatterhoarding of the seeds thus obtained by the agoutis enhances the survival of the trees, which in turn benefits the arboreal animals.

Agoutis and Seed Dispersal

Three important characteristics of the forest are relevant to a discussion of agoutis as seed dispersers: first, the relationship between the spacing of static organisms (the trees, their leaves, or their seeds) and the ease with which they may be encountered by potential predators or disease vectors; second, the relationship between forest maturity and seed size; and third, seasonality in the pattern of fruiting.

As Ridley (1930) and more recently Janzen (1970) have pointed out, the probability of plants suffering predation or disease decreases with distance between individuals. The same principle holds for seeds, seedlings, or adults, but is probably most important in the case of the seeds, which are not only most vulnerable as individuals but also contain the most concentrated source of high-value food. The density of fallen (nonself-dispersed) seeds is highest in the "seed shadow" directly under the parent and, in the absence of any kind of dispersal, would remain at zero elsewhere. Assuming roughly random dispersal in the direction away from the parent, the average density of the seeds of a particular species will eventually reach the point where it will be lowest, half way between fruiting conspecifics. It is along the line so described that the seeds and resulting plants will be minimally encountered by host-specific predators and disease vectors. Seed dispersal is thus of critical importance.

With regard to seed size and the maturity of the forest, Salisbury (1942:4–36) pointed out that, in general, seed size increases with the average height of the individuals in a given stand of vegetation. This is probably primarily due to the fact that the light levels on the forest floor decrease as the average height of the trees increases. Therefore, germinating seeds are more successful if they contain greater reserves of nutrient.

So we see that survivorship of a forest tree species is intimately related to two factors: the distance of dispersal of its seeds and their size. But the larger a seed becomes, the more difficult it is to move. A small seed can be blown by the wind, flung by an exploding pod, hooked onto a passing animal or swallowed and later deposited with a small amount of rich fertilizer far from its parent. As seeds become larger, each of the above dispersal methods becomes less efficient. How then can the largest seeds be transported? They can be made to float but, unless the water ebbs and flows (as it does over large areas of Amazonia), the distribution of the seeds will be unidirectional and thin. One occasionally reads of "gravity dispersal." Reliance on this would result in a gradual descent of the species in question until it existed in maladaptive densities at the lower ends of valleys. Animals could carry the seeds, but why should they? This brings us to the third consideration: seasonality.

The long-venerated assumption that tropical humid forests are aseasonal and constantly benign is gradually being put to rest, and we now know that, although the temperature may remain fairly constant, there are nonetheless fairly predictable seasonal changes throughout many, perhaps most, of

the lowland tropical forests. These are usually underlain by changes in the annual pattern of rainfall and through much of the range of agoutis there is a wet and a dry season each year. It is during the dry season that there is the greatest shedding of leaves from the trees, but decomposition of the forest floor litter is slowest then because of the lack of water. When the rain begins again the rate of decomposition is accelerated and, for a brief period, the soil surface becomes rich in its products. This is the optimal time for the germination of seeds and is thus the height of the fruiting season. After some months of heavy rains most of the surface litter is washed away and, as there is little or no topsoil, seeds dropped at this time would have a lowered probability of survival. They would also be more likely to be eaten since the seed-eating animals are short of food outside of the main fruiting season.

Climatic variation causes a season of scarcity and the agoutis hoard seeds to overcome this. The seeds are large enough to constitute a food resource during times of scarcity and are protected against decomposition, or attack by unspecialized predators, by a tough seed coat. (Or, perhaps in some cases, by toxins that may deteriorate after some months in the ground.) Agoutis are able to chew through this seed coat with their incisor teeth and, in this case, the embryo is destroyed. More seeds are hoarded, however, than are recovered, so dispersal is accomplished. The seeds have evolved so that, in most cases, a dual reward is offered to the potential disperser. The primary reward consists of a soft, sweet pericarp or pulp surrounding the seed and serves to attract the animal to the fruit. It is usually consumed immediately. The second reward is in the rich endocarp which, protected either by the tough exocarp or containing its own toxins, remains edible until it is needed some months after being hoarded. The agouti could not survive without such a hoardable resource; the plant could probably not survive without its agent of dispersal. The average distance that agoutis move the seeds that they hoard might seem small, but since the spacing of the seeds only increases until they are moved halfway toward the nearest fruiting conspecific, the distances are probably perfectly adequate.

The Adaptive Value of Monogamous Pairs

The adaptive value of remaining mate-tolerant throughout the year probably arises from the following factors. Since seeds are scatterhoarded to protect them from exploitation by other animals and to constitute a food source in times of scarcity, they must also be guarded from exploitation by conspecifics. This necessitates the maintenance of a fairly high level of intraspecifiec aggression. Moreover, the maximum survival rate of offspring occurs when parturition takes place near the beginning of the season of fruit abundance. Since the agouti has a gestation period of approximately three months, this means that conception must have taken place at a time when there was practically no fresh fruit available, and defense of the hoarded seeds was most rigorous. It would be difficult for the animals to mate at that time if they lived separately, defending separate hoards. Animals remaining together throughout the year do not have to go through the lengthy courtship that would be necessary to overcome the high level of intraspecific aggression and they can produce young when their chances of survival are greatest. Kleiman (1974:190) has suggested that agoutis probably have a very short period of estrous. If this is the case then it also is of obvious advantage for the pair members to be in one another's company at the time of estrous.

The manner of partitioning energy expenditure may also favor the formation of a long-lasting pair bond. Most of the defense of the hoard is performed by the male, but the fitness of the population is a function of the well-being of the female. The most highly adaptive strategy is probably for the male to defend the hoard and for the female to derive the greater proportion of nutritional energy from it, and to expend her energy in the raising of their young.

It may also be advantageous for the species as a whole if some young are produced throughout the year. Very few of the young born outside of the period of abundance survive but, while the seasons and the degree of food deprivation are usually fairly predictable, aberrant years are not uncommon. In the population of agoutis that I watched, some young were born in every month of the year and mortality was high for those born between September and March (when food is gen-

erally scarce). It is probably, however, that there are years when food is more abundant during what is usually the lean season, and that the young born at that time suffer reduced mortality. The survivors would be at an advantage over young born later, since they would be larger at the beginning of the regular season of abundance and more able to profit from it.

Limitations Imposed by the Necessity of Hoarding

The necessity of hoarding food against times of scarcity also contributes to the placing of a size limit on the agouti. Since the hoard is scattered it is reasonable to assume that there is an optimum density of buried seeds. If the mean distance between individual buried seeds is too low, the hoard will be concentrated enough that it will be profitable for peccaries to exploit it. If the mean distance between seeds is too high, there will not be sufficient food within the area of the hoard to support the resident agoutis.

Since the hoard must be defended, the resident must be able to detect the encroachment of a conspecific over a certain distance. This does not mean that he must be able to detect the other animal anywhere within the defended area, but he must have a high probability of doing so during one of his periodic patrols, and he cannot spend all of his time patrolling. The distance over which one animal can detect (or communicate with) another is a function of such environmental factors as visibility, air movements, and ambient noise levels. These factors are thus important in delimiting the maximum size of the defendable area. A larger agouti living in the same environment would need a greater quantity of stored food to tide it over seasonal shortages, but it would not be able to economically defend a larger area. Nor could it benefit from storing seeds at a higher density. For the same reason, the strategy of raising the reproductive potential by polygyny would be impractical, if the area defendable by one male can only support one additional animal.

The Status and Future of the Agouti

In conclusion, I feel it necessary to express my opinion as to the status and future of the agouti. Since it is the commonest and one of the most widespread of those Neotropical forest mammals that are considered to be desirable food by man, many factors affecting its well-being are generalizable to other animals that are also considered to be desirable food.

A range map of the genus *Dasyprocta* serves equally to illustrate the distribution of the Neotropical, moist, lowland, and premontane forest. The comparison is supported on a microgeographic scale: the agouti is absolutely dependent upon the existence of this type of forest. The conservation journals are constantly reminding us of a fact that is all too evident to any naturalist who has traveled in Latin America: the forests are disappearing at an almost incredible rate. The cult of progress holds as one of its most sacred tenets that a standing tree is anathema, and there is probably no way to stop the destruction of most of the forests. With them will go all their dependent species and we will be left with those that have the potential to exist as man's commensals.

The foregoing view is held by many to be cynically pessimistic. Perhaps that is true. There are still, even in Central America, vast tracts of forest that look, from an airplane or to the casual visitor, as though they are practically unmolested by man. I have visited some such areas to attempt the observation of agoutis in conditions even less artificial than those of Barro Colorado Island.

In 1966 I traveled with a botanist, Dr. James Duke, some 160 km up the Chucunaque, a river that bisects part of Darien Province, in eastern Panama. It is an area widely regarded as being among the most pristine in Central America. Along the river, as far as we went, we met several canoeloads of natives every day. As they traveled the river, particularly if they were going downstream, the women and children remained in the canoe while the men with their dogs hunted both banks of the river. Periodically we stopped and went ashore and I searched the area within a few hundred meters of the riverbank for signs of agoutis. During the entire trip I found one footprint and, at another location, heard one alarm call. During the same year the Atlantic-Pacific Interoceanic Canal Studies Commission was investigating the possibilities of building a sea-level canal across the Isthmus in Darien Province (Route 17). I had the opportunity to visit the area for a week. A road was

being built along the proposed route, and I spent the days and much of several nights around the head of this road, about 10 km inland from the tiny village of Santa Fé, walking as far into the forest as I could get, searching for agouti signs. I employed a local hunter to take me out with him and to show me the areas where his experience indicated we would see the most agoutis. During the entire time that I was in the area I caught glimpses of two agoutis, heard two alarm calls, and saw six different sets of tracks. I found more domestic dog tracks than agouti tracks!

In 1976 I paid two separate visits to the site of a proposed dam (La Fortuna) in Chiriqui Province in western Panama. The proposed damsite is a 2- to 3-hour walk, through progressively older looking forest, from the nearest village. This village of a few houses is itself about an hour's walk from the end of a very rugged dirt road. I walked around the damsite in all directions during a total stay of 10 days. I did not see an agouti, nor even a track. The tracks of domestic dogs were common. Local hunters asured me that it was only necessary to go 5 or 10 km further into the forest before game became plentiful; not as plentiful as it was a few years ago, and somewhat further away, but with a good set of dogs and perhaps a headlamp, one could be certain of shooting agoutis, pacas, peccaries, tapirs, etc.

Agoutis undoubtedly exist in all of these areas, but their numbers are abnormally low. The point of the foregoing is to show that complacency about there being plenty of undisturbed forest left is unwarranted. Moreover, it is not true of Neotropical forest game animals that, if their habitat is left more or less intact, their populations will survive in spite of indiscriminate hunting. This is because dogs and headlamps are being increasingly used and the mammals have evolved no defense against such things. Agoutis have no natural predator (and therefore no natural responses to one) that combines the abilities of high-speed odor-trail following with interindividual cooperation in the hunt. A hunter can visit the same area repeatedly with two or three dogs and can eradicate the local agouti population. Similarly, no mammal has evolved defenses against predators using lights. The use of headlamps is not as widespread as the use of dogs, but it is becoming increasingly common to meet hunters who live a day's walk from the nearest battery supplier and who regularly use headlamps.

A few countries in Latin America have instituted hunting regulations, but I have not seen more than token enforcement. (I have visited two "reserves" where the men charged with the enforcement of the regulations were, by their own admission, regularly hunting on the reserves.)

Thus, agoutis and the other game animals are indiscriminately hunted throughout the year, and the reduced populations have little chance to recover. If it was possible to preserve reasonable tracts of forest and to enforce regulations prohibiting the use of dogs and headlamps, and restrict hunting to the season of minimum reproduction (which may vary from one region to another, but probably is similar for most species within a given region), then there would be a fair probability of preserving the game animal species.

If the remaining forested areas must be exploited to produce food for burgeoning populations, it may well be that cutting down the trees is the less productive method of exploitation. In most cut-over areas where agoutis, pacas, tapir, and brocket deer would have thrived, cattle have been found to do poorly. It is possible that, by efficiently managing these areas and exploiting the naturally evolved ecosystem, a higher protein yield could be sustained. Management and law enforcement would be difficult and some species would suffer, but it would be better to preserve at least incomplete ecosystems, containing some of the animals, than to destroy them all.

Literature Cited

Allee, W. C.
1926. Distribution of Animals in a Tropical Rain Forest with Relation to Environmenal Factors. *Ecology*, 7(4):445–468.

Bourlière, F.
1973. The Comparative Ecology of the Rain Forest Mammals in Africa and Tropical America: Some Introductory Remarks. Pages 279–292 *in* Meggers, Ayensu, and Duckworth, editors, *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Washington, D. C.: Smithsonian Institution Press.

Cabrera, A., and J. Yepes.
1960. *Mamiferos Sudamericanos*. Volume 7, 160 pages. Buenos Aires: Ediar.

Daanje, A.
1950. On the Locomotory Movements in Birds and the Intention Movements Derived from Them. *Behavior*, 3:48–98.

Dubost, G.
1968. Les niches ecologiques des forêts tropicales sud-americanes et africaines, sources de convergences remarquables entre rongeurs et artiodactyles. *La Terre et la Vie*, 1:3–28.

Eibl-Ebesfeldt, I.
1958. Das Verhalten der Nagetiere. *Handbuch der Zoologie*, 10(13):1–88.

Eisenberg, J. F.
1974. The Functional and Motivational Basis of Histricomorph Vocalizations. *Symposium of the Zoological Society of London*, 34:211–244.

Eisenberg, J. F., and G. M. McKay
1974. Comparison of Ungulate Adaptations in the New World and Old World Tropical Forests with Special Reference to Ceylon and the Rainforests of Central America. *In* V. Geist and F. Walther, editors, The Behavior of Ungulates and Its Relation to Management. *International Union for Conservation of Nature and Natural Resources Annual Report*, new series, 24:585–602.

Eisenberg, J. F., and R. W. Thorington, Jr.
1973. A Preliminary Analysis of a Neotropical Mammal Fauna. *Biotropica*, 5(3):150–161.

Enders, R. K.
1930. Notes on Some Mammals from Barro Colorado Island, Panama Canal Zone. *Journal of Mammalogy*, 11(3):280–292.
1931. Parturition in the Agouti, with Notes on Several Pregnant Uteri. *Journal of Mammalogy*, 12(4): 390–396.
1935. Mammalian Life Histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 78(4):385–502.

Goldman, E. A.
1920. Mammals of Panama. *Smithsonian Miscellaneous Collection*, 69(5):1–309.

Hediger, H.
1955. *Studies of the Psychology and Behavior of Captive Animals in Zoos and Circuses*. 154 pages. London: Butterworths.

Howard, W. E., R. E. March, and R. E. Cole
1968. Food Detection by Deer Mice Using Olfactory Rather Than Visual Cues. *Animal Behavior*, 16: 13–18.

Janzen, D. H.
1969. Seed Eaters Versus Seed-size, Number, Toxicity, and Dispersal. *Evolution*, 23:1–27.
1970. Herbivores and the Number of Tree Species in Tropical Forests. *American Naturalist*, 104:501–528.

Kaufmann, J. H.
1962. Ecology and Social Behavior of the Coati (*Nasua narica*) on Barro Colorado Island, Panama. *University of California Publications in Zoology*, 60(3):95–222.

Kirchshofer, R.
1960a. Das Grosse Mara. *Umshcau*, 7:198–201.
1960b. Uber das "Harnspritzen" der grossen Mara (*Dolichotis patagonum*). *Zeitschrift fur Saugetierkunde*, 25:112–127.

Kleiman, D. G.
1971. The Courtship and Copulatory Behaviour of the Green Acouchi (*Myoprocta pratti*). *Zeitschrift fur Tierpsychologie*, 29:259–278.
1972. Maternal Behaviour of the Green Acouchi (*Myoprocta pratti* Pocock), a South American Caviomorph Rodent. *Behaviour*, 43:48–84.
1974. Patterns of Behaviour in Histricomorph Rodents. *Symposium of the Zoological Society of London*, 34:171–209.

Morris, D.
1962. The Behavior of the Green Acouchi (*Myoprocta pratti*) with Special Reference to Scatter Hoarding. *Zoological Society of London, Proceedings*, 139(4): 701–732.
1965. *The Mammals: A Guide to the Living Species*. 448 pages. London: Hodder & Stoughton.

Murie, J. O.
1977. Cues Used for Cache Finding by Agoutis (*Dasyprocta punctata*). *Journal of Mammalogy*, 58:95–96.

Murray, M. D.
1961. The Ecology of the Louse *Polyplex serrata* (Burmeister) on the Mouse *Mus musculus* (L). *Australian Journal of Zoology*, 9:1–13.

Oliver, J. A.
1962. *The Natural History of North American Amphibians and Reptiles.* 358 pages. Princeton, New Jersey: van Nostrand.

Ridley, H. N.
1930. *The Dispersal of Plants throughout the World.* 744 pages. Ashford, England: Reeve.

Rood, J. P.
1972. Ecological and Behavioural Comparisons of Three Genera of Argentine Cavies. *Animal Behavior Monographs,* 5(1):1–83.

Roth-Kolar, H.
1957. Beitrage zu einem Aktionssystem des Aguti (*Dasyprocta aguti aguti* L.). *Zeitschrift fur Tierpsychologie,* 14:362–375.

Salisbury, E. J.
1942. *The Reproductive Capacity of Plants.* 244 pages. London: Bell.

Simpson, G. G.
1945. The Principles of Classification and a Classification of Mammals. *Bulletin of the American Museum of Natural History,* 85:1–350.

Smythe, N.
1970a. On the Existence of Pursuit Invitation Signals in Mammals. *American Naturalist,* 104:491–494.
1970b. Relationships between Fruiting Seasons and Seed Dispersal Methods in a Neotropical Forest. *American Naturalist,* 104:25–35.
1970c. The Adaptive Value of the Social Organization of of the Coati (*Nasua narica*). *Journal of Mammalogy,* 51:818–820.

Southern, H. N.
1948. Sexual and Aggressive Behaviour in the Wild Rabbit. *Behaviour,* 1:173–195.

Walker, E. P.
1968. *Mammals of the World.* 1500 pages. Baltimore: Johns Hopkins University Press.

Weir, B. J.
1971. Some Observations on Reproduction in the Female Agouti (*Dasyprocta aguti*). *Journal of Reproduction and Fertility,* 24:203–211.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI–36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

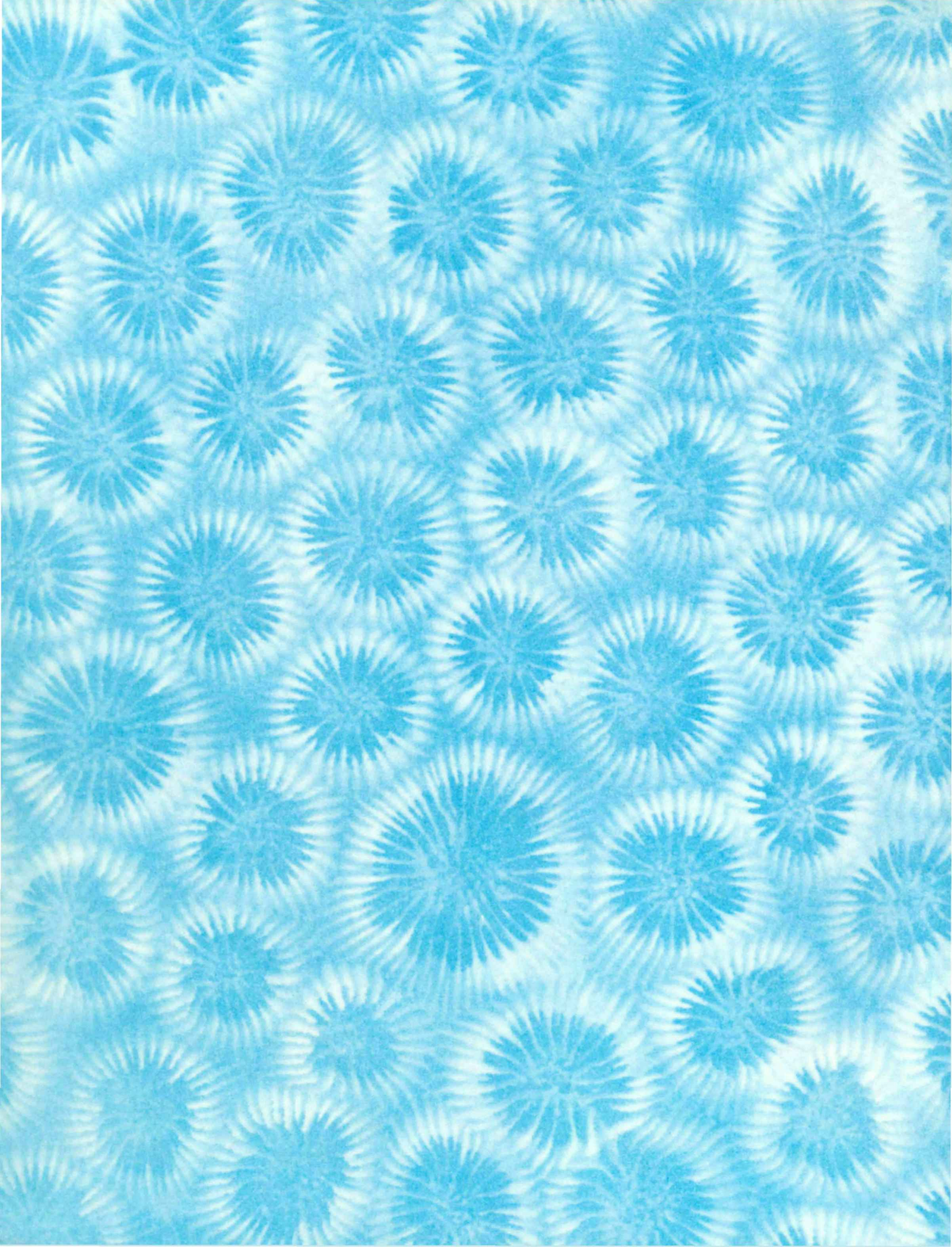
Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9b." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9b." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.