

STUDIES ON THE FAUNA OF CURAÇAO AND OTHER
CARIBBEAN ISLANDS: No. 195

THE BIOLOGY OF THE MONGOOSE
IN THE CARIBBEAN

by

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	Pages
INTRODUCTION	3
Taxonomy and Description	3
History of the Mongoose in the New World.	4
New World Distribution (Table 1)	5
Present Status.	7
GEOGRAPHY	10
St. Croix (Fig. 1).	10
Trinidad (Figs. 2-6).	13
Grenada (Figs. 7-9; Table 2).	20
TRAPPING AND GENERAL PROCESSING	28
Capture (Figs. 10-11)	28
Immobilization, Killing, Captive Handling and Laboratory Processing	29
BIRTH AND DEVELOPMENT	33
Breeding Season (Figs. 12-14; Table 3)	33
Gestation	38
Litter Size (Table 4).	39
Sex Ratio (Tables 5-6).	42
Birth and Early Development (Figs. 15-19; Table 7)	45
Development of the Male (Fig. 20; Table 8)	49
Development of the Female	55
Age Determination (Figs. 21-23; Tables 9-10)	57
Adult Weights and Measurements (Table 11)	65
FOOD AND FEEDING HABITS	68

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PHYSIOLOGY	75
Energy Requirements (Tables 12–13)	75
Thermal Tolerance	77
Milk Composition (Table 14)	78
Blood Characteristics (Table 15)	81
Other Organ Systems	81
Mongooses as Food	82
BEHAVIOUR.	84
Circadian Activity	84
Postures and Movements (Figs. 24–29)	84
Swimming	91
Vocalizations	92
Sexual Behaviour (Fig. 30)	93
Maternal Behaviour	95
Marking (Figs. 31–32)	100
Play	101
HOME RANGE AND MOVEMENT (Figs. 33–34; Tables 16–17)	102
POPULATION STRUCTURE AND DENSITY.	110
Age Structure (Figs. 35–36)	110
Population Density (Fig. 37; Tables 18–22)	112
PARASITES AND DISEASES	125
Ectoparasites (Table 23)	126
Endoparasites.	129
Rabies (Table 24)	131
Leptospirosis	136
Other Diseases and Pathogens	138
CONCLUSION	142
ACKNOWLEDGEMENTS	147
BIBLIOGRAPHY	149

INTRODUCTION

On most of the islands on which it has become established, the small Indian mongoose has commanded more attention than all indigenous mammals and introduced exotics. As a consequence of its impact on the neotropical single island ecosystems, both as a predator and as a vector of human and animal diseases, the mongoose is uniquely significant.

The present study of the mongoose was initiated in 1968 when EVERARD was appointed by the United Kingdom Medical Research Council (MRC) to the Caribbean Epidemiology Centre (CAREC), formerly the Trinidad Regional Virus Laboratory (TRVL). The terms of the appointment included a study of the biology of the mongoose in Trinidad and Grenada, surveillance of mongoose rabies in Grenada, and an investigation of methods to control mongoose rabies. Coincidentally, in 1968 NELLIS was contracted by the Government of the U.S. Virgin Islands to investigate the wild hosts of the African Bont Tick *Amblyomma variegatum* (the mongoose being of primary concern). The study was continued in a survey of wild animal parasites and diseases of concern to man or livestock, and it gained impetus as part of the rabies contingency plan for the Virgin Islands. Throughout the course of their work, the investigators continuously exchanged ideas, opinions, data and techniques.

TAXONOMY AND DESCRIPTION

The mongoose studied has been referred to by a variety of taxonomic names. A member of the family Viverridae, it was originally described by HODGSON (1836) as *Mangusta auropunctata*. Its name was revised to *Herpestes javanicus auropunctatus* by POCOCK (1937), who listed the mongoose's areas of distribution as northern India from Kashmir to Bhutan, Assam, Manipur, and Bengal south of the Ganges as far as Chilka in Orissa. Later, POCOCK (1941) referred to the introduced West Indian mongoose as *H. j. auropunctatus* on the basis of specimens collected in Jamaica, St. Lucia, and Barbados and housed in the British Museum (Natural History). ELLERMAN & MORRISON-SCOTT (1951) listed *M. auropunctatus* of HODGSON as *H. auropunctatus auropunctatus*, giving its range as essentially that reported by POCOCK (1937). PEARSON & BALDWIN (1953) identified the mongoose introduced in Hawaii from Jamaica as *H. a. auropunctatus*. HALL (1981) revised his earlier (1959) work and now refers

to the mongoose as *H. auropunctatus auropunctatus*. HINTON & DUNN (1967) listed the West Indian and Hawaiian mongoose as *H. a. auropunctatus*, and skeletal material from St. Croix has been identified by the staff of the American Museum of Natural History as that of *H. a. auropunctatus*. URICH (1914) called the mongoose introduced to Trinidad *Herpestes mungo*; but use of this nomenclature seems to be an error in identification rather than a taxonomic decision. Karyotypes of mongooses from Trinidad, prepared by NELLIS and examined by BAKER (personal communication), are not different from those of mongooses from other Caribbean islands whose populations are known to be derived from the original Jamaican introductions. For this monograph the nomenclature of ELLERMAN & MORRISON-SCOTT will be used.

Herpestes a. auropunctatus is long and slim with short legs and a tapered tail. The head is elongated with a pointed muzzle. The ears are small and rounded, lying close to the head. The claws are long, sharp, and non-retractile. Hair is short and alternately banded grey-brown and yellow, giving a speckled appearance to the fur. Females have three pairs of mammae; males have a baculum. Both sexes have an extensible anal pad with ducted glands lateral to the anus (POCOCK, 1916). The dental formula is i. 3/3, c. 1/1, p. 4/4, m. 2/2 (2/3). The presence of a third molar in the lower jaw is rare. Of 516 males examined 10 had 2 third molars and 12 had one. Of 406 females 7 had 2 third molars and 4 had one m3.

HISTORY OF THE MONGOOSE IN THE NEW WORLD

A century ago the economy of the majority of the Caribbean islands was based on the production of sugarcane. Damage to this vital crop by rats was severe. A variety of solutions to the problem was tried in Jamaica, including the hiring of rat catchers and poisoning and trapping rats. Biological control, documented by ESPEUT (1882), was attempted with the introduction of several potential predators. An unidentified South American carnivore (possibly the grison) was introduced, but its identity was lost by 1882 when ESPEUT wrote of it. *Formica omnivora* imported from Cuba was purported to be effective in preying on young rats, but the ants were difficult to move and were harmful to many other animals. *Bufo marinus* was introduced because it was thought to eat young rats, but it probably never played a significant role in rodent control. European ferrets proved to be ineffective as they suffered severely from the attacks of chigoes or burrowing fleas.

TABLE 1
CURRENT DISTRIBUTION OF THE MONGOOSE IN THE WESTERN HEMISPHERE
Caribbean and Hawaiian islands

Mongoose present	Year of introduction where known	Mongoose absent
Antigua		Anegada
Barbados	1877-1879	Anguilla
Beef Island		Aruba
Buck Island (St. Croix)	1910	Bahamas
Cuba	1886	Barbuda
Grenada	1872-1882	Bermuda
Guadeloupe		Blanquilla
Guiane Francaise		Bonaire
Guyana		Buck Island (St. Thomas)
Hawaii	1883	Cayman Brac
Hispaniola	Before 1895	Cockroach (Virgin Islands)
Jamaica	1872	Culebra
Jost Van Dyke		Curaçao
La Désirade		Dominica
Lovango		Dutchcap (Virgin Islands)
Marie-Galante		Frenchcap (Virgin Islands)
Martinique		Grand Cayman
Maui (Hawaii)	1883	Grenadines
Molokai (Hawaii)	1883	Hassel Island (St. Thomas)
Nevis		Kauai (Hawaii)
Oahu		Lanai (Hawaii)
Puerto Rico	1887	Little Cayman
St. Croix	1884	Margarita
St. John		Mingo (St. Thomas)
St. Kitts	1884	Mona
St. Lucia		Montserrat
St. Martin	1888	Niihau (Hawaii)
St. Thomas		Redonda
St. Vincent		Saba
Suriname	1900	Savannah (Virgin Islands)
Tortola		Sombrero
Trinidad	1870	St. Barthélemy
Vieques		St. Eustatius
Water Island		Testigos
		Thatch (St. Thomas)
		Tobago
		Tortuga
		Virgin Gorda

The mongoose was first introduced to the New World when an unstated number was brought to Trinidad from India by the owners of a sugar estate in Naparima (URICH, 1914), but most of the mongoose populations in the New World derive from five female and four male mongooses brought from Calcutta to Jamaica in 1872 by ESPEUT. Within 6 months of their introduction there was a noticeable reduction in cane damage, and within 3 years the estate was almost free of rodent damage. At this time neighbouring estates were finding similar relief and were purchasing mongooses from poachers. Although ESPEUT acknowledged several other importations to Jamaica after 1872, he maintained that the mongooses were few in number, and some were known to have died out; thus the Jamaican population was derived primarily from those originally introduced by him.

NEW WORLD DISTRIBUTION

The mongoose is probably the only animal which has been introduced so widely in such a short period of time. The Jamaican population is considered to be the source of mongoose introductions in the Western Hemisphere. In a period of less than 30 years (1872 to 1900) all Caribbean islands with a major sugar industry had acquired a mongoose population. The mongoose was introduced in Martinique and St. Lucia (DE VOS *et al.*, 1956) and Suriname (HUSSON, 1978) in an apparent attempt to control the populations of fer-de-lance, *Bothrops atrox*. Table 1 shows the present known distribution of the mongoose in the Western Hemisphere. Much of the information in Table 1 is taken from HINTON & DUNN (1967) and has been updated and expanded to its present form. WEST (1972) states that mongooses were introduced into Panamá, but we can find no corroborating evidence of this. There have also been reports, as yet unconfirmed, of mongooses in Colombia and Venezuela.

The mongooses on the mainland of South America are generally limited to the agricultural areas near the coast and are not likely to extend their range into the interior rain forests or past swampy coastal areas (HUSSON, 1960). However, as agricultural clearing or other developments proceed along the coast, mongooses are likely to follow. Once the range is north or south of the rain forest, the population is likely to expand to the limits of thermal endurance (NELLIS & MCMANUS, 1974). Mongooses have been introduced to North America but have been eliminated before becoming established (NELLIS *et al.*, 1978; VAN GELDER, 1979).

PRESENT STATUS

Many characteristics of the mongoose indicate its suitability for life in a tropical grassland, yet it is a sufficiently generalized animal that it can thrive in a wide variety of habitats. The mongoose has been most successful when introduced to islands which have limited numbers of species. As might be expected, when a small predator, such as the mongoose, is introduced to an island ecosystem which formerly had no predators except hawks, great devastation of wildlife frequently takes place.

Within two years of releasing the original nine animals in Jamaica, ESPEUT (1882) found that the rat problems in his sugarcane fields were almost completely eliminated. Eight years later he was able to estimate that the beneficial results of the mongoose introduction exceeded 150,000 pounds sterling a year. ESPEUT did comment, however, that "Unfortunately, ground-nesting birds, the Quail and others, have been diminished; but the loss of poultry is not as great from the Mungoos [*sic*] as it was from rats, snakes, etc., before the introduction of the former."

LEWIS (1953) recorded further depredations on the native fauna. ALLEN (1911) observed that mongooses had greatly reduced the population of *Ameiva* lizards in Grenada. He also pointed out that on Barbados the mongoose was a great menace to the raising of chickens, turkeys and ducks because the young birds fall easy prey to the mongoose; he further stated, "on St. Vincent, the mountain ground dove (*Geotrygon*) has disappeared, and the common ground dove (*Columbigallina*) and the ani (*Crotophaga*) have been reduced in number supposedly by the ravages of this animal." The destruction of native fauna by the mongoose has not always been frowned upon, however. BARBOUR (1930) recorded that the fer-de-lance, once very common on Martinique and St. Lucia, had become distinctly uncommon on St. Lucia and very rare on Martinique. MYERS (1931) records the adverse influence of mongooses on wildlife and suggests that money should be spent on research for control rather than bounties.

URICH (1931) has given an analysis of the effect of mongooses on a native animal population. Working in Trinidad, which has a large South American mainland fauna with a variety of small predators, he found that rats were uncommon in canefields but remained common in towns and around estate buildings. The three genera of opossum (*Didelphis*, *Philander* and *Marmosa*) remained common. No species of bird was extermi-

nated, although the tinamou and certain other ground-nesting or -feeding birds were somewhat reduced. The ground lizard, *Ameiva surinamensis*, was not as common as formerly, except around towns and villages where its greatest enemy was the domestic cat. Many of the small ground-inhabiting snakes have become rare. However, mongooses have been found in the stomachs of fully grown boas, which URICH believed could exercise valuable control on the increase of mongooses. Tree frogs of course did not suffer at all, but there was a decrease in the numbers of *Bufo marinus* and members of the genus *Leptodactylus*. There is little evidence that the mongoose was responsible for all the changes he reports in the avian and reptilian faunas. A case in point is that URICH records the lizard *Tupinambis nigropunctatus* to be extinct or very rare, yet at the present time this animal is common despite the continued presence of the mongoose.

A statement by the West Indian ornithologist JAMES BOND in a letter to WESTERMANN (1953, p. 33) regarding mongooses and ground-nesting birds is a good summary. "The initial impact following its introduction on an island is often severe on ground nesting species, but most of these evidently adapt themselves to the presence of the creature, and I don't feel that ground nesting birds as a whole are in any more danger from the mongoose in the West Indies than they are among other predators here in North America."

WESTERMANN (1953) documents recently extinct and endangered vertebrate species in the West Indies. Although extirpation of many species has occurred on major islands having mongooses, remnant populations frequently continue to exist on small adjacent keys. Cases of actual extinction in which the mongoose probably played a large role are few. *Solenodon cubanus* disappeared from Cuba in about 1910, probably due partly to the mongoose, though *Oryzomys* species and other forest rodents are abundant in Trinidad along with the mongooses. The snake *Alsophis sancte-crucis* seems to be extinct on St. Croix, possibly as a result of predation by the mongoose. The extinction of *A. ater* from Jamaica and extirpation of *A. rufiventris* from St. Kitts and Nevis can almost certainly be attributed to mongoose predation. *A. rufiventris* is still found on nearby St. Eustatius and Saba, which do not have mongooses. Various endemic species of snakes of the genus *Dromicus* are extinct on Martinique, Guadeloupe, Marie-Galante, and St. Lucia due to the mongoose.

Another case of extirpation caused by the mongoose is the edible frog,

Leptodactylus pentadactylus, locally called mountain chicken, which originally occurred on the islands of St. Kitts, Guadeloupe, St. Lucia, Dominica, and Montserrat. These frogs have been eliminated from the first three islands, but they continue to exist on the latter two, which are free of mongooses (BARBOUR, 1930).

GORMAN (1975) reports that the Barred-wing rail was generally distributed in Fiji in 1875 but has not been seen since the 1880's, when the mongoose was introduced. Four other genera of rails now survive only on islands free of the mongoose.

Ameiva polops has been extirpated from St. Croix by the mongoose, but it continues to maintain viable populations on nearby Green and Protestant Keys, the latter being less than 122 metres from the shore.

It is interesting to note behavioural modifications which have come about in various species as a result of the presence of mongooses. *Rattus rattus* is now almost completely arboreal on St. Croix, and the moustached quail dove, *Geotrygon mystacea*, which previously nested on the ground and which was thought to be extinct in 1921, now nests in low trees and has become moderately common.

The status of the mongoose in the Caribbean has changed over the years. Within 10 to 15 years of its introduction it was already considered an agricultural pest (URICH, 1914), and in succeeding years several islands (including Jamaica, Barbados, St. Vincent, Antigua, Barbuda and Trinidad) introduced legislation to destroy the mongoose or prohibit its importation (ANONYMOUS, 1918). By the early 1930's, however, mongoose control seems to have been no longer a governmental concern. Population sizes have fluctuated: in Trinidad, records of mongooses trapped for bounty (URICH, 1931) suggest that the population was considerably larger in the past than it is now.

Although the mongoose has profoundly influenced the biota of its new habitat, it seems to have come into an ecological equilibrium, and populations of both mongooses and their prey will probably remain stable indefinitely. The mongoose's present importance lies in its potential threat to endangered species and in its potential as a vector of disease, especially rabies.

GEOGRAPHY

ST. CROIX

The island of St. Croix is politically part of the U.S. Virgin Islands and is located in the Caribbean Sea at 17° 44' N Latitude and 64° 44' W Longitude. The sun is north of the island at noon from 31 May to 12 July. Due to the proximity of the equator, the seasonal variation in the day length is relatively slight, there being 13 hours 12 minutes of daylight on 19 June and 11 hours and 3 minutes of daylight on 22 December. The nearest land is St. Thomas, 64 km to the north. A trench over 4,000 metres deep separates the islands, which show no geologic affinity.

The island is an approximate isosceles triangle having the apex to the east, a length of 45 km and a width to the west of 11 km, giving a resulting area of 220 km². A hilly mountainous ridge runs the length of the island. The physiography of St. Croix is fairly sharply divided between mountains and plains, 60 percent of the land having slopes of 0 to 10 percent and 36 percent having slopes greater than 30 percent (ZUBE, 1968).

St. Croix, being located in the trade wind belt and surrounded by sea, has a very mild uniform climate. Most climatic factors vary more on a daily basis than they do seasonally. The mean annual temperature of St. Croix is 26.1° C. The mean daily temperature range of 7.2° C is more than twice the range of the annual mean monthly variation of 3.4° C.

The prevailing wind is from the east, fluctuating seasonally between east-southeast and east-northeast. The wind speed varies through the day with an average of 6.3 knots at midnight, increasing to a peak of 13.0 knots at midday.

Rainfall is generally spread throughout the year with a tendency for more rain from August to November. Variation is such that any month can be the wettest or driest month of a particular year.

The orographic effect of the island on the rainfall pattern is significant, producing a cline of rainfall from less than 25 cm annually at the east end to greater than 130 cm annually at the western end of the northern mountain range (BOWDEN, 1968).

The mean monthly humidity at 2:30 p.m. varies from 63 percent in February to 73 percent in September.

Inland, on the drier end of the island, dense brush covers the land. This is made up of many types of drought-resistant shrubs, especially species of *Croton* and *Acacia* interspersed with the official flower of the Virgin Islands, ginger thomas (*Tecoma stans*), and cacti of the genera *Cephalocereus*, *Opuntia*, and *Melocactus*.

In the mountains of the wet western end of the island a luxuriant forest occurs. One of the most conspicuous trees is the silk cotton (*Ceiba pentandra*) with its giant buttressed trunk and heavy horizontal limbs frequently draped thickly with epiphytes. Other common deciduous trees are the sandbox (*Hura crepitans*) with its exploding seed pods and the hog plum (*Spondias mombin*) known for its aromatic fruits. A large number of evergreens, chiefly representatives of the genus *Ficus*, also occurs. The understory includes many smaller trees and shrubs, including the edible guavaberry (*Eugenia floribunda*) and lime-berry (*Triphasia trifolia*).

The open pastures, generally maintained in guinea grass (*Panicum maximum*) by mowing, have mango (*Mangifera indica*), saman (*Pithecellobium saman*) and thibet (*Albizia lebbek*) interspersed periodically as shade trees. The abandoned sugarcane fields on the southern coastal plain are gradually reverting to a forest vegetation, but they are at present still in a mixture of regenerating sugarcane and tantan (*Leucaena glauca*).

Except for four species of bats (*Artibeus jamaicensis*, *Brachyphylla cavernarum*, *Noctilio leporinus*, and *Molossus molossus*), the entire mammal population has been introduced by man. *Rattus norvegicus* is found primarily in the two towns of Frederiksted and Christiansted, while *Rattus rattus* occurs in rural settings where trees and tall shrubs provide escape from mongooses. *Mus musculus* is ubiquitous. Deer (*Odocoileus virginianus*) are found throughout the island in areas where thick vegetation inhibits poaching.

Reptiles are predominantly represented by the lizards *Anolis acutus* and *Iguana iguana*, and four geckos *Thecadactylus rapicauda*, *Hemidactylus mabouia*, *Sphaerodactylus macrolepis*, and *S. beattyi*.

The small burrowing blind snake, *Typhlops richardii*, is occasionally unearthed. Amphibians are represented by *Bufo marinus*, *Leptodactylus albilabris*, *Eleutherodactylus lentus*, *E. antillensis*, and *E. coqui*.

Mongooses are found everywhere on St. Croix, even in the luxuriant forest on the wetter, western end of the island, which is comparable to the

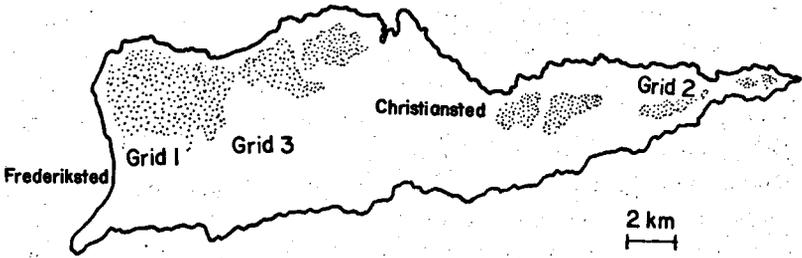


Fig. 1. Map of St. Croix showing grid locations and forested areas.

mountain forest zone of Grenada. They have been observed to inhabit the spacious courtyards and gardens in the middle of towns, and they can be seen foraging on the foreshore.

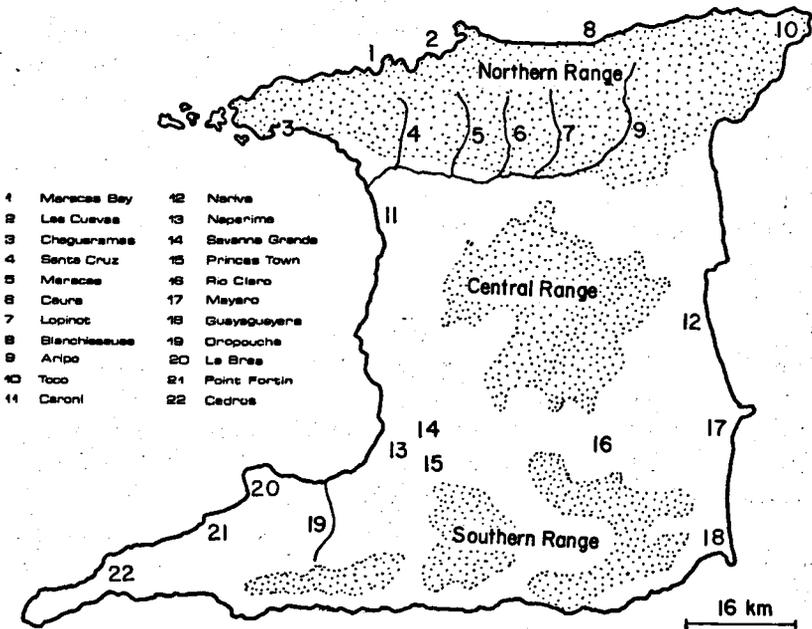


Fig. 2. Map of TRINIDAD showing major geographic features.

On St. Croix a 2.2-ha study area (Grid 1) in Estate Prosperity on the wet western end of the island (Fig. 1) was sampled with a 25-trap grid. The vegetation was composed of mahogany forest (*Swietenia mahagoni*) with lime-berry (*Triphasia trifolia*) and acacia scrub. From 18 April 1969 to 29 June 1970, trapping took place at irregularly-timed intervals.

On the dry eastern end of the island at Estate Slob, a 17-ha study area (Grid 2) composed of *Acacia tortuosa* and tantan (*Leucaena glauca*) scrub with interspersed guinea grass (*Panicum maximum*) was sampled with a 36-trap grid (Fig. 1). Trapping was conducted for 15 days. Movement into and out of the area was considered to be reduced by the water and open lawn boundaries. Where the natural scrub habitat was contiguous with the study area, the boundary used for population estimation and movement was considered to be a half trap-interval outside the line of peripheral traps.

A third grid of 30 traps covering 13-ha (Grid 3) was set out on a heavily grazed weedy pasture with bushy fence-lines bisected by a heavily wooded ravine. The weed species were predominantly *Croton* and regrowth of *Jatropha*, *Psidium* and *Acacia*.

TRINIDAD

Trinidad lies to the south of the Windward Island group in the southern Caribbean between 10° 3' and 10° 44' N and 60° 55' and 61° 44' W. The day length varies from 12 hours 45 minutes to 11 hours 30 minutes. At its nearest point to the South American mainland it is not more than 13 km from Venezuela, being separated from it by the shallow Gulf of Paria. The minimum length of the island is approximately 77 km, and the minimum breadth is approximately 51 km, the island covering in all an area of about 4,828 km². The Northern Range of Trinidad forms an extension of the Venezuelan Cordillera (Paria Peninsula) of pre-tertiary origin; thus both Trinidad and perhaps Tobago may be classed as continental islands with an obvious land-bridge connection between the former and the mainland during the Pleistocene.

There are three ranges of hills (Fig. 2). The Northern Range, the most prominent, extends the whole east-west length of the island up to a width of 19 km at its widest point, and it reaches its maximum height at Mt. Aripo (940 metres) and El Tucuche (936 metres). There are several river

valleys running either south to north or north to south. The Central Range of limestone hills reaches a maximum height of 307 metres at Mt. Tamana and is separated from the Northern Range by a wide belt of flat cultivated land mostly devoted to sugarcane, rice and garden vegetables in the west, and to tree crops in the east. The Southern Range follows the south coast hinterland in a low rolling mass, reaching its maximum elevation in the Trinity Hills at just under 300 metres in the southeast near Guayaguayare (KENNY, 1969) (Fig. 2). The main vegetational zones follow the topographical features fairly closely. Thus, the three hill ranges are forest-clad, and the flat alluvial plains are used for cultivation or cattle rearing except in those areas where impeded drainage has given rise to impoverished savannah or seasonal marsh forest.

Two seasons are defined in the calendar year, a wet season between May and December and a drier season between January and May. Average monthly maximum temperatures range between 30.2° C in January and 32.1° C in May; the usual range is between 21° and 32° C, with minimum and maximum temperatures in any one year about 15° C and 35° C, respectively (BEARD, 1946). There is usually a slight drop in temperature after dark. The sun shines for an average of more than 6 hours daily and relative humidity is usually about 90 percent, except on hot afternoons when it may drop to 60 percent. Annual rainfall may exceed 330 cm in the northeast and some central areas, and just over 127 cm in the extreme western parts of the island. The prevailing winds are usually northeasterly in the dry season and southeasterly in the wet; the windward (eastern) Atlantic coast is typically breezy, but the leeward (western) Caribbean coast bordering the Gulf of Paria is far more sheltered.

The fauna of Trinidad is mostly of South American origin, comprising some 40 mammalian species exclusive of bats (AITKEN, unpublished MS), 58 species of bats (ALKINS, pers. comm.), 38 species of snakes of which four are truly venomous (BOOS, pers. comm.), 16 species of lizards (UNDERWOOD, 1962), and 25 species of amphibians (KENNY, 1969).

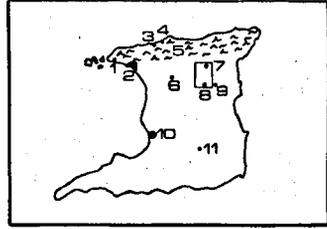
URICH (1931) noted that the mongoose, which had then been in Trinidad for 60 years, was found throughout the island but most commonly near cultivated and abandoned land. It was rare in forests. His data on the hunting of mongooses for bounty indicate that by 1913 mongooses had not reached Cedros, Mayaro, Oropouche, or La Brea; and they were rare

at Toco, Blanchisseuse, and even Naparima, where they were first introduced.

We have found that mongooses are distributed from Chaguaramas in the west eastwards to Sangre Grande and beyond towards Toco on the northeast coast. They do not enter the forests adjacent to cultivated land and the savannahs in the north, but are found some way up the valleys of the Northern Range, particularly in areas of mixed cultivation as in the Santa Cruz and Maracas valleys. Northwards, they are found in the shallow hinterlands of Maracas Bay and Las Cuevas before the forested hills start to rise steeply. Trapping along the north coast road within the rain forest has not resulted in the capture of mongooses, yet these animals have penetrated through the Northern Range to the limits of the north coast, presumably by way of the many north-to-south valleys. Southwards, mongooses are found beyond Rio Claro and Princes Town except in the many large forested areas. They have not penetrated the major coastal swamps of Nariva on the east coast or Caroni on the west coast, but they are to be found in sugarcane which is normally cultivated in areas adjacent to the latter.

Grid-trapping was conducted exclusively at Waller Field near the Aripo Savannahs (Fig. 3). The Aripo/Waller Field area was chosen because it is relatively remote from human habitation and therefore from interference; mongooses are comparatively abundant, the system of paved roads of the former airbase is well developed, and the available Government-owned terrain is large and flat. The Aripo Savannahs occupy some 10 to 20 km² northeast of Cumuto about 35 km east of Port-of-Spain. Waller Field lies due north of Cumuto and approximately halfway between there and Valencia. The area is derived grassland and scrub which arose after the forest was cleared in the early 1940's for the construction of the airbase. The true short-grass savannahs, however, were in existence long ago and resulted from impeded drainage, waterlogging, and leaching of soil nutrients. Mongooses inhabit only the areas of scrub, tall grass, and secondary vegetation. They are not found in the marsh forest or palm-marsh, and the true short-grass savannahs are not a favoured habitat because they are waterlogged during the wet season and there is insufficient cover. The area receives about 250 cm of rain a year.

- disused railway line
- Aripo river
- forest margin
- main road
- roads
- tracks
- Waller Field
- air-strips
- grid I
- grid II
- 45-trap line
- savannah with forest islands



- 1 Chegueramas
- 2 Port of Spain
- 3 Maracas
- 4 Las Cuevas
- 5 Northern Range
- 6 Piarco
- 7 Valencia
- 8 Cumuto
- 9 Sangre Grande
- 10 San Fernando
- 11 Rio Claro

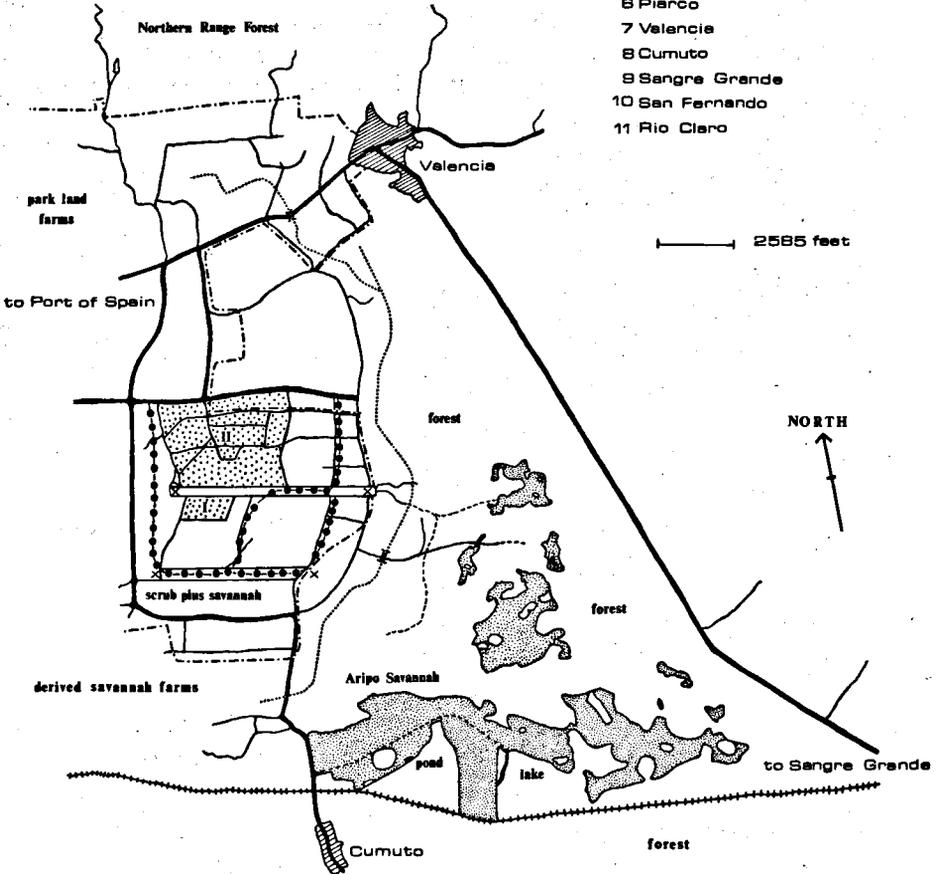


Fig. 3. Map of the Aripo Savannah and Waller Field, TRINIDAD, showing Grids I and II.



Fig. 4. TRINIDAD: Derived savannah with an abrupt change to original riverine forest.

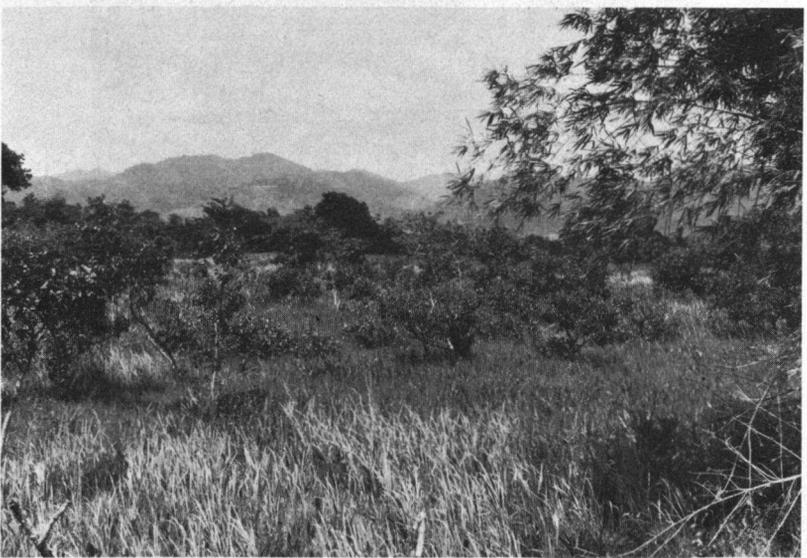


Fig. 5. TRINIDAD: Derived savannah with *Byrsonima* trees.



Fig. 6. TRINIDAD: Derived savannah with *Coccoloba latifolia* in the left foreground, *Ilex arimensis* and *Byrsonima*.

The vegetation of the true savannahs consists of an association of grasses and sedges (*Paspalum pulchellum* and *Lagenocarpus tremulus*) and various *Rhynchospora* spp. There may be a few small gnarled shrubs growing to a few feet, and two common herbaceous plants *Perama hirsuta* and *Sauvegesia sprengelii*, with the small insectivorous *Drosera capillaris* and *Utricularia* spp. (RICHARDSON, 1962). From these short-grass savannahs there is an abrupt change to palm-marsh and marsh forest characterized by the moriche palm (*Mauritia setigera*). There may also be a gradual transition to thicket-like forest 3 to 10 metres high, composed of small trees and shrubs with long rambling branches (BEARD, 1946). The trees here are cocorite palm (*Maximiliana elegans*), timite palm (*Manicaria saccifera*), agalie or matapal (*Clusia rosea*), olivier (*Terminalia amazonia*), and cajuca (*Myristica surinamensis*).

On the forest floor the so-called tirite, *Ischnosiphon arouma* and *Monotagma spicatum* (Marantaceae), forms masses of undergrowth. In the derived savannah and along forest margins and tracks, common large shrubs and small trees include *Chrysobalanus icaco*, *Coccoloba latifolia*, *Ilex arimensis*, *Bactris savannarum*, *Byrsonima crassifolia*, *Palicourea crocea*, and *Isertia parviflora*. *Comolia veronicaefolia*, *Heliconia parviflora*, *Miconia ciliata* and *Cephaelis tomentosa* are common small shrubs found in addition to grasses and sedges. The most conspicuous features of the Waller Field base itself are the guava trees (*Psidium* sp.) lining the disused runways and service roads, and the emergent *Byrsonima* in greenswards of *Heliconia*. A list of the most common plants in the area is given by RICHARDSON (1962), and some of the plants mentioned are described by WILLIAMS & WILLIAMS (1969). Figs. 4 to 6 show typical features of the Aripo/Waller Field area.

Two grids were laid down at Waller Field (fig. 3), one on each side of the main runway.

Grid I occupied an area of 10.4 ha (427 × 244 metres) on the south side of the runway, and comprised 72 traps at 30-metre intervals with 61-metre spacing between rows. Altogether it was operated for 15 weeks between 1 June and 11 September 1970, and the traps were serviced 5 days a week. With allowance for the acceptable one trap-width outside the perimeter of the grid, the area used for population estimation was 14.8 ha.

Grid II, on the north side of the runway, was very much larger and covered approximately 104 ha of woodland, secondary vegetation, scrub and grass-sedge savannah with the community association already mentioned. It comprised eight rows of nine traps (72) and was open for 23 weeks between 19 October 1970 and 26 March 1971. Fire burned out a large part of the grid at the end of March during the dry season. To collect any marked mongooses that moved away, a series of 45 widely spaced traps was set outside the grid (Fig. 3) except in the north, which was thick secondary forest. The 45 traps were operated for 19 weeks between 29 March and 6 August 1971. Vegetation had recovered by September, and the grid was reopened between 6 September 1971 and 14 April 1972 for a total of 32 weeks. All these traps were usually in operation from Monday to Friday, but the grid was not operational for seven of the total 55 weeks. It was thought unnecessary to add a trap-width to the perimeter of Grid II because it was such a large area. In any case, mongooses were not caught in the forest on the northern edge of the grid; thus, the area used for population estimation was reduced to 90 ha.

GRENADA

Grenada and the Grenadine Islands as far north as Carriacou form a political unit. The Grenada Bank stretches from Bequia in the north to Reindeer Shoal in the south, and it is thought to comprise a single volcanic entity separated from St. Vincent, the Barbados Ridge, and Trinidad and Tobago by submarine cliffs and bottom troughs (GROOME, 1970). The paucity of an indigenous terrestrial fauna confirms the absence of a former land-bridge connection with the mainland. The islands are thought to be surface remnants of what was once a single oceanic volcanic island of the late Miocene. If it is assumed that sea level was over 91 metres lower during the early Pleistocene glaciation in the Northern Hemisphere, the greater area of the Grenada Bank would have been above water at that time. The volcanic nature of Grenada and the smaller neighbouring islands can be discerned from both the rock and soil types present and the explosion craters of extinct volcanoes; the most notable of these are Grand Etang, Lake Antoine, and St. George's Harbour (GROOME, 1970).

Grenada itself is the most southerly of the Windward Islands, lying approximately 195 km north of the northwestern Chaguaramas peninsula of Trinidad. The 12° 00' N line of latitude just cuts through the southernmost peninsulas, and the approximate centre of the island lies at 61° 41' W. The day length varies from 12 hours 51 minutes to 11 hours 25 minutes. Grenada and the Grenadines together comprise a land area of 395 km², while Grenada itself is about 310 km², with a length and breadth nearing 26 × 11 km, exclusive of contours. Fig. 7 shows the topography and vegetation zones of Grenada. The interior of the island is occupied by a central mountain mass which is divided by a low col along which runs the Belvidere road. Morne St. Catherine, the highest point of the island at 838 metres, is located in the northern massif and is surrounded by lesser peaks, while the southern massif rises to several prominent peaks, the highest of which is Fedons Camp at 766 metres. The land descends fairly regularly from these mountains to the sea. No coastal plains are evident though there are undulating lowlands particularly in the southwest and northeast (BEARD, 1949).

Seasonal changes and temperatures are similar to those experienced in Trinidad. The winds are almost invariably easterly, so that many of the houses are completely open on the leeward side. Rainfall varies in different parts of the island from 400 cm near Grand Etang to less than 100 cm at the extremities of the southern peninsulas.

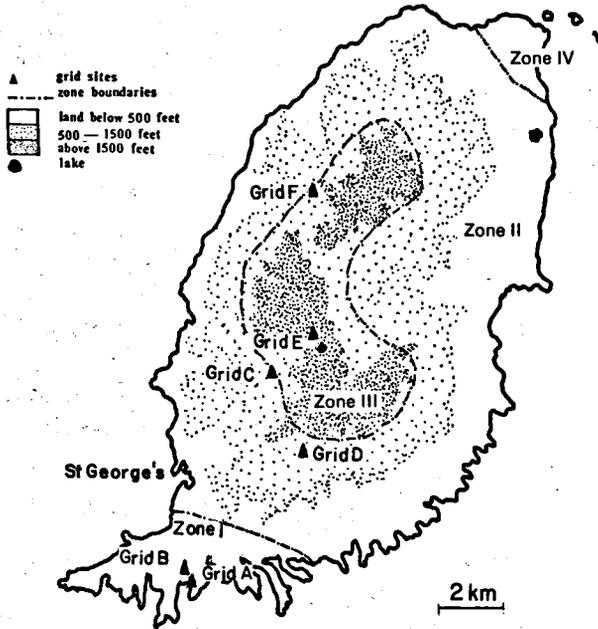


Fig. 7. Map of GRENADA showing grid locations, elevations and vegetation zones.

Except on the higher mountains and steeper slopes and ridges, much of the land has been cleared for cultivation at one time or another, with tree crops of bananas, nutmeg, citrus, and cocoa predominating. Cloves and cinnamon are also grown, giving the Spice Island its common name.

GROOME (1970) lists the native trees and shrubs of Grenada and also the fauna, which includes five species of amphibia, eight species of lizards, six species of snakes, twelve terrestrial mammalian species of which seven are rodents, and eighteen species of bats. Only *Dasyprocta* (Agouti) among the rodents, and possibly *Marmosa mitis* and *Dasypus novemcinctus* among the remaining five terrestrial mammal species, are thought to be indigenous (DE VOS *et al.*, 1956).

Within the past 15 years trapping has been carried out in almost every accessible area of Grenada as part of mongoose reduction programmes. There is no evidence to suggest that mongooses have not penetrated even the remotest hilly area of thick rain forest, where the annual rainfall may

be over 400 cm. PRESNALL (1969) gives details of mongoose population surveys conducted for short periods between 1965 and 1969 in 20 widespread and varied localities in the island. Because it was evident from his results that mongooses are found throughout the island, it was decided to sample the population in several vegetational zones (Fig. 7). These are: a dry zone in the southwestern part of the island (Zone I); a major area of habitation extending round the island, with cultivation and forest on the lower hill slopes (Zone II); a largely uninhabited and forested zone in the central mountainous area which is perceptibly cooler at the summit (Zone III); and a second small dry zone at the northeastern tip of the island (Zone IV). Zones I and IV are ecologically very similar.

Altogether, six grids were laid down in Grenada, two in Zone I, two in Zone II, and two in Zone III. Zone IV was not sampled because it is similar to Zone I. The locations of the grids are shown in Fig. 7.

Zone I (dry zone):

Zone I may be defined as the triangular projection of land southwest of the base line joining Belmont Lagoon, Morne Jaloux, and Westerhall Estate. Particular importance is attached to it as it is similar to the indigenous habitat of the mongoose in parts of India and very similar to the dry scrub areas of St. Croix; furthermore, residential development there coupled with the tourist trade and a high incidence of rabies in the area in 1973 has brought it into prominence on public health grounds. The rainfall in this zone does not exceed 150 cm per annum.

BEARD (1949) describes this dry belt zone in the southwest corner of the island as having impoverished growth, which at best consists of scrub woodland 9 to 12 metres high on the rocky hilltops (Figs. 8 and 9). BEARD mentions the peeling bark gomier *Bursera simaruba* and individuals of *Lonchocarpus latifolius*, *L. benthamianus*, *Albizzia caribaea*, *Citharexylum spinosum*, *Pisonia fragrans*, *Tabebuia pallida*, *Chlorophora tinctoria*, *Genipa americana*, and *Cordia collococca*. The undershrubs or small trees include *Bauhinia ungula*, *Pithecellobium unguis-cati*, *Tecoma stans*, *Amyris elemifera*, *Randia mitis*, *Jacquinia barbasco*, and *Annona squamosa*. *Haematoxylum campechianum* is usually present in areas which have been severely degraded, and poor grazing land is colonized by *Acacia nilotica*, *A. farnesiana*, *Haematoxylum*, and various shrubs including the prickly pear *Opuntia dillenii* and the columnar cactus *Cephalocereus*. The Point Salines peninsula is covered by alternations and mixtures of these types, with some pure stands of *Hippomane mancinella* to a height of 15 metres on raised sandy beaches. The predominant plants from this dry zone are listed in Table 2. The area is easily penetrated on foot during the dry season, but considerable care has to be exercised because of thorns. Fire could prove a hazard, but some of these areas are little frequented, and sugarcane, where present, is not burnt in Grenada prior to harvesting. During the past decade there has been considerable reduction in the rural area, with much land being cleared



Fig. 8. Southwest dry zone of GRENADA.



Fig. 9. Grazing land in the southwest dry zone of GRENADA.

for hotels, housing developments, shopping facilities, and restaurants. Nevertheless, there are still large tracts of land at Point Salines, Mt. Hartman, and the hinterland of Grande Anse which have been left untouched.

Grid A: The Mt. Hartman Estate is an abandoned sugarcane cultivation which has grown up into a continuous belt of prickly scrub up to 8 metres high, the most notable trees and undershrubs being *Acacia* spp., *Bauhinia*, and *Randia*. The area was chosen because it is remote from human habitation and because it is a characteristic mongoose habitat (Fig. 8). Grid A was opened on 20 July 1970 and closed finally on 26 March 1971, between which dates 28 weeks of trapping out of a possible 36 were completed. Seventy-two traps were placed at 30-metre intervals in nine rows with eight traps per row, so that the grid occupied 6.7 ha of ground. With a perimeter boundary strip of one trap-width, 9.3 ha were used for calculation of the population density. This grid proved to be too small for studies on movement, and consequently a second area (Grid B) was laid out in an adjacent part of the estate.

Grid B: This grid was operated for 25 out of 37 weeks between 24 May 1971 and 4 February 1972. The traps were placed at 61-metre intervals in ten rows of ten traps each, and the whole covered 30 ha. Because of the large area involved, no additional boundary strip was used for population estimation.

Zone II (cultivated and forested foothills):

Grid C: Sampling was undertaken at Annandale for 13 weeks between 13 March and 9 June 1972. This grid consisted of ten rows of ten traps spaced at 30 metres; it covered an area of 7.52 ha, which was increased as before to 11.2 ha for the purpose of population estimation. Part of this area is precipitous with two fast-flowing streams running through it, one in a deep ravine. The land slopes steeply upwards through cocoa cultivation into bamboo interspersed with clove trees and nutmeg (*Myristica fragrans*), and finally lower montane rain forest. There are a few gently-sloping clearings which were previously under cultivation, and several outcrops of large granite rocks.

Grid D: Grid D at Les Avocats was the same size as Grid C and also used ten rows of ten traps each. It was operational for 11 out of 13 weeks between 1 August and 27 October 1972. It was sited on a steeply-sloping Government forest reserve and was bisected by a watercourse leading to a

reservoir. Over half of the area is planted with well-established blue mahoe, *Paritium elatum* (*Hibiscus elatus*); the rest is lower montane rain forest.

Zone III (central forested mountains):

Grid E: This grid was located in the approximate centre of the island near the crater lake Grand Etang at an altitude of 550 metres. The area has an annual rainfall of over 400 cm. The vegetation consists of lower montane forest, rain forest, and some palm brake. The dominant trees are two rain forest types, *Dacryodes excelsa* and *Licania ternatensis*, and *Micropholis chrysophylloides* of montane thicket complex. The palm is *Euterpe* spp. including *E. globosa* (BEARD, 1949). Damage from the hurricane of 1955 is still evident. Grid E was the same size as grid C. Trapping was undertaken between 12 December 1972 and 27 February 1973.

Grid F: The grid was sited on Plaisance Estate at Piedmont/Florida and was the most precipitous; there is an average of 290 cm rain annually in the area. The lower portion of the hillside is gently sloping and under cocoa cultivation; the middle belt of chest-high grass and creeper is the steepest portion, and the upper part consists of rain forest and bamboo clumps. The cocoa occupied about one-third of the grid area. Nine weeks of trapping were accomplished between 13 March and 8 June 1973. The grid consisted of nine traps in seven rows at 30-metre intervals, with an additional nine traps placed in three rows of three along the baseline in the cocoa, giving a total of 72 traps. This unusual grid arrangement was necessary to meet the demands of the landowner. The grid area was 5 ha increased to 8.5 ha for calculation purposes.

TABLE 2
A LIST OF PROMINENT PLANTS FROM THE SOUTH-WEST DRY ZONE OF
GRENADA

(Point Salines, Mt. Hartman, Lance aux Épines and Grande Anse)

	Habitat
MIMOSACEAE	
<i>Acacia villosa</i> (?) (tree – rambler)	SW – ST
<i>A. tortuosa</i> (?) (tree)	SW – ST – RH
<i>A. macracantha</i> (tree)	SW – ST – RH
<i>Mimosa viva</i> or <i>bimucronata</i> (?) (tree)	SW – ST
<i>Pithecellobium unguis-cati</i> (tree)	RH – ST – SW
<i>Leucaena glauca</i> (tree/shrub)	OG – SW – ST – RH
CAESALPINIACEAE	
<i>Bauhinia ungula</i> (shrub – (T))	ST – RH – OG
<i>Tamarindus indica</i> (tree)	EC – SW – ST – RH
<i>Cassia biflora</i> (shrub/tree)	EC
<i>C. tora</i> (herb)	OG – UP
<i>C. patellaria</i> (shrub – (M))	OG – ST
LEGUMINOSAE	
<i>Haematoxylon campechianum</i> (tree)	ST – SW – RH
<i>Aeschynomene americana</i> (herb)	OG – UP
EUPHORBIACEAE	
<i>Euphorbia</i> sp. (shrub – (M))	ST
<i>E. tirucalli</i> (shrub)	EC – RH
<i>Croton</i> sp. (shrub – (S))	ST – OG
<i>Jatropha gossypifolia</i> (shrub – (M–T))	SW – ST
<i>Hippomane mancinella</i> (tree)	SC – ST
RUBIACEAE	
<i>Randia aculeata</i> (shrub – (M))	SW – ST
BORAGINACEAE	
<i>Cordia obliqua</i> (tree)	RH – EC
<i>C. curasavica</i> (shrub – (T))	ST – RH – OG – UP
<i>Bourreria succulenta</i> (tree)	RH – SW – ST
CAPPARIDACEAE	
<i>Capparis cynophallophora</i> (tree)	SW – ST

TABLE 2
A LIST OF PROMINENT PLANTS FROM THE SOUTH-WEST DRY ZONE OF
GRENADA

(Point Salines, Mt. Hartman, Lance aux Épines and Grande Anse)

VERBENACEAE		
<i>Lippia alba</i> (herb)		OG- UP
<i>Melochia</i> sp. (herb)		OG- UP
<i>Citharexylum fruticosum</i> (tree)		RH- ST - SW
TILIACEAE		
<i>Corchorus siliquosus</i> (herb)		RH- OG- UP
<i>C. aestuans</i> (herb)		RH- OG- UP
ANNONACEAE		
<i>Annona squamosa</i> (tree)		RH- ST
BIGNONIACEAE		
<i>Tecoma stans</i> (tree/shrub)		RH- OG- ST
BURSERACEAE		
<i>Bursera simaruba</i> (tree)		SW- ST - OG
MALVACEAE		
<i>Malvastrum cormandelianum</i> (herb)		OG- UP
APOCYNACEAE		
<i>Plumeria alba</i> (tree)		SC - ST
SCROPHULARIACEAE		
<i>Capraria biflora</i> (herb)		RH- OG
COMPOSITAE		
<i>Wedelia caracasana</i> (herb)		RH- OG
ERYTHROXYLACEAE		
<i>Erythroxylum ovatum</i> (shrub - (M-T))		SW- ST - RH
Scrub woodland	= SW	(T) Tall
Scrub thicket	= ST	(M) Medium
Road & trackside hedges	= RH	(S) Small
Untended pasture	= UP	
Open ground	= OG	
Escaped from cultivation	= EC	
Sea coast	= SC	

TRAPPING AND GENERAL PROCESSING

CAPTURE

On St. Croix, commercially available live-traps (15 × 15 × 45 cm) constructed from 2.5-cm square weld-mesh and baited with pork liver were used exclusively and found to be completely effective if somewhat expensive (available from National Live Trap, Tomahawk, Wisconsin). Removal-trapping for tick surveillance was conducted by up to 10 men 5 days per week in an assigned area until the catch was greatly reduced. Additional animals for necropsy were collected in an effort to trap out small samples of previously undisturbed populations.

On Grenada and Trinidad, mongooses were caught alive in locally made wooden box-traps which measured 20 × 15 × 45 cm (Fig. 10). The upper and lower surfaces were made of 2.5-cm square weld-mesh, and the door had a vertical handle, at the base of which protruded a horizontal bar. Tension was provided by a circular strip of tyre inner-tube looped around this protruding bar and a U-hook on one side of the trap. To hold the door open the top of the handle was hooked back to the upper surface by one end of a double S-hook; a chicken head was suspended inside the trap on the other end. A mongoose pulling on the bait dislodged the handle, and the contracting rubber closed the door and kept it firmly in place. The whole structure was durable, relatively cheap, and effective. For the removal-trapping programmes in Grenada one or two teams of five or more trappers, each with 10 to 40 traps, were sent out 5 days a week throughout the year, except on public holidays or when difficulties arose. The traps were checked daily, except on weekends, and all mongooses were taken to the laboratory on the day they were found in the trap. Trapping was conducted in one area until the number of mongooses caught diminished considerably.

Removal-trapping in Trinidad was conducted on a much smaller scale in the derived grasslands and abandoned cultivations near the Aripo Savannahs and elsewhere. A team of two or three people set a variable number of traps when specimens were required. Captured animals were brought to the laboratory in Port-of-Spain on the day they were found. Some were kept for experimental purposes, but the remainder were processed on the day after capture.

IMMOBILIZATION, KILLING, CAPTIVE HANDLING AND LABORATORY PROCESSING

In the laboratory mongooses were placed in a large glass jar containing a cotton pad with diethyl ether until sufficiently anaesthetized. Very young mongooses could be handled directly, but subadults had to be either anaesthetized or put into a stout canvas bag. This latter method was used only when mongooses had to be weighed. In Trinidad and Grenada, anaesthetization by ether proved a cumbersome and difficult technique in the field. One mg of succinyl choline chloride in 0.5 ml of distilled water was therefore injected intramuscularly into the thigh, and this treatment immobilized a mongoose of average size in 4 to 5 minutes. Usually, the animal was first wedged against the inside of the cage with a metal bar or stick and then the tail or one of the hind legs was pulled through the weld-mesh (Fig. 11). The whole procedure allowed rapid examination and recovery within 10 to 15 minutes.

In St. Croix, succinyl choline chloride was used initially for immobilization, but after a number of animals went into shock on recovery from the drug, ether anaesthesia was employed routinely. Near the end of the study, sufficient skill was developed that mongooses could be hand-held without drugs for most procedures. Animals were killed either by ether or by the injection of 5 mg of succinyl choline chloride in 0.5 ml of water, which usually caused death within less than 1 minute.

Sex, maturity, weight and external measurements were recorded for all removal-trapped mongooses. In females, lactation, uterine scars, and position, number, weight and length of embryos were recorded. For males, testicular weight was recorded and the penis was removed for processing. In Trinidad and Grenada the bacula were cleaned of excess tissue and then placed in a solution containing equal quantities of strong ammonia and 6 percent hydrogen peroxide for several days. The bacula were teased out, allowed to clean further in fresh solution, finally washed in water, and then allowed to air dry before being weighed. In St. Croix, bacula were cleaned by bacterial maceration in water before a final treatment with hydrogen peroxide and air drying.

On St. Croix, the skull and right hind leg of each animal were removed and rough-fleshed before being dried for final cleaning by dermestid beetles.

Eyes were removed in their entirety from selected males and females in

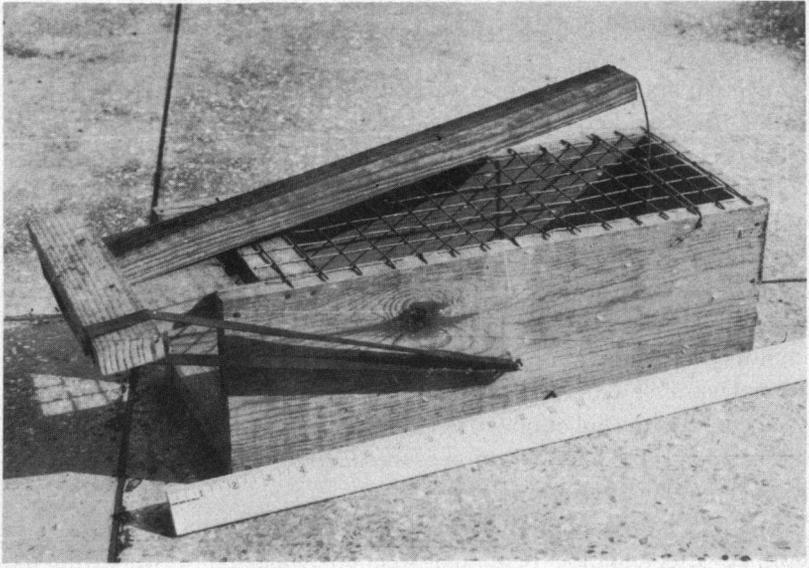


Fig. 10. Wooden box-trap as used in Trinidad and Grenada.



Fig. 11. Mongoose in box-trap about to receive an injection of succinyl choline chloride.

Trinidad and Grenada and from all animals in St. Croix. The lenses were stored and hardened in a solution of 10 percent formalin according to the methods outlined by LORD (1959) and SANDERSON (1961). The length of time that the eyes were in solution was not important provided that a minimum of 1 week was allowed; better hardening was obtained after longer storage. When hard, the lenses were dissected out by a single incision, rolled dry on a tissue, and placed in labelled Bijou bottles. Uncapped bottles were placed in a tray, and the paired lenses were oven-dried at 80° C for 24 hours or longer. Because lenses are hygroscopic, in Trinidad the caps of the bottles were screwed on tightly after the lenses were dried; in St. Croix lenses were stored in a desiccator. Each lens was weighed separately on a Mettler balance to 0.01 mg, and the lens weight per animal taken as the mean weight of the two lenses. Lenses removed from a frozen carcass were unsatisfactory.

Other laboratory processes and specialized techniques used are considered under the appropriate sections.

Captive mongooses were kept from a few days to over 3 years for several purposes. Primarily, as breeding does not take place readily in captivity, females which were pregnant on capture were used as a source of laboratory-born young. Captive animals and their young were also used in studies on behaviour, food preference, poisons, narcotics, chemosterilants, and for rabies investigation.

On St. Croix, mongooses were kept in individual cages, 33 × 77 cm, within a screened verandah. A 10-cm diameter plastic pipe or box was included in each cage for housing and play purposes. The animals were allowed to run free on the verandah, singly or in small groups, for a short period of time each day. Behaviour was observed closely in these semi-domesticated mongooses.

In Trinidad, captive mongooses were kept in individual wood and wire-mesh cages, 76 × 60 × 45 cm, which contained a housing-box of wood approximately 15 × 17 × 30 cm. Wood shavings were used as litter, and a water container was wired to the side of the cage. Access to the cage was through an upper hinged lid.

In Grenada, cages of a similar size with weld-mesh floors and sides were built together in three tiers against a back wall. Each cage had a removable galvanized tray fitted underneath for collecting urine, faeces, and discarded food. Cages used for housing mothers with young had flooring of 1.25-cm mesh, as the babies were liable to fall through the larger gauge. Unfortunately, the smaller mesh tended to retain the droppings. In the centre of each cage was a sliding plywood partition, and the front had two hinged doors. This arrangement allowed the mongoose to be enclosed in half the cage so that feeding and cleaning could be performed conveniently. Also, a mother could be segregated from her young easily. Each cage contained a housing-box similar to those used in Trinidad, and a plastic water pot.

On St. Croix, food consisted of a daily supply of condemned liver and other meats from the abattoir supplemented with mango and papaya (paw-paw). Old newspapers were used as floor litter, and were changed every day. The majority of the animals kept were in perpetual close proximity to NELLIS, and some were handled frequently.

In Trinidad and Grenada, the animals were normally fed and watered daily and the cages cleaned every 3 days. They were not usually fed on Sundays or on public holidays, but where two holidays occurred together not more than 24 hours were allowed to elapse between successive feedings. Extra food was provided on the day prior to that on which feeding would not occur. In Trinidad, captive mongooses were fed on plucked chicken heads and surplus white albino mice from the laboratory colony. Two adult mice or two chicken heads, or one of each, were considered a sufficient daily diet. In Grenada, no mice were available, and the staple food was unplucked chicken heads. Cases of food condemned by the Public Health Department were kept for stand-by feeding when chicken heads were in short supply. These varied from tinned ham, beef, Vienna sausage and meat paste to sardines and other fish. If sufficiently hungry, mongooses will eat most tinned protein, but highly spiced and oily foods like sardines and salt pork are generally not favoured. When nothing else was available tinned dog food and fresh fish were bought. On neither island was a fruit supplement generally given, but females with weanlings were given surplus food to ensure that they would not be tempted to eat their young.

BIRTH AND DEVELOPMENT

BREEDING SEASON

Pregnant female mongooses were found on Grenada during all months of 1970 and 1971, but with a considerable drop in numbers in November and December (Table 3). Three distinct breeding peaks were evident in the first 10 months of 1970, and this pattern was repeated in 1971, though slightly in advance (Fig. 12). When the data for 1970 and 1971 are considered separately and combined, there is no significant difference between the monthly frequency of pregnant females expected and that obtained during the first 10 months. This suggests the homogeneity of the breeding period despite the apparent peaks at February/March, May/June, and August/September. Statistically, there is insufficient variation between the three peaks and the alternating troughs to provide significant differences during the 10-month breeding periods. If, however, the expected monthly frequency and that obtained for 12 months in the 2-year period are considered either separately or combined, then a highly significant difference is apparent ($p < 0.001$), indicating that breeding takes place mainly between January and October.

In 1972, the three breeding peaks were repeated (Fig. 12). Again, there were few pregnant females in November and December, but the non-breeding period was apparently extended to include September and October, and most pregnant females were found in June. There is no significant difference when the first 8 months of 1972 are compared, but a highly significant difference ($p < 0.001$) exists when all 12 months of the year are considered. If the 3 years are combined, no significant difference is apparent for the first 8 months, a significant difference ($p < 0.05$ and > 0.02) exists when the first 10 months are compared, and a highly significant difference ($p < 0.001$) is indicated when all 12 months are compared. Because of the reduced catch in 1973, only 273 females were examined; of these, 28 were pregnant. This number is too small to allow monthly comparisons to be made, but nevertheless peak breeding was again apparent in June.

There was a fairly consistent drop in the proportion of pregnant females over the 4 years. In 1970, 25.8 percent of all females examined had developing embryos, compared with 15.9 percent in 1971, 13.7 percent in 1972 and 10.3 percent in 1973. No reason for this has been identified;

TABLE 3
ANALYSIS BY MONTH OF PREGNANT MONGOUSES ON GRENADA DURING 1970, 1971 AND 1972*

Month	1970			1971			1972			Mean Percentage pregnant
	Females examined	Females pregnant	Percentage pregnant	Females examined	Females pregnant	Percentage pregnant	Females examined	Females pregnant	Percentage pregnant	
Jan.	21	5	23.8	38	7	18.4	8	1	12.5	19.4
Feb.	45	19	42.2	37	11	29.7	53	14	26.4	32.6
Mar.	57	18	31.6	61	16	26.2	26	6	23.1	27.8
Apr.	52	13	25.0	45	6	13.3	34	7	20.6	19.8
May	56	15	26.8	30	7	23.3	19	2	10.5	22.9
June	30	12	40.0	38	6	15.8	33	10	30.3	27.7
July	23	6	26.1	26	3	11.5	30	3	10.0	15.2
Aug.	29	7	24.1	19	5	26.3	28	7	25.0	25.0
Sept.	27	13	48.1	30	6	20.0	51	2	3.9	19.4
Oct.	23	6	26.1	70	9	12.9	27	0	0.0	12.5
Nov.	60	3	5.0	70	4	5.7	52	1	1.9	4.4
Dec.	34	1	2.9	59	3	5.1	34	1	2.9	3.9
Total	457	118	(25.8)	523	83	(15.9)	395	54	(13.7)	(18.5)

* 1973 273/28 = 10.3%. Total for four years = 1648/283 = 17.2%.

several years of study would be required to postulate a long-term pattern relating fecundity to population growth or stability.

On St. Croix, the broad limits of the breeding season were determined by a compilation of approximate birth dates from three different categories of measurement (Fig. 13). Over the 3-year period 1969-1972 birth dates of embryos from 455 wild-caught pregnant females were estimated by the criteria of TOMICH & DEVICK (1970); birth dates from known-age animals were used; and birth dates of animals under 1 year of age were determined by eye lens weight. This information is collated in Fig. 14 and indicates that although parturition takes place throughout the year, most births occur in June and July, and the fewest in December and January.

From a sample of 321 female mongooses with an estimated age of 6 months or over, the highest percentage of pregnant females occurred in June, but preliminary peaks in April/May and in February are also evident (Fig. 13a). Fig. 13b shows the percentage of lactating females in the sample. Little reproductive activity occurred from August through to the following January, and the highest proportion of inactive females was found in November and December (Fig. 13c). These findings from St. Croix do not differ substantially from those from Grenada, particularly those from 1972 where little breeding occurred between September and December.

GORMAN (1976b) has studied the breeding behaviour of *H. auro-punctatus* on Viti Levu, Fiji (19° S), where pregnant females were found from August to January. He compared his results with those of PEARSON & BALDWIN (1953) from Hawaii (21° N) and of PIMENTEL (1955a) from Puerto Rico (18° N). In Hawaii, pregnant females were found between February and July, and in Puerto Rico between January and October. GORMAN concluded that mongooses breed on an increasing day length, and our findings from St. Croix (17° N) and Grenada (12° N) support this conclusion, even though in Grenada the difference between the number of daylight hours in June and December is only one hour and 26 minutes. SOARES & HOFFMAN (1981) found that Hawaiian male mongoose serum androgen levels were high from February to July, while the levels of luteinizing and follicle stimulating hormones increased prior to the winter solstice. The monthly figures for the percentage of females pregnant (Table 3) indicate that over a number of years breeding may become fairly uniform over the first 8 to 10 months of the year; nevertheless, one or more

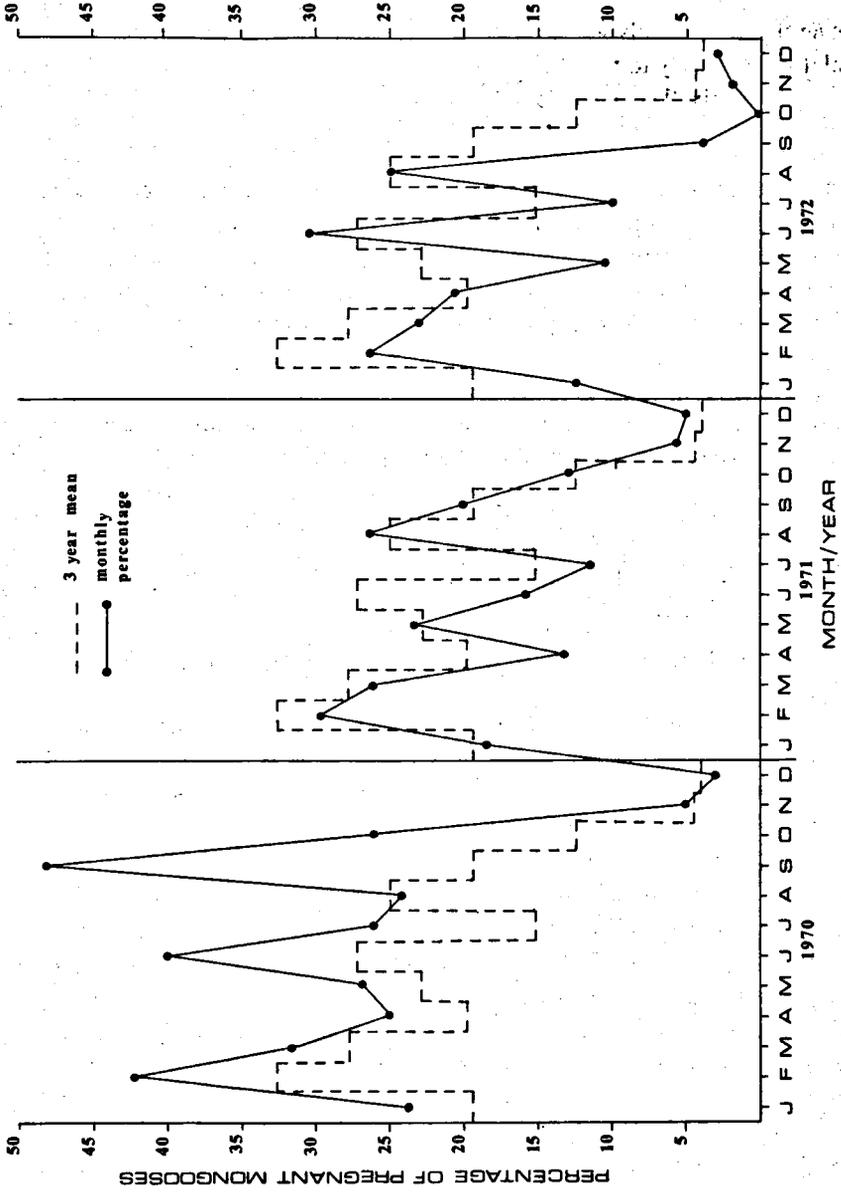


Fig. 12. Percentage of pregnant mongooses per month over a three-year period in Grenada.

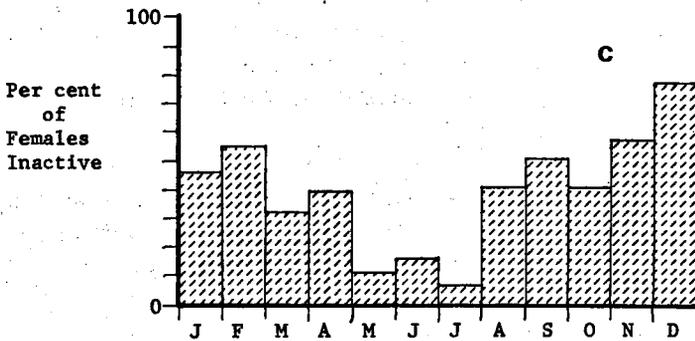
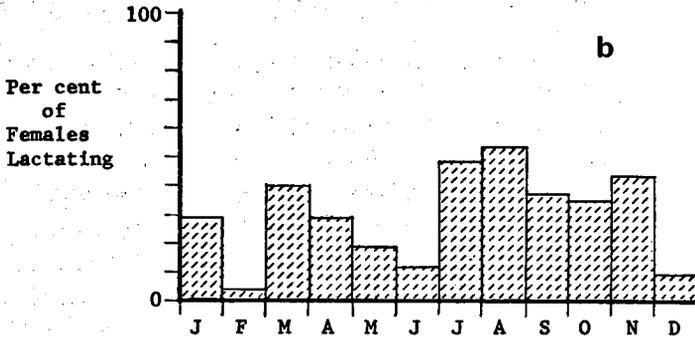
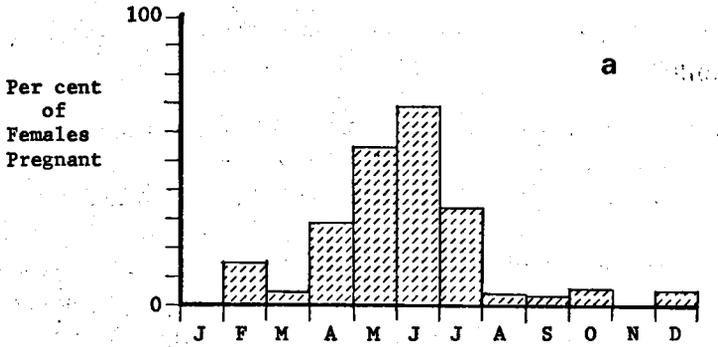


Fig. 13. Reproductive activity of female mongooses over six months of age from St. Croix: a - Percentage of females pregnant. b - Percentage of females lactating. c - Percentage of females inactive.

peaks of reproductive activity may be apparent even after several years of recording.

Two litters per year are possible. A female in captivity on St. Croix has twice produced litters at intervals of 4 months. Perhaps this is partly dependent on age, time of birth, and onset of the first breeding season.

Occasionally a mother and young have been caught in a trap together. Two such mothers were pregnant, and the young were not more than 6 weeks old at the time. Allowing for the gestation period, the peaks of Fig. 12, which occur nearly every 3 months of the breeding period, would indicate mating shortly after the young were born but not as late as the end of lactation.

FRERE (1929) observed that a semi-domesticated female *H. edwardsi* in India produced five litters between May 1927 and October 1928, and he suggested that she was probably born in mid-May 1926. HINTON & DUNN (1967) give the gestation period for *H. edwardsi* as 8 to 9 weeks, and ASDELL (1964) concluded that this species has no regular breeding season. Nevertheless, it appears to be comparable with that of *H. auropunctatus*. The latter has a 10-month breeding period and may also be capable of producing five litters in 18 months, especially as it has a shorter gestation period.

In Hawaii, the first breeding season extends from February to April and a second from May to July, with no breeding from October to January (BALDWIN, *et al.*, 1952). PEARSON & BALDWIN (1953) indicate that females breed twice in the year. PIMENTEL (1955a) gives the season in Puerto Rico as January to October, with most births in March/April and July/August.

GESTATION

POWELL (1913) reports an observed gestation period of 49 days in a free-ranging *Mungos auropunctatus* [*sic*] in India. The gestation period of *H. auropunctatus* has been reported from other workers by ASDELL (1964) as about 7 weeks, while TOMICH & DEVICK (1970) calculate the gestation period as 47 to 53 days.

Caged wild mongooses have not been induced to breed in the laboratory, although we have had some success with hand-reared animals kept in large enclosures. The female will copulate frequently on successive days

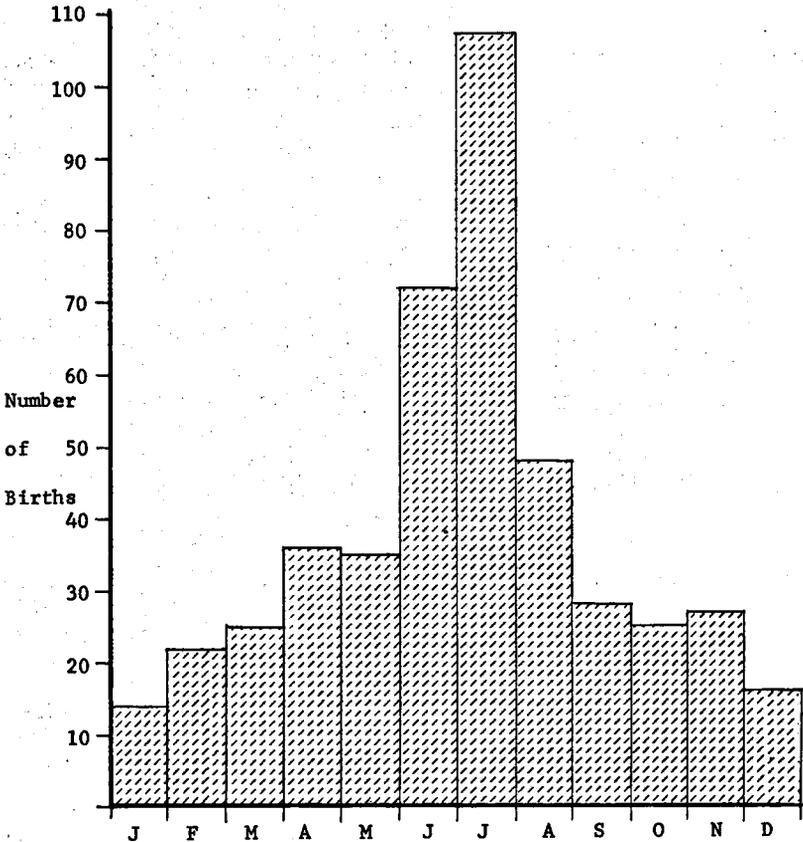


Fig. 14. Breeding season of mongooses on St. Croix shown by number of births per month.

during the period of oestrus, and unless she is carefully segregated after mating once, the day of conception cannot be determined. Of the three exact and reliable records for gestation periods of tame animals in St. Croix, two were 49 days and one was 50 days. All evidence seems to be in agreement that the gestation period is 7 weeks, with the expected variation for mammals of 5 percent.

LITTER SIZE

PIMENTEL (1955a) found an average of 2.1 embryos per pregnant female mongoose in Puerto Rico, and PEARSON & BALDWIN (1953) record a mean

TABLE 4
PERCENTAGE OF PREGNANT FEMALE MONGOUSES IN GRENADA WITH 1-5 EMBRYOS
DEVELOPING AT THE SAME TIME

	Number of embryos in litter										
	1970					1971					
	1	2	3	4	Total	1	2	3	4	Total	
Number of females	10	79	27	2	118	11	55	14	3	83	
Percentage of females	8.5	67.0	22.9	1.7		13.3	66.3	16.9	3.6		
Number of embryos	10	158	81	8	257	11	110	42	12	175	
Mean number of embryos per female per year		2.18					2.11				

	Number of embryos in litter												
	1972						1970 to 1972 combined						
	1	2	3	4	5	Total	1	2	3	4	5	3-year Total	
Number of females	9	27	15	2	1	54	30	161	56	7	1	255	
Percentage of females	16.6	50.0	27.7	3.7	1.9		11.8	63.1	22.0	2.7	0.4		
Number of embryos	9	54	45	8	5	121	30	322	168	28	5	553	
Mean number of embryos per female per year		2.24						2.17					

of 2.7 in Hawaii. ASDELL (1964), reporting the results of other workers, gives an average embryo count of 2.1 and a range from 2 to 4. HINTON & DUNN (1967), reporting the work of BRYAN (1908), record a maximum of 5 embryos.

Table 4 shows the numbers and percentages of pregnant females in Grenada with 1 to 5 embryos developing at the same time. In 1970 the mean number of embryos per trapped pregnant female was 2.18. In 1971 the mean changed slightly to 2.11. The mean for the 2-year period was 2.15, and there was no significant difference between the means for the 2 years. In 1972, the mean number of foetuses per pregnant mongoose was 2.24, and the overall mean for the 3-year period was 2.17. There was no significant difference between the observed and expected numbers of offspring in each of the three groups of pregnant females during the 3 years ($\chi^2 = 0.273$) and, accordingly, no evidence of change in the number of developing embryos. The mean number of embryos recorded by month over the combined 3 years did not differ significantly from the overall 3-year mean of 2.17. The lowest value was 2.00, and the highest was 2.53. From the meagre data for 1973, 28 pregnant females produced a total of 67 embryos ranging in number from one to four in each animal; the litter size averaged 2.39. Thus, the overall average for 1970 to 1973 is 2.19 (620/283) embryos per female. Despite the decrease in the percentage of pregnant females between 1970 and 1973, the mean number of embryos observed remained constant. The mean litter size of 2.25 for 27 laboratory-born young in Grenada is comparable to the island-wide averages.

When the Grenada results for the 4 years are combined, the percentages of females having one, two, three, four or five embryos are 11.3 (32/283), 61.8 (175/283), 23.7 (67/283), 2.8 (8/283), and 0.3 (1/283) percent, respectively. Thus nearly two-thirds of the pregnant female population have two embryos developing at the same time.

On St. Croix, the percentages of females having one, two, and three embryos developing at the same time were 5.8 (4/69), 73.9 (51/69), and 20.3 (14/69) percent, respectively; the mean litter size was 2.14. One post-partum animal had four uterine scars. We have received a report of a litter of five being born under a picnic table in the National Park on St. John (U.S. Virgin Islands).

Pregnant female mongooses in Trinidad were not examined for litter size because laboratory-born young were needed.

SEX RATIO

On St. Croix 405 female mongooses and 519 males were removal-trapped. Thus, 43.8 percent were females (with 99 percent confidence limits of 38.1 to 48.6), and the sex ratio was 1:1.28. At an earlier stage in this removal-trapping programme there were 212 females (46 percent) and 249 males (ratio 1:1.17), while a subsequent collection yielded 193 females (41.7 percent) and 270 males (ratio 1:1.40).

During 1970 in Grenada, 1,740 mongooses (mainly from the removal-trapping programme) were sexed, of which 458 (26.3 percent) were female. The sex ratio was 1:2.8. The corresponding figures for 1971 and 1972 were 523 females of 1,765 animals (29.6 percent, sex ratio 1:2.4) and 395 females of 1,416 animals (27.9 percent, sex ratio 1:2.6), respectively. The ratio for the three years combined was 1:2.58 (27.96 percent female). There is no significant difference between the sex ratios for each of the 3 years, and this confirms the results of an earlier assessment of a large sample of mongooses made at 3-monthly intervals between January 1970 and December 1971 (Table 5a). Here, there is no significant difference ($p > 0.10$ but < 0.50) between the numbers of females observed in each of the eight 3-monthly batches and the number expected from the total catch of males and females. The differences between the ratios are therefore well within the limits of normal variation. In 1973, 273 females and 537 males were sexed,

TABLE 5a
SEX RATIOS FROM A SAMPLE OF MONGOUSES TRAPPED IN GRENADA DURING
1970 AND 1971

Year	Months	Male	Female	Percentage female	Ratio (F:N)
1970	Jan.-March	240	88	26.8	1:2.7
	Apr.-June	361	140	27.9	1:2.6
	July-Sept.	247	80	24.5	1:3.1
	Oct.-Dec.	254	117	31.5	1:2.2
1971	Jan.-March	400	136	25.4	1:2.9
	Apr.-June	238	113	32.2	1:2.1
	July-Sept.	146	75	33.9	1:1.9
	Oct.-Dec.	456	199	30.4	1:2.3
Total		2342	948	28.8	1:2.5

a ratio of 1:2.0 or 33.7 percent female. The sex ratios for the 4 years are summarized in Table 5b. The mean sex ratio for Grenada for the whole period was 1:2.48 or 28.8 percent female.

Of 207 mongooses from all trapping sites on Trinidad, 95 (45.9 percent) were female, giving a ratio of 1:1.2. At an earlier point in the programme when only 163 animals (74 females) had been trapped, the ratio was comparable (45.4 percent females, ratio 1:1.2).

The sex ratios of first captures on Grenada grids A to F are shown in Table 5c, and the sex ratios of mongooses recaptured at the same grids are included for comparison. In most cases there was little change in the sex ratios of mongooses between first capture and recapture, except for Grid E (Grand Etang) and, to a lesser extent, Grid F (Florida/Piedmont). The sex ratio of first captures on the Trinidad grids combined was 1:1.13. The recapture ratio varied somewhat (1:1.77), but the sample size was considerably smaller than that in Grenada. The sex ratios of grid-trapped mongooses on St. Croix from Estates Slob, Prosperity and Mountain are shown in Table 6. As in the case of Grenada, there is variation between them; recapture ratios were similar to first capture ratios, except for Estate Slob where females actually outnumbered males.

The numbers of mongooses born in captivity were too small to use for comparison.

In Hawaii, TOMICH (1969) found 232 of 546 (42.5 percent) first captures to be female (ratio 1:1.35). This percentage differs markedly from the 28.8 percent females removal-trapped on Grenada, but it is close to the 43.8 percent and 45.9 percent obtained on St. Croix and Trinidad, respectively; the ratio is close to the birth ratio observed on St. Croix. PIMENTEL (1955a) on Puerto Rico found the sex ratio to be 1:1.06, while PEARSON & BALDWIN (1953) in Hawaii trapped 77 female and 144 male mongooses (ratio 1:1.87). Removal-trapping records from all over Grenada indicate a preponderance of males, and in some localities ratios as low as 1:7 (female:male) have been recorded. BALDWIN *et al.* (1952) also reported a greater number of males with even lower ratios of 4 females to 37 males (1:9.25). Nevertheless, grid-trapping results show that local populations frequently exist where the sex ratio is almost 1:1, and that females may even be in slight excess. The fact that first captures and recaptures on Grenada maintained an essentially uniform ratio in the same areas in-

TABLE 5b
SEX RATIOS OF REMOVAL-TRAPPED MONGOUSES IN GRENADA BETWEEN 1970
AND 1973

Year	Total mongooses	Females	Males	Ratio (F:M)	Percentage female
1970	1740	458	1282	1:2.8	26.3
1971	1765	523	1242	1:2.4	29.6
1972	1416	395	1021	1:2.6	27.9
1973	810	273	537	1:2.0	33.7
4 years combined	5731	1649	4082	1:2.48	28.8

TABLE 5c
SEX RATIOS OF MONGOUSES CAUGHT ON THE GRENADA GRIDS

* This includes animals that died either in the trap or during immobilization.

Grid	Female	Male	Total	Ratio (F:M)	Percentage female	Ratio of recaptures (F:M)
A	43	42	85*	1:0.97	50.6	1:1.1
B	43	41	84	1:0.95	51.2	1:1.1
C	20	40	60	1:2.00	33.3	1:1.9
D	22	19	41	1:0.86	53.7	1:0.7
E	13	34	47	1:2.62	27.7	1:5.4
F	13	50	63	1:3.85	20.6	1:2.7

TABLE 6
SEX RATIOS OF MONGOUSES CAUGHT ON THE ST. CROIX GRIDS

Grid	Female	Male	Total	Ratio (F:M)	Percentage female	Ratio of recaptures (F:M)
Slob	31	35	66	1:1.13	47.0	1:0.76
Prosperity	10	37	47	1:3.70	21.3	1:3.00
Mountain	11	33	44	1:3.00	25.0	1:3.33
Total	52	105	157	1:2.02	33.1	1:1.28

dicates that both sexes react to traps in a similar way. Also, as males and females entered the traps in approximately equal numbers on St. Croix and Trinidad and on some of the Grenada grids, trap-shyness of females was probably not the cause of the overall disproportion between the sexes on Grenada. Both TOMICH (1969) and PIMENTEL (1955a) have found that male movements exceed those of females; this must be taken into account. Farther-ranging males might be expected to encounter randomly-placed removal traps more often than females, and this could account for the ratio of 1:2.48 (female:male) found on Grenada, although it leaves the Trinidad and St. Croix ratios unexplained. Possibly, under the more competitive conditions of Grenada, females die more quickly, or are even attacked during their immature and subadult stages by the more aggressive heavier sibling males in the absence of the mother. We have seen this trend in the captive mongooses. Also, weanling females could be killed by adults of both sexes more easily than weanling males. BALDWIN *et al.* (1952) report several instances of cannibalism. We have found that mothers frequently become cannibalistic in captivity, particularly when unduly disturbed. This tendency may possibly be shown in the wild, the mother killing the weaker female members of the litter at times of stress.

As discussed in the section on population structure, until approximately 7 months of age females appeared to outnumber males on St. Croix. From 8 months onwards, males were more numerous. Similar results were not obtained on Grenada where the ratio of juveniles was approximately 1:1 (112 females to 126 males). On the attainment of sexual maturity, young females are stressed with pregnancy, parturition, lactation, and then looking after the young. Increased mortality may be a consequence. Greater male aggressiveness and activity (especially in searching for females) would also result in a proportionately higher male catch in a removal-trapping programme. Our conclusions are that all these factors contribute to the divergence between the observed sex ratio and the expected birth ratio of 1:1. Under some conditions, the already preponderant males are probably even more evident in the samples because of decreased female activity immediately post-partum.

BIRTH AND EARLY DEVELOPMENT

Pregnancy is not easily discernible unless mongooses are parturient; nevertheless, palpation was undertaken on St. Croix to detect uterine

swelling, but this was not done on Grenada because of the risk of bites from potentially rabid animals. Of the 27 young born in the laboratory to wild-caught mothers in Grenada (mean litter size 2.25), 16 were weaned successfully, 8 were killed and eaten by the mothers, usually after several females and 9 were males (43.8 percent females, ratio 1:1.3). Sometimes only one sibling was later, but on other occasions all were killed. For this reason, mother and young were usually left undisturbed as far as possible, and examination and weighing of the young were kept to a minimum. Domesticated mothers usually react quite differently and do not harm their young.

On Trinidad, five litters born or weaned under laboratory or domestic conditions allowed for the development of a total of 10 young with a sex ratio of 1:1 and an average litter size of 2.0. On St. Croix, 10 litters born in captivity produced 20 young with a sex ratio of 1:1.5 (female: male) and a mean litter size of 2.0.

The captive-born young of wild-caught or domesticated mothers from St. Croix and Trinidad provided our data on birth and early development. Maternal care is discussed in the Section on Behaviour.

The dorsal surface of well-developed embryos shortly before parturition, or of the young at birth, is covered with hair, but ventrally there are only sparse patches of golden hairs on the upper abdomen and thorax. The vibrissae are prominent. Eruptive cones of the canines are clearly visible, and the minute incisors can be seen and felt in both jaws; the claws are well developed. The ears appear to remain completely closed and flattened backwards against the head, and there is a distinct pale orange band in the region of the eyebrows. Eyelashes are visible. TOMICH & DEVICK (1970) have studied the immature and prenatal development of *H. a. auropunctatus* in detail, with particular reference to dentition. They note that the eight medial incisors (I^1 and I^2) are advanced in development at birth and assist with suckling. At 2 weeks the full complement of incisors is in place, and canines have erupted, although the latter may take a variable length of time to erupt completely. The full complement of permanent teeth is present 22 weeks after birth. The sequence of deciduous tooth replacement and growth of the molars is regular. EWER (1963a and 1963b) notes that the incisors of the South African meerkat (*Suricata suricatta*) are not felt until the fifth day, and upper and lower incisors (four) are

present on the eleventh day. Thirty days after birth the milk dentition of meerkats is complete.

HINTON & DUNN (1967), quoting POWELL (1913), note that the eyes of mongooses open after 16 to 17 days. In all our observations the eyes appeared to be still closed on day 15. They usually opened between 17 and 20 days after birth, mean $18.1 \text{ SE } \pm 2.4$ (range 15.7 to 20.6). By comparison, the eyes of the meerkat begin to open on the tenth day, and are completely open on the twelfth (HINTON & DUNN, 1967).

TOMICH & DEVICK (1970) record a birth weight of between 19.8 and 22.1 g from three term foetuses with crown-rump lengths of 51 to 58 mm. Birth weights of mongooses from St. Croix were exactly comparable to those on Hawaii. However, our observations on the wet weight of 18 unsexed foetuses from Grenada which were nearing parturition ranged between 22.3 and 36.4 g, figures which are in excess of those obtained by TOMICH & DEVICK. The weight increase of young captive male and female mongooses from Grenada up to 26 days after birth (at the time of artificial weaning) is shown in Fig. 15 by the two, almost parallel, regression lines which cut the abscissa at 33.1 g and 27.4 g for males and females, respectively. The equations for these lines, expressed as the square root of the weight, are $Y = 5.75 + 0.2106 X$ for males, and $Y = 5.23 + 0.2182 X$ for females. The weight increase of immatures up to 80 days of age is shown by the two diverging regression lines also in Fig. 15; since many of the points overlap, the more rapid increase in weight of males is not immediately obvious. The equations for these two regression lines, which should not be extrapolated to the abscissa, are $Y = 6.83 + 0.148 X$ and $Y = 6.92 + 0.129 X$ for males and females, respectively.

The subsequent weight increase beyond 250 g, expressed as the logarithm of the weight, is shown in Fig. 16, and again, these lines should not be extrapolated beyond the range taken. These regression line equations are $Y = 1.085 + 0.754 X$ for males, and $Y = 1.313 + 0.600 X$ for females. The divergence in the weight increase for the two sexes is now much more obvious. Table 7 shows the weights of males and females taken from these six regression lines at selected time intervals.

Because measurements of the young prior to weaning were limited, the two extrapolated birth weights are exaggerated, and the female average

probably approaches 25 g. Day 26 was chosen as the limit for the first set of regression lines in Fig. 15 since this was the approximate date of artificial weaning.

On St. Croix comparable growth curves for body weight (Figs. 17 and 18) and total length (Fig. 19) were constructed from the periodic measurements of 15 mongooses born in captivity. In captive mongooses, weaning is probably complete between 6 and 8 weeks, and the young may become independent of the mother between 10 and 12 weeks of age (or later) when the males and females should weigh at least 300 and 250 g, respectively. For animals less than 6 months of age, weight and, to a greater extent,

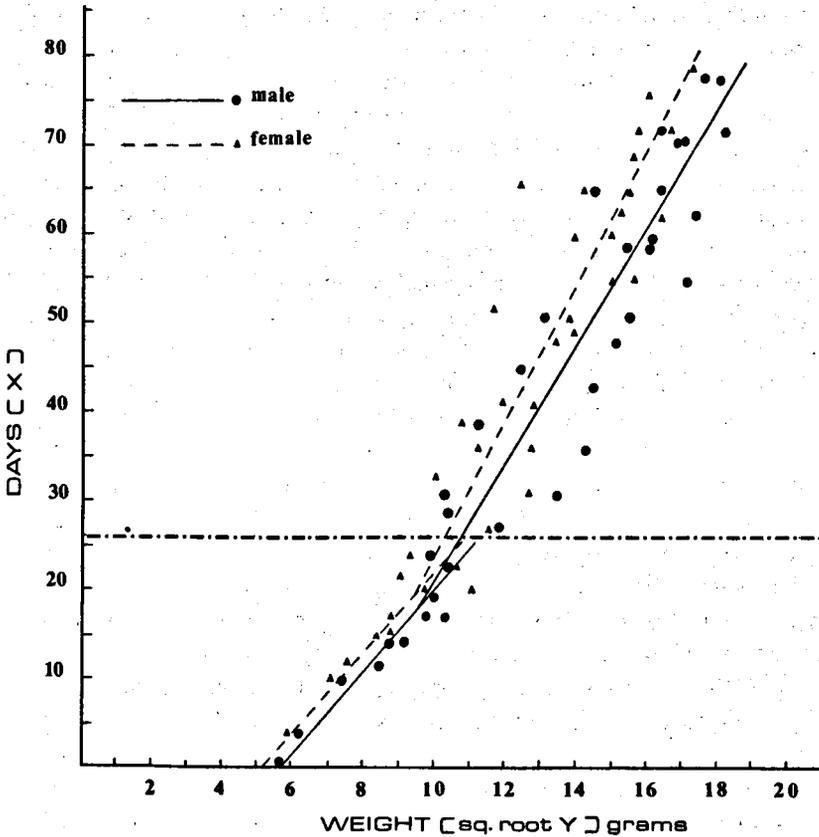


Fig. 15. Weight increase of young male and female mongooses on Grenada.

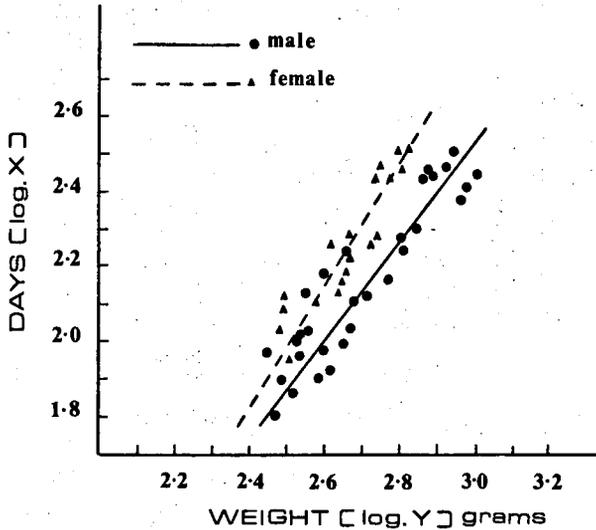


Fig. 16. Weight increase of Grenadian male and female mongooses beyond 250 grams.

length measurements provide a reasonably accurate estimate of age. The range of weight values for animals over 6 months old is probably too great to be a useful parameter for age determination. Only 1.4 percent of a sample of 552 trapped male mongooses on Grenada weighed less than 200 g; this also helps confirm the relatively long period of parental care in these animals. What can be considered a young adult weight is attained in approximately 5 months or 150 days.

DEVELOPMENT OF THE MALE

The male reproductive system of *H. auropunctatus* has been described by PEARSON & BALDWIN (1953). These authors found that males with testes 13 mm or over become sexually mature at between 4 and 6 months of age when they show cells in all stages of spermatogenesis including spermatozoa. We have observed mounting and copulating behaviour in animals less than 6 months old. Thus males are capable of reproducing within a year of birth but do not necessarily find sexually mature females of their own age. Whether they are capable of mating with older mature females is conjectural. Sperm production continues for the remainder of the individual's life.

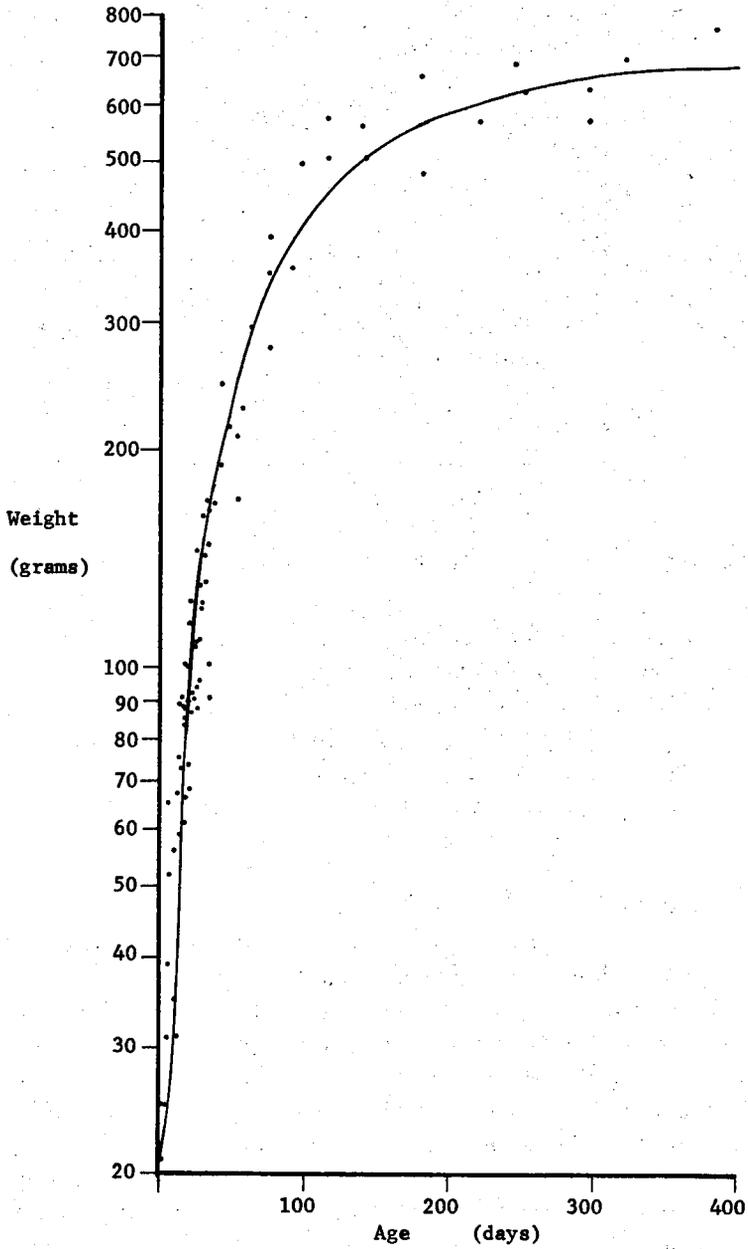


Fig. 17. Weight increase of male mongooses from St. Croix between birth and one year.

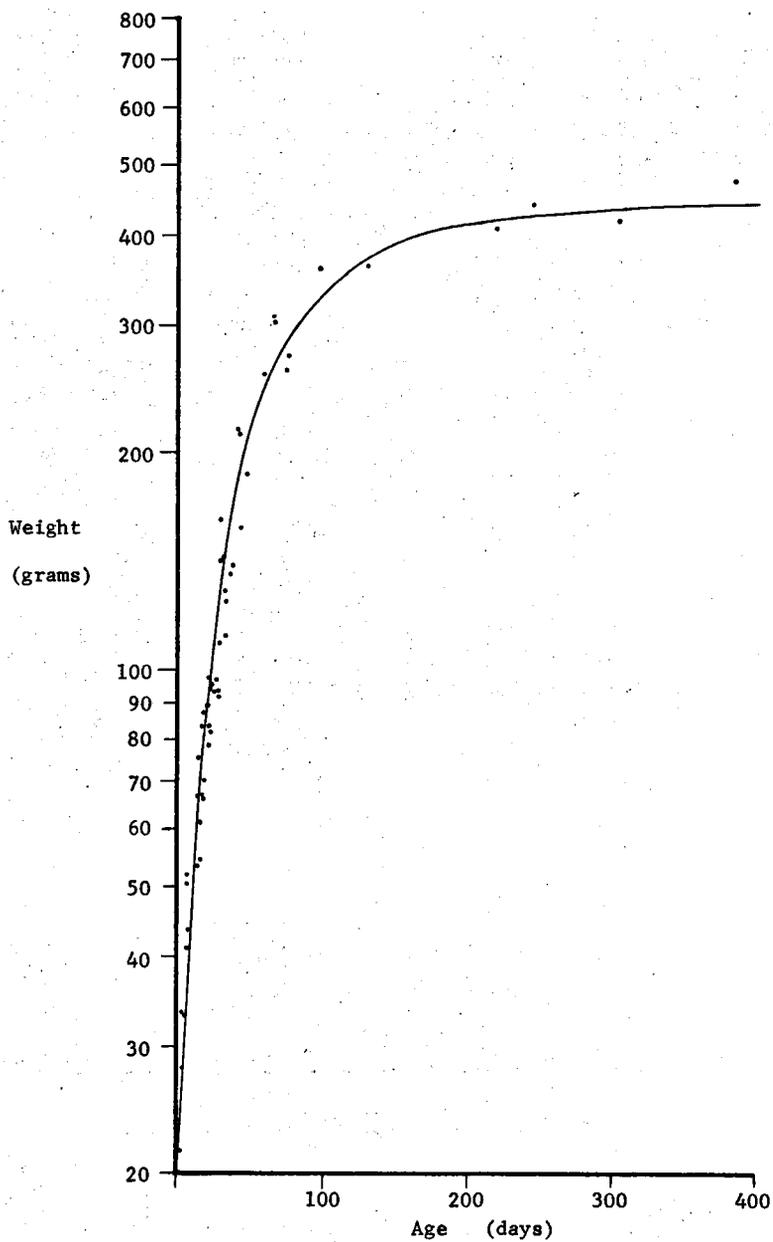


Fig. 18. Weight increase of female mongooses from St. Croix between birth and one year.

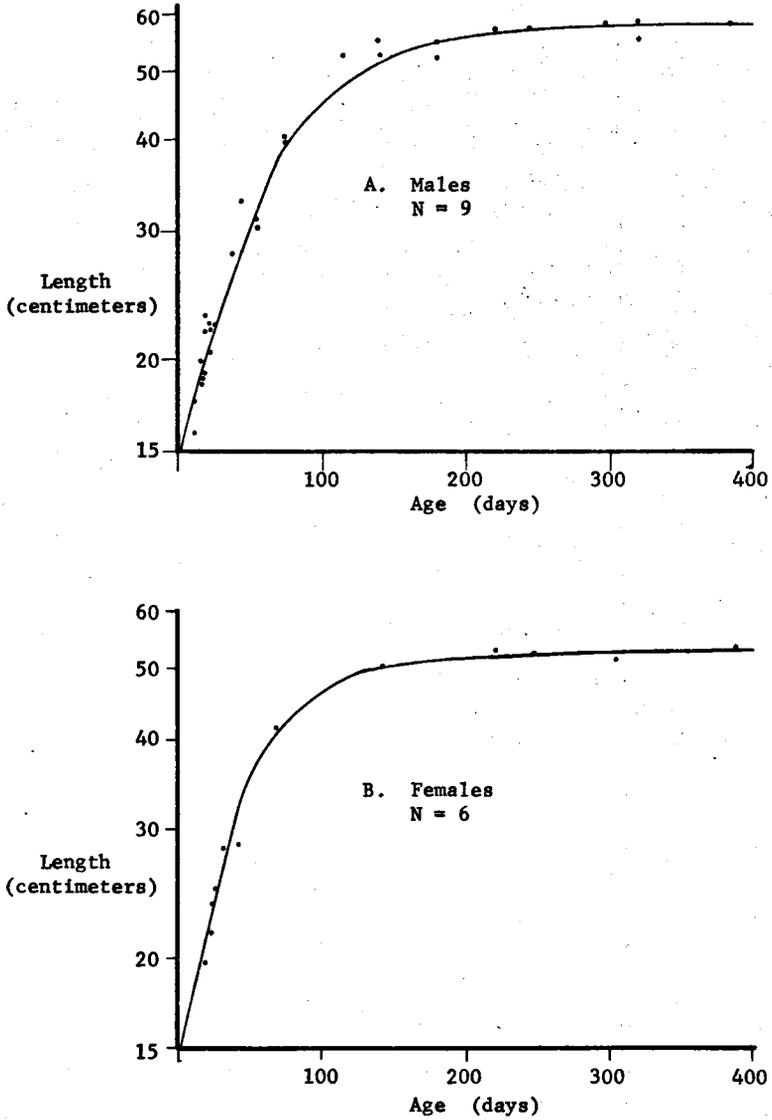


Fig. 19. Increase in length of mongooses from St. Croix between birth and one year: A - Males. B - Females.

In an attempt to correlate body weight with sexual maturity, testes were taken from 278 mongooses on Grenada and divided into two arbitrary groups of 136 and 142 individuals. The testes were collected during all months of the year, and the slight seasonal variation mentioned by PEARSON & BALDWIN (1953) was discounted. Figure 20 shows the weight of the paired testes plotted against mongoose weight for each of the two groups, the 95 percent confidence limits being given. The equations for these two regression lines are $Y = 0.00481 X - 0.983$ (group of 136) and $Y = 0.00613 X - 1.84$ (groups of 142), where Y represents testicular weight and X is body weight. The difference in orientation between these lines is accounted for by the slightly differing ratios of adults to immatures in the two groups. Table 8 shows the mean and range in weight of paired testes of mongooses in ten 100-gram weight groups; each of these mean testicular weights is also plotted in Fig. 20 against the corresponding mean of the ten body weight groups.

It is clear that there may be a wide range in testicular weight for a given weight of animal, and the regression lines are of value only in connection with specimens weighing more than 350 g. Males weighing less than 325 g have few spermatozoa and are obviously immature, and all mongooses are sexually mature by the time they attain a body weight of 600 g. Those weighing between 400 and 500 g may be either subadults or young adults, since spermatozoa are usually plentiful in the testes of animals within this weight range. From Table 7 it can be seen that this weight is reached in

TABLE 7
WEIGHTS OF LABORATORY-BORN HERPESTES ON GRENADA
taken from the regression lines in Figs. 15 and 16

Day	Weight of males (grams)	Weight of females (grams)
0	33	27
10	62	55
20	99	92
40	163	146
70	295	254
100	391	325
150	531	415
200	659	494
250	783	565

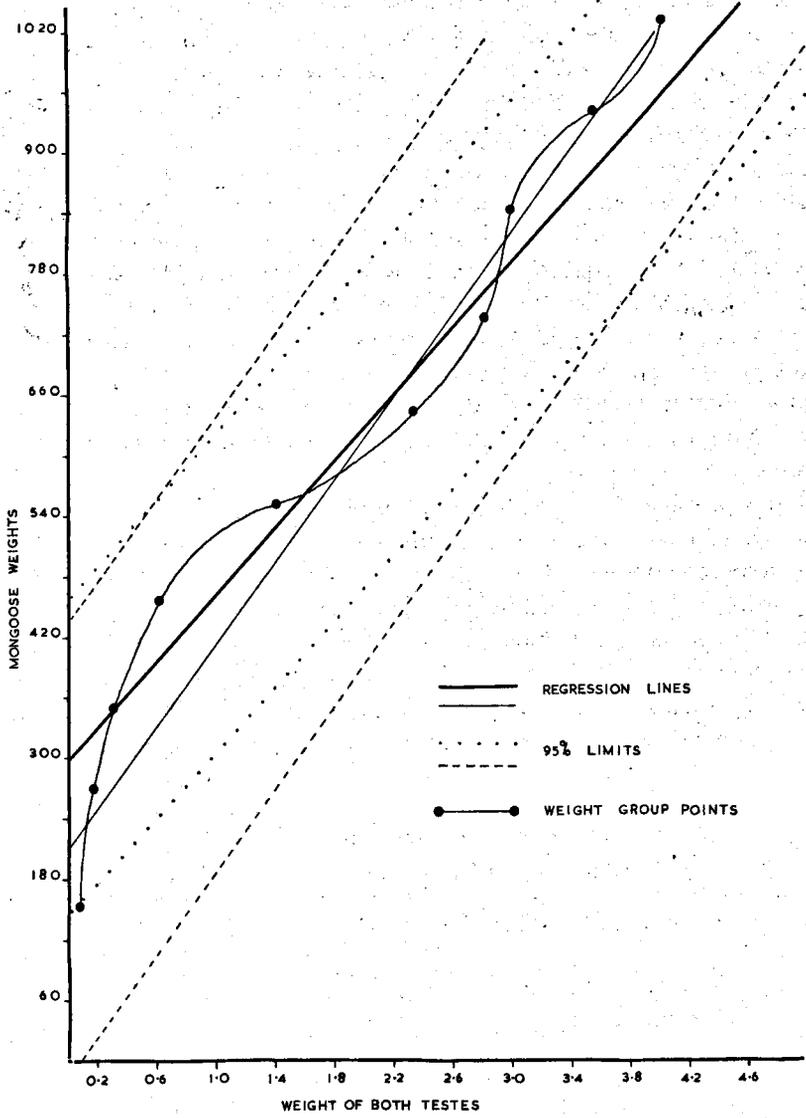


Fig. 20. Relationship between body weight and testicular weight of *H. a. auropunctatus*.

TABLE 8
THE MEAN AND RANGE IN TESTICULAR WEIGHT FOR SELECTED WEIGHT GROUPS OF
MONGOOSES ON GRENADA

	Weights of mongooses in 100-gram groups									
	100- 199	200- 299	300- 399	400- 499	500- 599	600- 699	700- 799	800- 899	900- 999	Over 1000
Mean weight of group (grams)	152.9	269.4	349.1	457.9	552.3	644.1	745.2	844.3	940.3	1030.0
Mean weight of paired testes (grams)	0.08	0.18	0.31	0.62	1.14	2.35	2.83	3.01	3.56	4.01
Weight range of paired testes (grams)	0.06 to 0.10	0.09 to 0.30	0.13 to 0.50	0.19 to 2.73	0.40 to 2.96	1.30 to 4.05	1.80 to 3.96	1.96 to 4.30	2.66 to 4.74	

about 4 months, confirming the finding of PEARSON & BALDWIN (1953).

Variations in the shape and size of the baculum, and the use of this bone in the determination of mongoose age, are considered in the Section on Age Determination.

DEVELOPMENT OF THE FEMALE

A comprehensive account of reproduction in the mongoose, including a description of the female reproductive tract, has been given by PEARSON & BALDWIN (1953). The most unusual features of the female tract, which most closely resembles that of mink and ferret, are the extreme lengths of the oviducts and ovarian ligaments, with the ovaries being located considerably anterior to the cephalic end of the bipartite uterus. Normally, ovulation appears to be as frequent in one ovary as the other, and corpora lutea may grow to 3 mm in diameter in mid-pregnancy. ASDELL (1964) suggests a 4-day oestrus period at 20-day intervals, and holds that ovulation is induced by copulation.

Our findings are substantially the same; we find a 3-day oestrus period repeated approximately every 3 weeks in the absence of conception and subsequent pregnancy. In three lactating females, oestrus was indicated by either turgid uteri or ripe ovarian follicles. Here, oestrus was post-partum

rather than post-lactational as found by PEARSON & BALDWIN (1953). (As it is sometimes difficult to express milk from the teats of some lactating females, it is possible that these authors misinterpreted their findings on a female which had corpora lutea and unimplanted embryos in addition to considerable mammary tissue development.) PEARSON & BALDWIN (1953) also maintained that the failure of corpora lutea to appear in non-mated captive mongooses suggests that ovulation does not occur in the absence of copulation. HOFFMAN & SEHGAL (1976) treated 53 mongooses with various doses and combinations of pregnant mare serum and human chorionic gonadotrophin and found formation of only one corpus luteum. Of six females cohabiting with males, three had litters, two of them at various times after treatment with pregnant mare serum. A possible confounding factor in the experiment was that it took place during a period of decreasing day length (see Breeding Season). Even so "the results suggest that the mongoose is an induced ovulator and the stress of captivity blocks pregnancy through lack of mating" (HOFFMAN & SEHGAL, 1976). The single exception casts some doubt on the conclusions, and whether ovulation in the Viverridae is induced or spontaneous remains to be determined, perhaps by an experiment involving mechanical stimulation of the vagina or cervix.

Transmigration of the blastocyst into the opposite horn of the uterus regularly occurs. NALBANDOV (1964) notes that the distances between implantation sites are approximately equal, being shorter when there are many embryos to be accommodated than when there are few. If more embryos find themselves in one uterine horn than in the other, the excess migrate from the one to the other; this spacing can be partly explained by the finding that once a blastocyst becomes implanted, adjacent areas of the endometrium are no longer receptive to further blastocyst implantation and development. In the mongooses we examined there were exceptions to these statements by NALBANDOV. In two cases there were three embryos in one uterine horn and none in the other; in one of these, all three ova originated from the same ovary. In the second case, an ovum from the opposite horn migrated to join the other two. In another observation, an animal with two embryos in one horn of the uterus had two corpora lutea in the opposite ovary. In two further cases corpora lutea were found in both ovaries, but both embryos were on the same side. This would indicate that transmigration of blastocysts in mongooses may be random rather

than determined by any uterine spacing mechanisms. For 93 corpora lutea accompanied by visible uterine swellings, there were 91 embryos, indicating an intrauterine loss of 2.2 percent. PEARSON & BALDWIN (1953) found the corpora lutea in a recent post-partum female to be degenerating, while near-term pregnant females examined on St. Croix had small or macroscopically undetectable corpora lutea. TOMICH & DEVICK (1970) confirm that delayed implantation is not known in the mongoose, and they believe that implantation occurs 8 to 10 days after insemination. However, delayed implantation does occur in several other carnivores, especially the Mustelidae, including species of *Mustela*, *Meles* and *Martes* (SADLEIR, 1969); but this phenomenon does not always take place even within species of the same genus, as is the case with *Mustela* and *Lutra*.

In *H. auropunctatus* implantation scars are visible in some females after parturition, but these are generally hard to detect later than 21 days post-partum. PEARSON & BALDWIN (1953) report that scars remain discernible for 4 months; our own observations indicate that scars even from the same litter are not equally prominent. They also report the resorption of the bony pubic symphysis during pregnancy to facilitate parturition, and the subsequent deposition of bone, reuniting the symphysis, before the end of lactation.

FREDGA (1965) reports an interesting sex-determining mechanism in *H. auropunctatus*. The chromosome number is 36 in females and 35 in males, with the female possessing two X-chromosomes and the male one. There is no visible Y-chromosome in the male. During meiosis in males, 16 bivalents and a unique type of trivalent are formed; the latter consists of the X-chromosome associated end-to-end with one chromosome arm of an autosomal bivalent. It is assumed that a part of the original Y-chromosome has been translocated onto an autosome.

Reproductive maturity in the female occurs at about 6 months of age or later. In a sample of 43 pregnant females aged by eye lens weight, three were less than 6 months old at the time of conception, the youngest being about 130 days. The conception dates of embryos were calculated using data provided by TOMICH & DEVICK (1970).

AGE DETERMINATION

The determination of the age of individuals in wild populations is essential for the understanding of population structure and dynamics.

Most of the techniques for age determination which might be applicable to large numbers of carnivores were examined in mongooses.

1. — The increase of body weight as a function of age has been discussed, with the conclusion that this parameter is useful only until puberty. Total length is a useful parameter on which to estimate the age of immature animals, but it loses reliability as maturity is approached. Fig. 19 shows increase of length with age, and has also been mentioned previously. When used together, the body weight and total length are useful parameters by which to approximate the age of young animals which are to be returned alive to the field.

2. — Length of the hind foot was found to be a less precise indicator of age than body weight or length, and subject to greater error in measurement.

3. — Testes weights were found to correlate only approximately with age (see Page 53). Mongooses whose paired testes weigh 2 g or over can be roughly categorized as adults.

4. — The baculum or *os penis* of several mammals, particularly carnivores, can be used to distinguish age groups within a species. The length, weight and volume of this bone increase with age, especially during puberty, until the maximum dimensions for an individual are reached at some time during adulthood. In the mongoose, the urethral duct in the penis is almost surrounded by the bony beak-shaped baculum, which is convex laterally and open along the ventral margin (Fig. 21). Some bacula have two foramina and a ventral indent immediately below these, while at the other extreme both foramina and the notch may be lacking. The ventral margins are frequently crenated, and there may be a proximal head with dorsal projections. The mean length of 232 bacula from Grenada was 11.2 mm (observed range 5.0 to 15.0). As PEARSON & BALDWIN (1953) point out, there is considerable variation, particularly in young animals, with lengths of 3 to 6 mm being associated with mongooses of the same age group. Further, the beak of the baculum sometimes curves forwards and downwards, resulting in foreshortened measurements.

The mean weight of the Grenada bacula was 26.4 mg (observed range 2.0 to 55.8). A sample of 357 bacula from mongooses from St. Croix with adult dentition had a mean weight of 26.91 mg with a standard error of

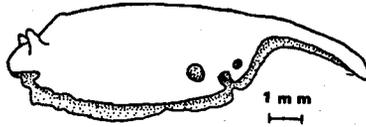


Fig. 21. The baculum of a mongoose.

0.54 and 99 percent confidence limits of 25.51 to 28.31. The observed range was 4.29 to 61.83 mg. The variation in baculum weight for immature animals at a given age is large. Baculum weights of 1.40 to 3.92 mg were recorded for mongooses determined to be 77 days old on the basis of tooth eruption. For animals 119 days old, baculum weights ranged from 3.44 to 6.29 mg. Two siblings raised together to 297 days old and having body weights of 566 and 625 g had bacula weighing 44.44 and 18.51 mg, respectively.

For the sample of 232 Grenadian individuals, the correlation coefficient (r) of baculum weight against baculum length is 0.896, a figure which is highly significant at the 0.001 percent level. For a further group of 86 Grenadian bacula, the correlation coefficient (r) for baculum weight (Y) compared with mongoose body weight (X) is 0.443, which is significant at the 0.001 percent level. The equation for the regression line expressed as units of Y milligrams and X grams is $Y = 2.38 + 0.03673X$. The orientation of this line is obviously biased by the greater number of weight recordings in the middle and upper range, as a baculum weight of 2.4 mg at birth is probably excessive. Baculum weights for mongooses weighing 100, 200, 300, 400, 600, 800, and 1000 g were calculated to be 6.1, 9.7, 13.4, 17.1, 24.4, 31.8, and 39.1 mg, respectively. It was thought that the regression line might have made age-class prediction in broad groups possible, but the residual variance (95 percent limits) about the regression line at 24.5 mg was too great to be meaningful.

In conclusion, full baculum size is probably not reached until the animal weighs at least 500 g and is over 5 months old. Bacula can probably be used only to segregate adults from immature animals, with lengths of less than 6.5 mm and weights of less than 14.3 mg being associated with immature animals.

5. — The weight of the lens of the eye in many mammals has been shown to increase throughout life at a decreasing rate. The weights of eye lenses

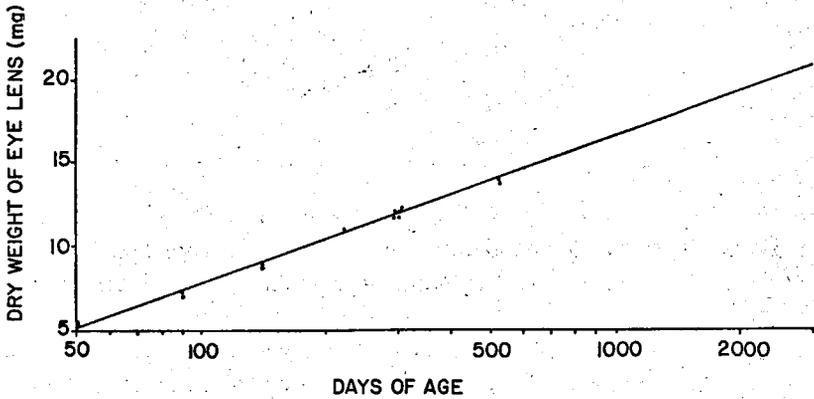


Fig. 22. Increase in weight of mongoose eye lenses with age.

from mongooses of known age from St. Croix were plotted against age in days by means of a log curve fit. The equation for the resultant regression line was $Y = 9.69 + 3.80X$.

The coefficient of determination (r^2) when the above equation is used is .99, indicating an excellent fit between the regression line and data points. Figure 22 shows the regression line plotted with data points and extrapolated to 3,000 days of age. This line should not be extrapolated below the data points at 50 days of age. The weight variation between lenses of individual animals was examined; of 106 animals in which both lenses were saved, the mean difference between the two lenses was 0.09 mg.

Lenses from an arbitrarily-selected sample of 73 female and 153 male live-trapped mongooses from Grenada were weighed. The mean weight of the lenses was $11.8 \text{ mg SE} \pm 5.2$ for females; and $12.7 \text{ mg SE} \pm 5.0$ for males. There is a significant difference between these two means at the 2 percent level ($p < 0.02$ but > 0.01). The standard error of the difference in the means is 0.3665. This difference in means could be a result of a difference in age distribution of the sexes.

Comparing mongoose body weight as an indicator of maturity with lens weight, the correlation coefficient (r) is 0.552 for males and 0.589 for females. Both figures are significant at the 0.001 percent level. Equations for the two corresponding regression lines are $Y = 7.37 + 0.00846X$ and $Y = 5.94 + 0.0140X$ for males and females, respectively. It appears that in both cases the predicted weights of the lenses at birth are probably too

high, a result of extrapolating from figures in the median and upper categories of the range.

The particular value of using eye lens weight as a technique for determining age lies in its potential for application to animals which have attained adult size, when most other techniques have lost their usefulness.

6. — The skull of the mongoose provides several characteristics useful in age determination. Tooth eruption of immature mongooses has been described by TOMICH & DEVICK (1970). We have confirmed the accuracy of their table which shows the full complement of adult teeth to be present at 22 weeks of age.

7. — Once the full adult dentition is attained, wear begins. We separated skulls into four categories of tooth wear.

Category 1 included all animals whose adult teeth had not fully erupted; ages of these animals were determined by means of data from TOMICH & DEVICK (1970). Eye lens weights were used to determine the absolute ages of animals in categories 2, 3, and 4.

Tooth wear category 2 contained all animals with adult teeth showing little or no wear. Males in this category varied in age (determined from eye lens weight) from 139 to 795 days, averaging 374 days. Females in this category ranged in age from 147 to 558 days, averaging 286 days.

Tooth wear category 3 contained animals whose teeth showed moderate wear. In this category, males averaged 610 days with a range of 290 to 1,368; females averaged 570 with a range of 332 to 1,000.

Tooth wear category 4 contained animals with very worn teeth, frequently worn to the gum line. Incisors and first premolars may be completely gone, the canines flat-topped stubs, and the entire body of the last premolars and molars may be completely worn away leaving only parts of the roots (Fig. 23). The mean age for males in category 4 was 1,289 days with a range of 607 to 1,755, the latter being the oldest animal in the study. Females averaged 873 days with a range of 595 to 1,350.

The large variation in tooth wear is probably due primarily to differences in individual food habits and preferences. A male and female maintained in captivity for over 2,500 days on relatively nonabrasive food still had teeth in wear category 2. Individuals whose diet includes large numbers of crabs or insects probably show the greatest tooth wear.

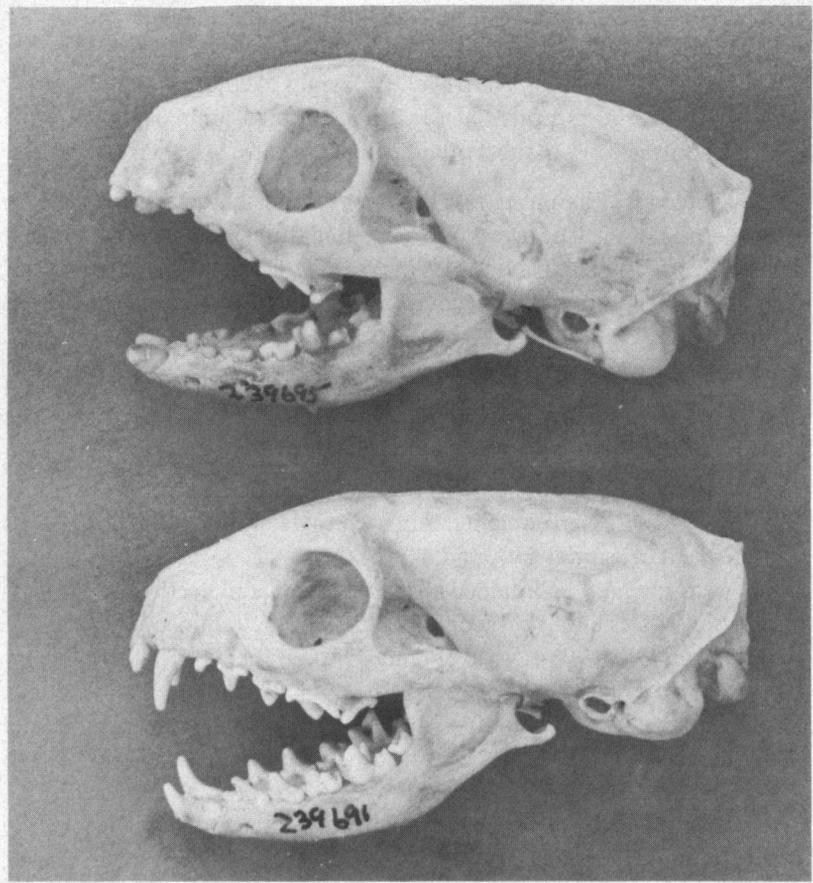


Fig. 23. Mongoose skulls showing tooth wear categories 2 (bottom) and 4 (top).

8. — It is known that incremental layers or annuli laid down in the tooth dentine or cementum can be used to determine age in certain mammalian species including the tropical vampire bat *Desmodus* (LINHART, 1973). Mongooses were investigated for annuli, although under natural conditions the life span of the mongoose is probably shorter than most animals to which this technique has been applied. Six canine teeth from five wild-caught mongooses were sectioned and stained in haematoxylin and eosin. As we could not detect any annuli, sections were sent to

LINHART who adjudged (pers. comm.) that in only one of six were some possible incremental growth lines present. CROWE (1972) used paragon stain successfully on bobcat teeth and agreed to process teeth from four mongooses. He found (pers. comm.) that the mongoose teeth appeared to have some annular deposition but that it was vague in most cases.

It seems unlikely that annuli would develop in captive animals that have not been subjected to the same environmental stresses and influences as those in the wild. Secondly, it is not known whether tropical terrestrial mammals develop growth lines similar to those of mammals in lands where seasonal changes are more pronounced. Periodic stresses such as the droughts in the Virgin Islands may produce growth lines on other than an annual basis.

9. — The closure of the skull sutures is known to occur at maturity in mammals. As the sutures close serially, the order and degree of closure were examined as a possible indicator of age. The order of closure of selected sutures in *H. a. auropunctatus* is: frontal-malar (touching), basioccipital-basisphenoid, median-palatine, median-nasal and frontal-parietal.

Table 9 shows that in a sample of 354 mongooses the median age at each suture closure is less for females than for males. While open skull sutures are a definite indicator of young or immature animals, this method is not sufficiently accurate to determine age precisely.

10. — The fusion of the epiphyses of the limb bones of mammals has been used by many investigators to determine approximate age. Epiphyseal fusion in the hind limb of the mongoose proceeds with the distal end of the tibia and proximal end of the femur fusing at the same time. The distal end of the femur and proximal end of the tibia then fuse simultaneously.

Table 10 shows that the epiphyses of females fuse before the equivalent epiphyses of males, and that, as in skull development, the series of events is useful for age determination only up to the age of 15 months. An example of age overlap in closure is provided by the greater trochanter on the proximal end of the femur. Of 12 females examined with this epiphysis open, 66.6 percent were less than 175 days of age. Of the 124 females examined with this epiphysis closed, 0.8 percent were less than 175 days. Of

TABLE 9
CLOSURE OF SKULL SUTURES IN *Herpestes a. auropunctatus* (N = 354)

Suture	Minimum age of closure (days)	Maximum age of closure (days)	Median age of closure (days)
<i>Female</i>			
Frontal-Malar (touch)	148	215	180
Basioccipital-Basisphenoid	180	268	220
Median palatine	188	400	300
Median nasal	194	520	279
Frontal-Parietal	194	410	335
<i>Male</i>			
Frontal-Malar (touch)	208	410	226
Basioccipital-Basisphenoid	180	426	275
Median palatine	244	538	361
Median nasal	275	540	386
Frontal-Parietal	275	596	470

TABLE 10
EPIPHYSEAL FUSION IN *Herpestes a. auropunctatus* FROM ST. CROIX

	Minimum age (days)	Maximum age (days)	Median age (days)
<i>Female</i>			
<i>Femur</i>			
Proximal end	165	210	175
Distal end	250	404	295
<i>Tibia</i>			
Proximal end	268	410	300
Distal end	168	204	170
<i>Male</i>			
<i>Femur</i>			
Proximal end	221	314	250
Distal end	276	566	484
<i>Tibia</i>			
Proximal end	275	566	485
Distal end	185	270	225

26 males with this epiphysis open, 69.2 percent were less than 250 days, and of 190 males with this epiphysis closed, 3.2 percent were less than 250 days.

The great utility of skull suture closure and epiphyseal fusion in age-grading lies in their application to specimens which are too severely decomposed for most of the other age determination techniques. Thus, even parts of specimens recovered in the field months after death can be assigned approximate ages.

ADULT WEIGHTS AND MEASUREMENTS

Of a sample of 873 trapped female mongooses from Grenada, 163 were pregnant. The pregnant mongooses ranged in weight from 301 to 853 grams with a mean of 480.3 g (S.E. 2.55) and 99 percent confidence limits of 471.9 to 488.7. If a normal distribution is assumed, 99.0 percent of the pregnant females weigh more than 301 g. In the non-pregnant sample of 710, 613 animals weighed over 305 g; if it is assumed that these are mature, the mean weight of adult non-pregnant females was 434.1 g (S.E. 3.40) (422.9 to 445.3 for 99.9 percent limits).

A sample of 406 females from St. Croix had only three females with adult dentition that weighed less than 305 g; thus, as in Grenada, this is probably a reasonable lower limit to weight to use as a criterion of maturity. A sample of 100 non-pregnant females with adult dentition had a mean weight of 432.9 g (S.E. 5.47). The range in weight observed in non-pregnant females with adult dentition was 252 to 662 g.

The range in weight of 38 non-pregnant Trinidadian females which weighed over 305 g was 315 to 640 g with a mean of 409.8 g. (S.E. 11.1). There is no significant difference between any of the groups of the females.

The weights of 552 male mongooses in Grenada were recorded. Fifteen animals (2.7 percent) weighed less than 300 g and were therefore considered to be immature. The remaining 537 animals had a mean weight of 661.8 g (S.E. 5.0). The calculated range for 98 percent limits would be 393 to 930 g. Outside the range covered by this sample 7 of 2,524 (0.28 percent) male mongooses weighed over 1,000 g; the heaviest animal weighed 1,049.5 g.

One hundred male mongooses with adult dentition from St. Croix had a mean weight of 640 g (S.E. 12). Of 519 males examined, the weight range of those with adult dentition was 396 to 1,221 g. The heaviest individual was abnormal in having become extremely obese through thieving at an egg farm. The heaviest normal male was 1,028 g.

TABLE 11
SKULL MEASUREMENTS IN CENTIMETRES OF MALE AND FEMALE *Herpestes*
FROM ST. CROIX

	Mean	Standard error	Range	
			Minimum	Maximum
<i>Female</i>				
Condylobasil length	6.182	0.002	5.908	6.456
Zygomatic width	3.032	0.010	2.839	3.206
Toothrow width	1.923	0.008	1.792	2.072
Braincase width	2.210	0.007	2.088	2.310
Postorbital constriction	1.052	0.011	0.903	1.285
Rostral width	1.075	0.006	1.001	1.210
<i>Male</i>				
Condylobasil length	6.648	0.022	6.344	6.935
Zygomatic width	3.419	0.018	2.982	3.639
Toothrow width	2.064	0.011	1.923	2.243
Braincase width	2.344	0.010	2.134	2.467
Postorbital constriction	1.093	0.011	0.927	1.285
Rostral width	1.189	0.007	1.082	1.310

Forty-five Trinidadian male mongooses over 300 g ranged in weight from 437 to 863 g with a mean of 641.5 g (S.E. 16.6).

In summary, the data from all islands indicate sexual dimorphism, with females reaching sexual maturity by about 305 g and averaging 434 g as adults. Most males are mature at 395 g and weigh about 650 g as adults.

The total length (excluding tail-tip hair) of 100 females from St. Croix with adult dentition ranged from 50.9 to 57.8 cm with a mean of 54.0 cm (S.E. 0.15). One hundred males had a mean total length of 59.1 cm (S.E. 0.23), and an observed range of 54.4 to 67.1 cm.

The head and body length (excluding tail) of 246 female mongooses from Grenada ranged between 21.4 and 38.5 cm (mean 30.3 cm), S.E. 5.5. The range of head and body length in 739 male mongooses was 22.2 to 44.6 cm (mean 34.0 cm), S.E. 5.3.

Head and body length (excluding tail) of 45 Trinidad males ranged from 25.0 to 39.5 cm with a mean of 34.7 cm (S.E. 4.1). The head and body of the 38 Trinidadian females ranged from 22.9 to 37.2 cm with a mean of 30.9 cm

(S.E. 6.2). A comparison with the Grenadian means showed no significant difference.

Hind foot length of 100 females with adult dentition from St. Croix ranged from 4.9 to 5.8 cm with a mean of 5.3 cm and a standard error of 0.019. Males ranged from 5.3 to 6.6 cm, with a mean of 5.9 cm and a standard error of 0.023.

Samples of 50 skulls from each sex with completely fused sutures were measured with a dial caliper reading to 0.005 cm. Readings were interpolated to 0.001 cm. The results are shown in Table 11 and demonstrate the trend towards sexual dimorphism but with a consistent overlap of features between the sexes. Male skulls tended to have more conspicuous saggital and lambdoidal crests, and the brain case tended to be more flattened dorsally; however, these characteristics could not be used consistently as a basis for differentiating the adult skulls of the two sexes.

FOOD AND FEEDING HABITS

Herpestes a. auropunctatus is an omnivorous carnivore and by choice preys on small rodents and birds. However, as a mongoose population eliminates the easily available components of this food source, it then turns to other vertebrates and arthropods, principally lizards and Orthoptera.

The fact that the mongoose has sharp angular molar cusps and thoroughly chews its food, renders studies on its food habits difficult. Nevertheless, some excellent work has been completed, although our own work has been limited to general observations. Some of the most notable reports are the following.

WILLIAMS (1918) in Trinidad compared the food habits of mongooses living in cacao plantations (forests) with those in sugar plantations. He found 22 rats in 118 stomachs on the sugar estates compared with three in 48 stomachs in the cacao districts. This difference may have been due to there being a greater number of rats in the sugar districts, but the greater facilities for escape afforded to the rats by the trees in the cacao districts will also have affected the result. He further found that the total number of birds ingested was relatively higher in the cacao districts, but this finding was entirely due to the greater numbers of domestic fowl around the numerous small houses of the cacao plantation than were present on the sugar estates. The number of frogs and toads destroyed was relatively much higher in the sugar districts than in the cacao, while the number of snakes destroyed was relatively higher in the cacao districts.

WOLCOTT (1953), an entomologist, examined the stomach contents of 42 mongooses shot on St. Croix and 56 collected from a similar habitat at Roosevelt Roads, Puerto Rico, and found a variety of items including rats, mice, frogs, lizards, snakes, crabs, centipedes, spiders, and six orders of insects of which the Orthoptera, Coleoptera, and Diptera were most common.

PIMENTEL (1955a), in an analysis of mongoose stomachs from Puerto Rico, reported: "Of a total of 315 specimens in the 56 stomachs, 88.9 percent were animal and 11.1 percent plant material. Insects made up 56.4 percent of the animal specimens and the remainder included: reptiles 17.1, myriapods 12.1, arachnids 7.9, mammals 2.9, crustaceans 1.4, asteroids 1.1, and amphibians 1.1 percent." PEMBERTON (1933) and KAMI (1964) found similar results in Hawaii.

SEAMAN (1952) reported that "a breakdown of the foods found in 36 mongoose stomachs. . shows":

Lizards	0.5%	Poultry	2.8%
Toads	13.9%	Insects	83.0%
Mice	13.9%	Crabs	11.1%
Rats	13.9%	Fruit	11.1%
Birds	2.8%	Vegetable matter	5.5%

In 1962 SEAMAN & RANDALL published a further report on the mongoose as a predator with dramatic accounts of mongoose preying on deer fawns.

During field work in the past years, we have gained the general impression that mongooses are very opportunistic foragers. When living near the sea, crab remains are a conspicuous component of stomach contents.

On St. Croix, while studying the circadian activity patterns of mongooses visiting a feeder in dry weather, several days of heavy rainfall in the area produced a lush growth of vegetation and a related increase in insect populations. During this period, feeder visitations dropped from about 15 per hour in daylight hours to less than one per hour. When certain fruit trees such as mango (*Mangifera indica*) or hog plum (*Spondias mombin*) are in fruit, mongooses are abundant in the vicinity, feeding both on the fallen ripe fruit and on the insects attracted to it.

Although mongooses are generally considered to be strictly terrestrial, they have been seen to climb into low bush-like trees when seeking ripe fruit of soursop (*Annona muricata*) and sugar apple (*Annona squamosa*). Guava (*Psidium guajava*) grows vigorously on St. Croix and is frequently a serious nuisance brush plant in pastures. When guava is fruiting, it is rare to find a ripe fruit left which is within reach of a mongoose. Contrary to other reports, we have found that some mongooses are very willing to eat papaya (*Carica papaya*). GORMAN (1975) reports that most scats of mongooses in the Fijian islands contain seeds of papaya or guava. Papaya fruit made up half of the diet of the captive animals on St. Croix for three years. However, some wild-caught animals refused papaya at first, but later would eat it. Under natural conditions, depredations by fruit bats probably prevent most papaya from becoming available to mongooses.

With their omnivorous food habits, mongooses are a potential pest to agricultural crops. In addition to native fruits, mongooses in captivity will readily eat tomatoes, sweet peppers, ripe bananas, okra, corn, cabbage, and chunks of pineapple, but they usually will not eat citrus fruits. It seems that a combination of parental training and a preference for animal food have prevented mongooses from feeding on crops. One can hypothesize, however, that if mongooses supplement their diet with crops at times of drought or when conventional food sources are scarce, the habit of eating crops might be passed on to other mongooses by food envy, and to future generations by maternal training and learning.

An example of the opportunistic feeding of mongooses was noted on a construction site in Grenada, where 20 to 30 workers threw the remains of their lunch down a steep wooded hillside over a period of a few weeks.

Following an attack on one of them by a rabid mongoose, removal-trapping was instituted and 27 mongooses were caught in the area on the first day. These animals had presumably been eating the discarded food.

A further example of opportunistic feeding was seen at a St. Croix egg farm where hens were maintained in small wire cages with sloping bottoms which allowed the eggs to roll to the front of a rack for periodic collection. Several persons reported that mongooses would jump up on the rack, pick up an egg with one front leg and jump to the ground, carrying the egg to a place of cover for consumption. Mounds of egg shells were found under a pile of scrap lumber adjacent to the premises. In five days at this egg farm, 37 mongooses were trapped and removed, including the fattest individual (1221 g) ever collected on St. Croix. This extremely obese mongoose was an old male with very worn teeth; he quite possibly began eating eggs after it became difficult to capture other prey. Mongooses do not suck eggs as is commonly believed. A mongoose can open its jaws sufficiently wide to encompass an egg with its canines. It then punctures the egg and licks the contents. When a mongoose has completely consumed an egg, the shell is in very small fragments in a limited area, almost as though the egg had been stepped on.

Studies on food habits show that centipedes can make up a fairly large proportion of a mongoose diet. These centipedes (primarily *Scolopendra subspinipes*) are capable of inflicting a very painful and poisonous bite. On first seeing a centipede in the open, a mongoose swiftly approaches, bites the centipede in the head, and flings it aside. The bite and toss are extremely rapid and do not allow the centipede sufficient time to give a retaliatory bite. The mongoose immediately rushes to the new location of the centipede and repeats the bite and toss. After four or five bites, when the centipede has become incapacitated, the mongoose picks it up by the head and munches rapidly down the entire length of the body, generally causing the centipede to stop writhing. Once the centipede is relatively immobilized the mongoose eats it, beginning with the head. If a mongoose uncovers a centipede while digging, or if it takes refuge under litter, the mongoose unhesitatingly scratches it out into the open with its long claws. Millipedes are totally rejected.

Snakes are also potentially retaliatory prey items in the mongoose diet. The behaviour of mongooses faced with a pugnacious snake was studied with large brown water snakes (*Natrix taxispilota*) captured in Florida and transported to the Virgin Islands. Encounters of mongoose and snake took place in a glass-fronted box (0.6 × 1.2 by 0.6 metres high). Several early encounters were recorded on cinematographic film, but as the mongooses became more adept at dispatching snakes, the action was frequently over before the filming could be initiated.

When first encountering a snake, the mongoose weaves back and forth and is extremely intent on the snake, paying particular attention to the head. Any sudden movement of the snake results in great excitement in the mongoose. When the mongoose finally attacks the snake, a bite is directed at the base of the snake's skull. GREGORY & HELLMAN (1939) state, "Such is the dental apparatus of these famous snake killers, eminently fitted to inflict small but grievous bites in the head of serpents." The mongoose tenaciously hangs on despite the writhing or thrashing of the snake. A mongoose which has never seen a snake will show a general interest in it, sniffing all parts of its body, but when the snake begins to move, the mongoose becomes very alert. Any rapid movement on the part of the snake incites attack from the mongoose. After the mongoose has had the opportunity to kill several snakes, mere exposure to a snake, even in a lethargic condition, is adequate to incite kill behaviour. In this case the mongoose warily approaches the snake and attacks the head at the first opportunity. In Martinique the speed and accuracy of this attack is regularly demonstrated to tourists in staged contests between a mongoose and a large (over 1.5 metre) fer-de-lance (*Bothrops atrox*) described in detail by PINCHON (1967). The mongoose is almost never envenomed by the snake, either before the attack or later while the snake is furiously lashing about. This attack, directed at the base of the skull, seems typical of that on several other prey items.

When exposed to live rats (*Rattus rattus*), even inexperienced mongooses will invariably direct a killing bite at the base of the skull. This killing bite is generally associated with a very firm hold on the rat. When attacking birds, the killing bite is also directed at the base of the skull, but inexperienced animals may grip the neck.

In the case of snakes, rodents, and birds, feeding normally begins on the head with special attention being paid to the brain, possibly because blood

from the killing bite is present. When mongooses are given uninjured rats which have been killed by an injection of succinyl choline chloride, feeding may begin at either the head or the abdomen, but usually at the head. Mongooses consume the entire prey if hungry, but if near satiation, they discard skins of rats or snakes. Birds are entirely consumed except for the feathers.

It is not unusual to observe mongooses eating parts of road-killed or live *Bufo marinus*. While driving down a gravelled road in St. Croix, NELLIS observed a mongoose which was attacking a large, live, but apparently slightly injured, *Bufo*. Returning to the site, he observed the mongoose in some tall grass eating from the hind legs of the still struggling toad. Eventually, the mongoose noticed the observer's presence and ran deeper into the bushes, leaving the toad which began to make its way off into some thick vegetation. At this point the observer moved the toad to the centre of the road and stepped back into the bushes. Shortly afterwards, the mongoose came forward and resumed its attack upon the toad, eventually carrying it back into the tall grass. The toad was removed to open ground three times before the mongoose eventually carried it deeper into the bushes out of sight. In final observations of this event it was noted that the toad was moribund, most of one hind leg had been completely consumed, and the second hind leg had been severely chewed. The entire anterior half of the toad was untouched and seemed uninjured. It would thus seem that when mongooses do on occasion prey on *Bufo*, they may try to avoid the toxic secretions of the parotid glands by eating only the nontoxic parts of the toad.

BALDWIN, *et al.* (1952) state that mongooses consume entire *Bufo marinus* with impunity, and GORMAN (1975) found remains of toads in scats from all habitats which contained toads in Fiji. On Grenada, five mongooses were given toads on four successive days while the normal diet was withdrawn. One animal born in the laboratory and which had never encountered toads refused to eat them. The other four animals ate all 16 toads presented without showing any adverse effects. Some ate the toad including the skin, while others opened the abdomen and ate the viscera, head and limbs, but they discarded the skin and body carcass. Domestic cats ignore these toads, and dogs that bite or eat them suffer to a greater or lesser extent with extreme salivation, buccal irritation, vomiting and

sometimes death. How mongooses can consume these noxious creatures without harm remains to be investigated.

We have found that mongooses are unable or perhaps unwilling to prey upon adult land crabs (*Cardisoma guanhumi*). This conclusion is reached after these crabs were introduced to caged mongooses and remained unharmed, even sharing the mongooses' food for several days at a time. These crabs live in large holes which would easily admit a mongoose; yet, in areas which are not easily accessible to humans, the crabs thrive in the presence of mongooses. Possibly the *Cardisoma* remains found in a mongoose stomach (WOLCOTT, 1953) were derived from carrion or were misidentified. Small specimens of coconut crabs (*Gecarcinus lateralis*) are preyed upon to the extent that they maintain large populations only in areas rarely frequented by mongooses, such as the vicinity of houses with dogs. The large adults with carapace widths over 4 cm seem exempt from mongoose attack.

The adults of the large, heavily armoured, terrestrial hermit crab (*Coenobita clypeatus*) are also resistant to mongoose predation. They are commonly found everywhere on the islands and at times are extremely abundant during their annual migrations to the sea. Ghost crabs (*Ocypode quadrata*) and rock crabs (*Grapsus grapsus*) maintain normal populations along the coasts, avoiding mongooses by their rapid retreat. Small immature crabs of various species living among the flotsam on beaches are very susceptible to mongoose attack; the contents of digestive tracts from mongooses collected near beaches are often composed entirely of remains of small crabs. RIVERS (1948) reports co-operative crab-hunting by mongooses in Hawaii.

Of the two large molluscs found on Grenada, mongooses do not eat *Strophocheilus oblongus*, but they do eat the more fragile-shelled *Oxystylus* species.

The hunting behaviour of mongooses varies immensely depending on the species sought. Mongooses dig vigorously for beetles and grubs in appropriate substrates. When a lizard is sighted in an exposed position, it is attacked with a headlong rush. It is not unusual to see a mongoose run more than a metre up the side of a tree or a fence post in pursuit of a lizard. However, when approaching a bird on the ground, a mongoose uses a

stalking pattern very similar to a felid, using all cover available and approaching in a low slink ("*Herpestes*" is derived from the Greek word for creep) with a final attack. This is seldom successful, and adult mongooses frequently give up the pursuit of certain birds. In an area where a pack of hunting hounds were fed, dog food was frequently scattered on the ground. It was not unusual to see mongooses and doves (*Zenaida aurita*) feeding on this dog food within two metres of each other. Approaches to within one metre occasionally occurred before the doves showed signs of uneasiness.

Mongooses are also attracted to bat roosts. The chittering of bats in a large colony probably lures mongooses to the vicinity. Once in the roost, they have access to multiple food sources. In addition to the occasional sick, injured or immature bats which drop to the ground, coprophagous insects attracted to the bat guano are available. In feeding trials, mongooses eagerly attacked, killed and consumed both *Artibeus* and *Brachyphylla* bats.

PHYSIOLOGY

ENERGY REQUIREMENTS

The energy requirements of mongooses were determined by the study of two captive-born specimens (male and female 2-year-olds) maintained in large aquaria on St. Croix as previously described. The animals were weighed to the nearest gram before and after the studies.

Two experiments were undertaken, during both of which the animals were maintained on a diet composed of equal parts by weight of raw pork liver and peeled ripe papaya. NELLIS had previously found that this diet would maintain the animals in good health for long periods of time without the need for additional water. Food was weighed before being placed in the cages. Faeces were removed twice daily, air-dried, and stored in envelopes for later analysis. In the laboratory, faeces were dried at 50°C in a vacuum oven, then ground in a Wiley mill to 60 mesh. After further drying in a desiccator, they were pelletized and burned in a Parr adiabatic bomb calorimeter. Samples from three papayas were freeze-dried and then treated in the same way as the faeces.

Papaya was found to have a mean water content of 85.9 percent and a caloric value of 509 calories per gram wet weight. Pork liver has a caloric value of 1310 calories per gram and a water content of 71.6 percent (WATT & MERRILL, 1963).

The first experiment had many problems. Mice were suspected of eating and carrying away the faeces which were being dried. A mongoose managed to jump into the drying tray and scatter the faeces, resulting in a probable loss of material. When the faecal material was ground in the Wiley mill, a sand-like residue remained which could not be ground to pass through the 60 mesh screen and was excluded from the sample burned in the calorimeter.

The second experiment progressed more satisfactorily. The sand-like residue in the Wiley mill was mixed thoroughly with the ground material before being pelletized for the calorimeter, and no material was lost to other influences. The results of the experiments are shown in Table 12. As expected with a reduced quantity of faeces, the calculated caloric requirements per day were higher in the first experiment. The data in the Table are all biased somewhat high because the caloric value of the urine excreted has not been subtracted from the total. These findings of a mean energy

TABLE 12
 METABOLIC REQUIREMENTS OF *Herpestes a. auropunctatus* ON A DIET OF
 LIVER AND PAPAYA

Measurement	Experiment 1		Experiment 2	
	Male	Female	Male	Female
Weight (grams)	753	440	745	425
Duration of study (days)	17	17	10	14
Kcal papaya consumed	551.8	378.4	328.7	276.3
Kcal liver consumed	1473.5	1013.4	845.0	708.3
Kcal faeces	122.3	112.1	97.8	86.3
Weight gained (grams)	15.7	4.9	13.5	8.8
Kcal* consumed in weight gain	109.9	34.3	94.5	61.5
Kcal/kg/day metabolized	139.9	166.5	131.7	140.5
Grams water** consumed per day	102	70	101	61

* Based on caloric value of 7 Kcal/g of animal fat (WATT & MERRILL, 1963).

** Based on percentage of water in diet consumed (WATT & MERRILL, 1963).

consumption of 144 Kcal/Kg/Day compare reasonably with the subsequent work of LIN & KOBAYASHI (1976) and EBISU & WHITTOW (1976). LIN & KOBAYASHI (1976) found a resting oxygen consumption of 16.9 ml/min/Kg. If production of 4.8 Kcal per litre of O₂ is assumed, the resting metabolic rate would be 116.81 Kcal/day/kg. Similar calculations from the results of EBISU & WHITTOW give a resting metabolic rate of 76.03. Both of these findings are values for animals at rest, whereas ours are for animals given daily exercise. We would attribute the difference in values to the energy used in daily activity.

KLEIBER (1961) presented the formula $M = 70W^{0.75}$ where M is the metabolic rate in kilocalories per day and W is body weight in kilograms. When applied to a mongoose of 650 g, this formula predicts a lower metabolic rate of 50 Kcal per day. The cardiac output of 334 ml/min/kg found by LIN & KOBAYASHI is also higher than expected for other mammals of similar size. The intense, vigorous nature of the mongoose thus seems to be supported by a metabolic rate higher than that of other animals of equivalent size.

Stores of reserve energy to support such a high metabolic rate would seem to be a necessity, but fat deposits would hamper the agile sinuous movements required to capture active prey in thick cover. Evolutionarily

TABLE 13
EXTRACTION OF TAIL AND BODY FAT FROM *Herpestes a. auro punctatus*

Specimen number	Sex	Body fat index	Tail fat index	Ratio	
				Body fat index	Tail fat index
960	Male	44.01	121.84	1:2.77	
961	Female	20.17	148.29	1:7.35	
962	Female	32.63	88.35	1:2.71	
963	Female	22.38	103.20	1:4.61	
964	Male	59.55	179.83	1:3.02	
Mean				1:4.09	

the mongoose seems to have solved the problem by depositing fat reserves in the thick, strongly tapered muscular tail. To quantify this general impression, we sent five mongooses to the University of Georgia Institute of Ecology laboratory where fat extractions were performed by SUZANNE BEST. Various tissues of the mongoose were extracted with a 5:1 solution of petroleum ether-chloroform. Results were expressed as a fat index, i.e. the ratio of extracted fat to 100 g of lean dry residue after extraction.

Data shown in Table 13 demonstrate that results were variable but that the tail always had more than twice the fat content of the rest of the body. In one instance, it had over seven times the concentration. The mean ratio of body fat index to tail fat index was 1 to 4.1.

THERMAL TOLERANCE

The concentration of fat in the tail rather than over the whole body also reduces the body insulation and allows greater heat dissipation at the expense of reduced cold tolerance. Thermal tolerance in *Herpestes* has been investigated by NELLIS & MCMANUS (1974) and EBISU & WHITLOW (1976). As might be expected of a small elongate mammal with no under-fur, the thermoneutral zone is quite narrow. The normal body temperature of 39.5° C is maintained by an increased metabolic rate as the ambient temperature drops below the thermoneutral zone of 28 to 38° C. At 5° C the metabolic rate increases by a factor of 3, but as the environmental temperature falls to 0° C the metabolic heat production is unable to

compensate for increased heat loss, and the body temperature begins to fall. Lengthy exposure to temperatures of -9°C results in frost damage to the extremities, or even death. Mongooses react to low temperatures by decreasing their activity and by curling into heat conserving postures, with the tail and feet drawn towards the body and the snout pressed against the ventral surface. Tolerance of high environmental temperatures is limited by poor body insulation and limited cooling mechanism. The resting respiratory rate of mongooses is 63 per minute and the heart rate is 252 per minute. As the ambient air temperature is raised the mongoose begins to pant, and as stress increases it assumes a heat dissipating posture, lying prone with limbs extended. The heavy salivation accompanying panting saturates the snout and gular areas only. We have seen no evidence that mongooses sweat. At rectal temperatures of 40°C and above the respiratory rate may exceed 500 per minute during the panting associated with high heat stress. MATSUURA *et al.* (1977) found that the increase in respiratory frequency was associated with an increased minute volume but that the tidal volume diminished. As might be expected with such rapid panting, the respiratory evaporative heat loss increases dramatically. The total evaporative water loss may increase by as much as a factor of 3 under high heat stress (EBISU & WHITTOW, 1976). Heat stress seems to be extreme at air temperatures of 45°C , as two of four mongooses died soon after a 2-hour exposure to this temperature. When exposed to direct midday sunlight in a wire cage on St. Croix, heat stress became evident after 15 minutes or less in an ambient air temperature of 33°C . Thus, traps should always be located in the shade. Mongoose habitat must have consistently available shade in the tropics and can probably extend poleward to the 10°C mean winter isotherm. In the Americas, this would extend from the Gulf coast states of the U.S.A. south to the Argentine pampas near Buenos Aires.

MILK COMPOSITION

We have not been able to find any reference in the literature to the composition of viverrid milk. To correct this deficiency we collected samples of milk from a captive 19-day postpartum female and a wild-caught lactating female. The milk was manually expressed while the mongooses were under light ether anaesthesia. Milking was further assisted by the intramuscular injection of oxytocin. The milk was im-

TABLE 14
CONSTITUENTS OF MILK FROM *Herpestes a. auropunctatus*

Total solids (percent)	24.3	Fatty acid composition	
Ash (percent)	1.1	Short chains (percent)	1.0
Lactose (percent)	2.4	Palmitic (percent)	21.8
Protein (percent)	8.9	Palmitoleic (percent)	4.2
Fat (percent)	12.0	Other long chains (percent)	4.2
Citrate mg/100 ml	180	Unknown (percent)	1.6
Calcium mg/100 ml	202	Stearic (percent)	9.1
Phosphorus mg/100 ml	161	Oleic (percent)	45.0
NPN mg/100 ml	210	Linoleic (percent)	13.1

mediately sealed in a glass vial and held frozen until delivered to ROBERT JENNESS of the University of Minnesota who performed the analysis using standard techniques as discussed by JENNESS & SLOAN (1970).

The mean values of the results are shown in Table 14. The gross analysis is not greatly different from that found for other fissipede carnivores, the

TABLE 15a
CHARACTERISTICS OF THE WHOLE BLOOD OF ADULT MALE
Herpestes auropunctatus
taken from PALUMBO & PERRI, 1974.

Whole blood characteristics (Adult males)	Mean	Standard deviation
PCV (%)	48	± 4
Haemoglobin (g/dl)	14.7	± 1.2
WBC/cmm × 10 ³	10.4	± 2.2
RBC/cmm × 10 ⁶	11.6	± 0.1
Eosinophils	0.42	± 0.80
Basophils	0.00	± 0.00
Juvenile neutrophils	0.00	± 0.00
Band neutrophils	3.37	± 1.38
Segmented neutrophils	53.06	± 7.05
Lymphocytes	42.35	± 8.48
Monocytes	0.84	± 0.75
Platelets	100% adequate	

closest resemblance being to that of the genus *Mustela*. The milk fat composition is also similar to that of other carnivores. The principal sugar is lactose with a significant amount of inositol and traces of glucose and galactose. The gel electrophoretic pattern of whey proteins differs from that for milk of other carnivores in that it indicates fewer proteins.

TABLE 15b
CHARACTERISTICS OF THE SERUM OF *Herpestes a. auropunctatus*
taken from LENZ & NELLIS & HABERZETTL, 1976

Serum characteristics	Mean	Standard error
Glucose (mg/dl)	104	13.1
Triglycerides (mg/dl)	41	5.3
Cholesterol (mg/dl)	247	9.9
BUN (mg/dl)	49.5	7.78
Uric acid (mg/dl)	2.6	0.26
Creatinine (mg/dl)	1.3	0.07
Total bilirubin (mg/dl)	0.5	0.06
Direct bilirubin (mg/dl)	0.2	0.02
Sodium (mEq/L)	164	1.1
Potassium (mEq/L)	6.4	0.3
Chloride (mEq/L)	125	1.4
Calcium (mg/dl)	9.7	0.14
Phosphorus (mg/dl)	5.8	0.276
Magnesium (mEq/L)	2.6	0.12
Iron total (μ g/dl)	114	16.9
Specific gravity	1.035	
Total solids (%)	9.9	0.21
Osmolality (mosmol/L)	367	5.4
Freezing point depression	0.683	
Total protein (g/dl)	7.6	0.18
Albumin (g/dl)	2.7	0.06
alpha-1 globulin (g/dl)	0.6	0.013
beta globulin (g/dl)	1.6	0.015
gamma globulin (g/dl)	2.2	0.07
Lactic dehydrogenase (IU/l@ 30°C)	1528	253.3
alpha-hydroxybutyrate dehydrogenase (IU/l@ 30°C)	1119	164.4
Glutamate-oxalacetate transaminase (IU/l@ 30°C)	139	25.6
Glutamate-pyruvate transaminase (IU/l@ 30°C)	161	18.0
Creatinine phosphokinase (IU/l@ 30°C)	847	142.0
Alkaline phosphates (IU/l@ 30°C)	25	2.4

BLOOD CHARACTERISTICS

The characteristics of the blood of mongooses are not profoundly different from those of other carnivores and can be compared to those of the palm civet, *Paradoxurus hermaphroditus* (RAMAKRISHNA & NAIR, 1971). The results of standard laboratory blood tests are shown in Table 15. HINSLEY & YOKOYAMA (1970) found that mongoose blood can be divided into three groups according to the presence of isoagglutinogens or isoagglutinins. The presence and pattern of agglutinins compared with human blood groups indicate that mongoose blood has antigenic properties similar to the human ABO blood group substances. LENZ *et al.* (1976) found a high serum osmolality which was due partly to the occurrence of high concentrations of sodium and urea nitrogen attributed to the urine concentrating mechanism in the mongoose kidney.

OTHER ORGAN SYSTEMS

The mongoose was found to be capable of achieving a urine concentration greater than 4,500 mosmoles when deprived of water. This value is higher than expected for carnivores, but the ability to concentrate urine to this degree is certainly advantageous to a mongoose in its normally preferred arid habitat. The kidney shows some rather unusual anatomical specializations. It is unilobular with a single papilla, but the length of the papilla and relative medullary thickness are not as great as one would predict from the maximum urine concentrations found. The renal arterial supply is conventional, but the venous drainage is unusual in that the cortex and medulla have separate venous outlets. After leaving the efferent glomerular arteriole, one encounters the typical capillary bed, but rather than coursing deep into the medulla as vasa rectae, many of these capillaries drain by a series of even larger vessels towards the surface. Immediately subjacent to the capsule these veins form a network on the cortical surface, reaching the hilus before entering the renal veins. The medulla has typical venous drainage. This separation of cortical and medullary drainage (present in some felids) may enable the mongoose to maintain higher concentration gradients in the kidney and hence achieve higher urine concentrations than possible for more typical kidneys of similar dimensions (HORST *et al.*, 1975). Other sources of water loss are minimized to the extent that captive mongooses with no drinking water are able to exist without any perceptible dehydration. On a diet of fruit and

raw liver, the mean ratio of water intake to body weight per day, based on the water content of the food, is 0.1512 for the female and 0.1355 for the male (NELLIS, 1973). These figures can be compared with 0.106 for *Dipodomys* and 0.230 for the carnivorous desert mouse *Onychomys* (BOICE, 1972).

Mongoose adrenals are anatomically similar to those in the dog and cat and may be typical of those in the order Carnivora. The right gland is about 80 percent of the size of the left. The relative weight of the adrenals decreases in all age and sex classes as body weight increases. Adrenals are only slightly larger in young females than in young males, but at sexual maturity they enlarge greatly in females and remain much larger than those in males. In lactating females the adrenals are significantly larger than those in all other classes of adult females (MCKEEVER & TOMICH, 1963). Sexual maturity seems to have no major effect on adrenal gland size in males. The weight of the adrenal glands seems to show a remarkable stability to environmental stress (TOMICH, 1965).

Ulcers caused by acute gastric stress in mongooses were presumed to be attributable to trapping, but the presence of healing ulcers suggests that ulceration also occurs in the wild (STEMMERMANN & HAYASHI, 1970).

Mongooses in the wild are able to recover from major traumatic injuries and continue to maintain good condition. On St. Croix, animals with missing tails or a front or rear foot, or with fractured femurs, all seemed to have well-healed wounds and normal body weight. *Acacia* thorns lying against the skull at the base of the masseter muscle were common, and fragments of a carabid beetle were found in a healed wound of the masseter in one specimen.

Albinism does occur in mongooses. NELLIS observed an almost white individual on St. Croix, and other residents of St. Croix and St. Thomas have reported albinism. A local calypso also concerned a white mongoose. On Trinidad a pale ginger mongoose has been captured. Total melanism has not been seen, but dark plumbaceous individuals occur. The muzzle of old animals may become grizzled.

MONGOOSES AS FOOD

The mongoose as a food source seems to have been widely but not completely overlooked. Among the Pedi tribe of South Africa the consumption of viverrids is confined to men and boys, who claim they are very

tasty (QUIN, 1959). JARDIN (1967) mentions that mongooses are eaten sporadically in other areas of Africa. Both as a possible food source and as a potential control measure, the consumption of mongooses has been promoted in the Virgin Islands. A group of young mongooses were dressed, frozen and delivered to the Consumer Evaluation Division of the U.S. Department of Agriculture, where a tasting panel found mongoose flesh to be comparable to chicken or veal. Recipes suggested for mongoose preparation were then distributed to the public at an agricultural fair on St. Croix. Subsequent international food fairs on St. Thomas have featured mongoose, which has proved to be a popular dish, but it has not yet become a commonly consumed item in the Virgin Islands.

BEHAVIOUR

CIRCADIAN ACTIVITY

Daily activity patterns of captive mongooses were determined with a red light beam which bisected the living space of the mongooses, and a photocell. Interruption of the light beam activated an electric counter which totalled and printed the results once an hour. A similar apparatus was used to monitor the visits of wild mongooses to a feeder. Our captive mongooses were found to be diurnal, but they became active if disturbed by lights or other activity at night. They also tended to be late risers and could often be found in a sleeping posture as late as an hour after sunrise. The wild mongooses were found to be strictly diurnal in their visits to the food source. The first feeder visits of the morning began when the ambient light level reached 5 footcandles, and the final visits of the afternoon occurred at about the same light level.

These observations confirm and complement the detailed experimental work of KAVANAU (1975) who found captive *Herpestes* to be most active from 10:00 to 16:00 h. Over 99 percent of the mongooses' total activity was diurnal, with the balance at twilight, and no activity was recorded at night. The diurnal nature of the mongoose is further demonstrated by DÜCKER (1959) who found that histologically *Herpestes* has rods and cones and experimentally shows colour vision.

In the course of other duties, NELLIS was frequently active in the field at night using spotlights. Even on bright moonlit nights, mongooses were never seen more than an hour after sunset. However, movement at night has been recorded in Grenada and is indicative of rabies, as are other aberrant behavioural patterns.

POSTURES AND MOVEMENTS

The normal gaits of a mongoose are a fast walk or trot, but when in the open away from cover, a low slink is used (Fig. 24) in which the head, trunk and tail are held less than a centimetre from the substrate, and forward progression is by a series of dashes interspersed with periods of immobility. The body is not elevated during the dashes. The gallop is seldom used except when an animal is startled at some distance from cover. When in thick short grass, the mongoose moves through it sinuously rather than bounding over it. When in cover more than 10 cm high, the mongoose may

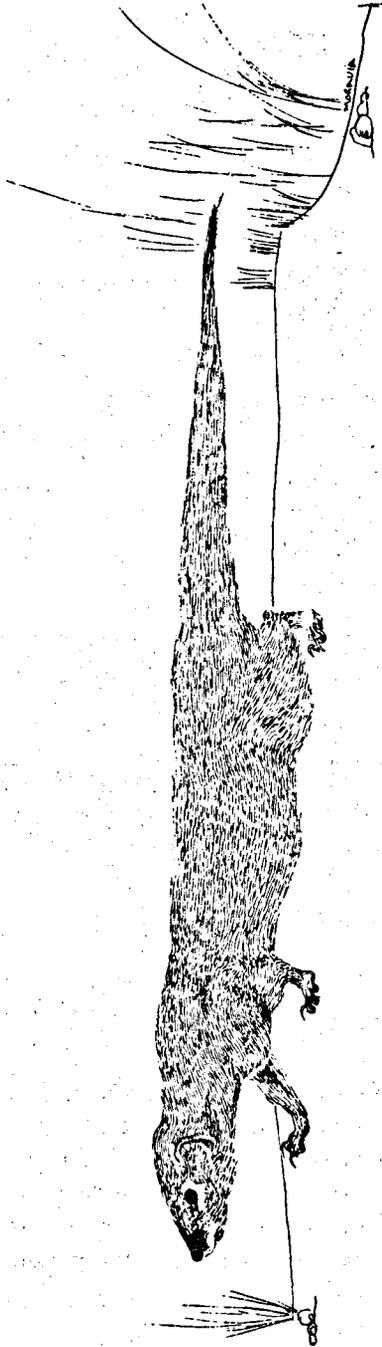


Fig. 24. Low slinking gait of a mongoose.



Fig. 25. Mongoose in low sit posture.

sit erect on its hindquarters ("low sit" of EWER, 1963b) (Fig. 25), while if in taller grass, or very curious, the mongoose may stand bipedally erect (high sit Fig. 26). Commonly in the two erect postures, and occasionally in other stances, the mongoose will weave its head from side to side while staring fixedly at an object. We attribute this to the need to extend the visual parallax base for improved distance and depth perception.

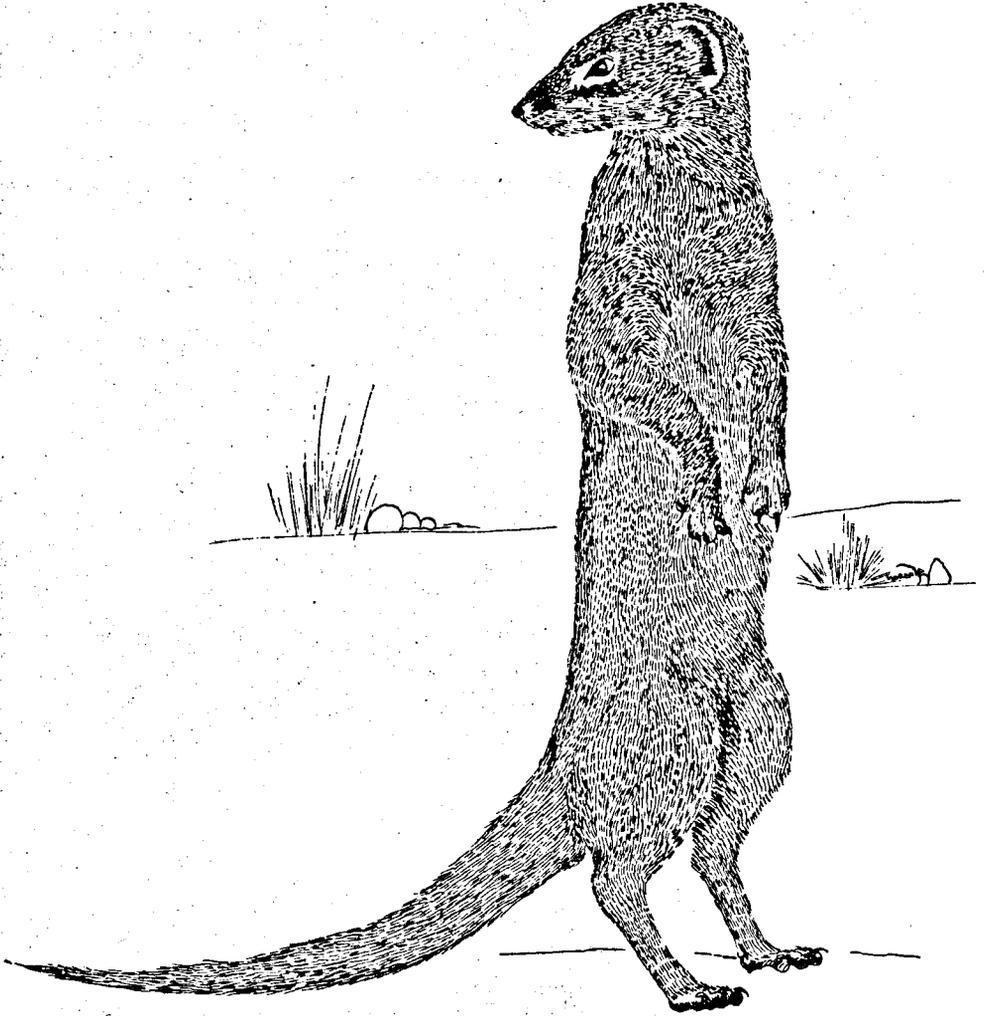


Fig. 26. Mongoose in high sit posture.

Although generally plantigrade, when highly aroused in an agonistic situation mongooses may become somewhat digitigrade, arch the back and tail, and erect the tail and body hair (Fig. 27). The lateral aspect of the body is then presented to the opponent. If being attacked, the mongoose



Fig. 27. Agonistic threat display of a mongoose.



Fig. 28. Mongoose sleeping in a vertical tuck.

presents the dorsal surface of the back to the opponent and turns the head away, watching the opponent over the off-side shoulder.

Mongoose jump very well. Captive animals were able to reach the top of a 1.2-metre vertical barrier. Horizontal jumps of close to a metre have been observed for wild mongooses chasing lizards on a boulder pile.

On cool or damp mornings, mongooses bask in direct sun. They choose an exposed spot such as a log or rock, and lying with the ventral surface on the substrate, they orient the body perpendicular to the sun and erect the body hair. Identical behaviour has been observed in *Herpestes sanguineus* in South Africa by NELLIS. Mongooses in the wild will also rest stretched out in a "museum skin" posture while leisurely watching something of interest. A similar posture is shown when an animal is exposed to extreme heat stress; maximum contact of the ventral surface of the body with the substrate is sought by extending the hind legs rearward and the front legs forward.

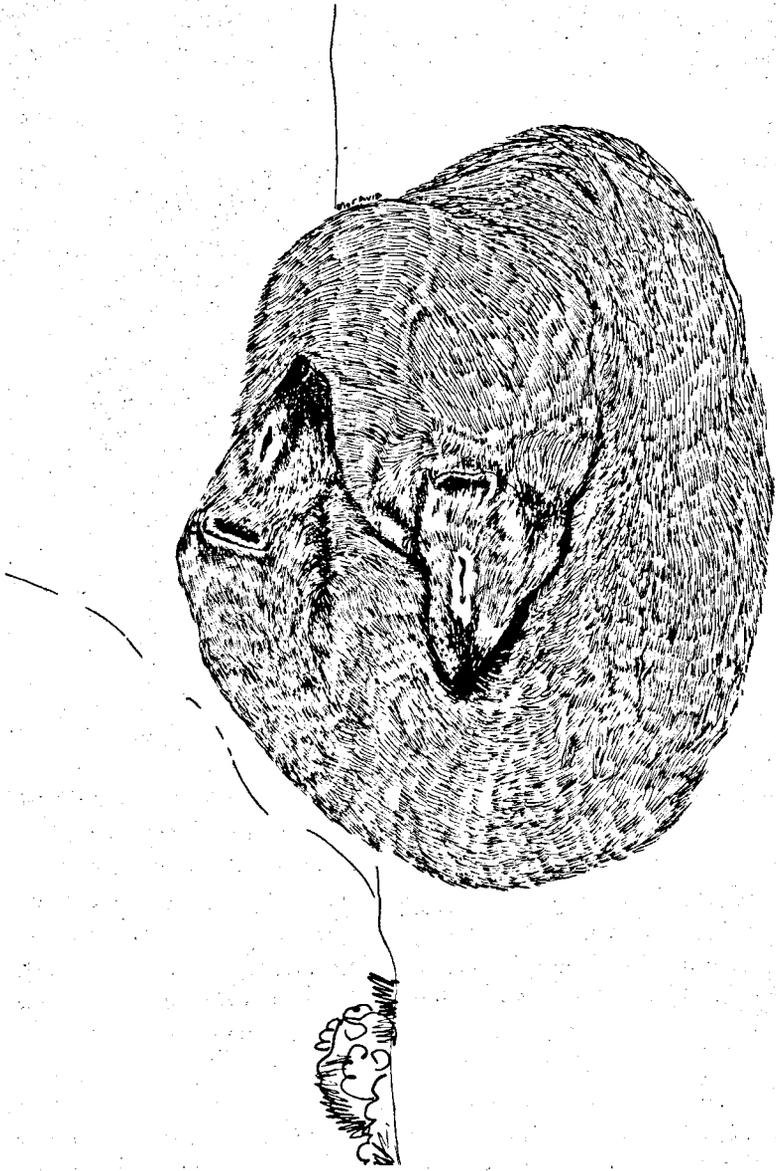


Fig. 29. A pair of sleeping mongooses.

Mongoose sleep in two basic postures. Lying on its side, the mongoose curls into a coil with the tail behind the head and shoulders, or alternatively it tucks its head between its forelegs and assumes a vertical C position with the weight supported on the hind legs and dorsal aspect of the shoulders (Fig. 28). The orientation of the head is vertical with the tip of the snout visible against the flank. When two mongooses are kept in the same cage, they usually sleep with bodies in contact, so that the arousal of one immediately alerts the other. Fig. 29 shows two mongooses sleeping with sides touching but facing in opposite directions.

The short coarse hair of the mongoose does not require frequent grooming. When grooming does take place it may be with a few swipes of the long agile tongue, by scratching with the claws of the hind feet, or by nibbling with the incisors to kill fleas. Mutual grooming has never been observed in the wild except between mother and offspring. In captive animals caged together, mutual grooming has been observed between animals of the same and opposite sexes. DÜCKER (1965) notes that *H. edwardsi* cleans the teeth with the front claws. We have also observed this in *H. a. auropunctatus*, but only if tough or stringy food is caught in the teeth.

Mongoose scratch and dig vigorously under the slightest provocation. Both paws may be used simultaneously in a soft substrate, or they may be used alternately. When reaching into a hole or crevice most mongooses are right-handed. As the result of digging in an attempt to escape, the wire mesh floor of a trap is frequently covered with a mound of soil.

SWIMMING

Mongoose will voluntarily wade in water which is up to about 5 cm deep if they can do so without wetting the fur of their ventral surface, but they do not willingly swim or wet their bodies. The swimming ability of mongooses was investigated from the end of a dock extending 26 metres into a calm, sheltered saltwater lagoon. Mongooses were released from live-traps directly into the water although they frequently needed urging. They immediately began to swim to shore. The swimming time was recorded, and the mean swimming speed of four mongooses was 34.5 metres per minute. If a human stood on the beach in line with the mongoose's swimming route, the direction and speed of swimming was not altered. The mongoose would begin growling as it approached the human and would eventually come ashore at the human's feet, then rush across

the beach to cover. A mongoose was released 80 metres from shore in calm water. Rather than swimming directly to the beach, which had low vegetation cover, the mongoose turned to a patch of mangroves which were conspicuous on the horizon at a diagonal to the beach. Near the end of its swim, the mongoose was allowed to rest for 15 seconds on a floating board while it was reoriented to come ashore on a small beach. The board was submerged and the mongoose resumed swimming to the beach. When the mongoose finally reached land, it crawled clear of the water and lay down. Gentle nudging elicited only faint growls. The mongoose was replaced in the live-trap, and two hours later appeared tired but otherwise fully recovered. The distance of the swim was determined to be 97.5 metres, and the rate averaged 19.5 metres per minute. As the initial rate was nearly 35 metres per minute, the very slow speed at the end of the swim is evident.

A reluctance to swim, coupled with poor endurance, can account for the failure of mongooses to become established on Protestant Key, 120 metres from shore in Christiansted harbour, St. Croix. It thus seems likely that the many small keys adjacent to larger mongoose-inhabited islands will remain free of mongooses unless deliberate introductions take place.

The mongoose's general avoidance of water is also evident when trapping. In a good habitat when trap success is in the range of 30 to 50 percent, rainy weather will reduce trap success to zero, even if the rain continues for several days. When the weather returns to normal, trap success is frequently greater than that before the rain.

VOCALIZATIONS

Adult mongooses have been found to produce 12 different categories of calls (MULLIGAN & NELLIS, 1975). Many of these calls have a wide range of amplitude and tonal quality indicating variations of behavioural significance. As an example, the growl can vary from a barely perceptible mutter indicating mild uneasiness, to a ferocious exclamative warning of imminent attack.

A list of the calls with brief descriptions follows:

- 1) Weep – a clear birdlike call. In the wild it is commonly heard as a contact call between mother and offspring.
- 2) Squawk – a scratchy call widely used in a variety of circumstances, the most commonly heard call in the wild.
- 3) Honk – a clear mellow call of discontent or frustration.

- 4) Weeonk – a sound with components of both the weep and the honk indicating discontent.
- 5) Conversation – extremely varied low level communication between two individuals.
- 6) Ruck a Ruck – stuttering call associated with feeding. Probably what KIPLING was referring to in his Jungle Book as the call of Rikki-tikki-tavi.
- 7) Pant – produced as a distinct sound not associated with respiratory distress.
- 8) Spit – an explosive defensive sound similar to a cat spit, and most frequently heard in newly-caught mongooses within the trap.
- 9) Bark – a short sharp defensive call.
- 10) Chuck – a harsh intense call of a highly aroused animal.
- 11) Scream – a loud harsh call used under conditions of extreme stress. In contrast to the findings of EWER (1963b) this call is produced in response to physical pain or extreme fear. Also commonly heard in newly-trapped animals.
- 12) Growl – A pulsed throaty sound typical of disturbed small carnivores.

SEXUAL BEHAVIOUR

Observations were made on the sexual and reproductive behaviour of a female offspring of a live-trapped pregnant mongoose, hand-raised with her male sibling, and other similarly-acquired semi-tame mongooses. This particular female had produced seven litters up to the time of writing and had been uninhibited by observations of her sexual and maternal behaviour.

Behaviourally, oestrus seems to be well-defined. When in heat the female becomes very active, pacing back and forth in her cage and giving an increased number of honks. When released for exercise with males, the female shows greatly increased marking behaviour. The males are usually decidedly interested, following and sniffing under her tail frequently.

In early oestrus when the female is not yet fully receptive, she may repulse a particularly persistent male by facing him, then with noses about 5 cm apart both animals give a ululating scream. If the female is in a receptive state and the male does not show adequate interest, she will tease flirtily and constantly place herself in front of him until he is adequately aroused to take the initiative. Squabbles between competing males are

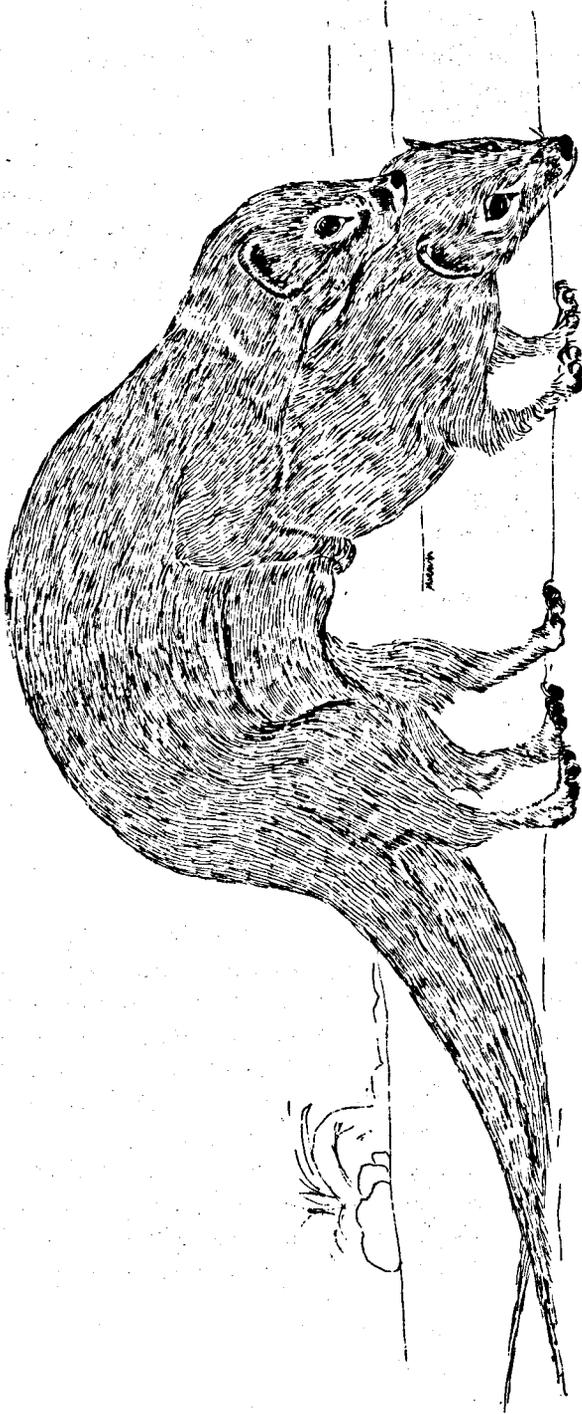


Fig. 30. Mongooses copulating.

frequent and are manifested by barks and screams accompanied by piloerection and chasing, but no injuries have been observed as a result of these encounters.

The successful male seems to be chosen by the female and is not necessarily the dominant male in the courting group. Once mounting takes place it is seldom interrupted by competitors. Several mountings take place before copulation succeeds. Occasionally a second male will mount in the intervals between the first male's mountings, although the female usually will not allow this. During mating the male grasps the female behind the rib cage with his forepaws and bends his body into a "C", while the female occasionally rests her forequarters and chin on the substrate (Fig. 30). The female may emit very low-level vocalizations, which are often accompanied by growls from the male. When copulation is successful, the male may lick the female's mouth and occasionally gently bite the nape of her neck during the more intense later stages. After copulation, both sexes lick their genital areas.

If conception does not take place, behaviour typical of oestrus is repeated at 3-week intervals. Each receptive period lasts about 3 days. These observations generally confirm the laboratory findings of PEARSON & BALDWIN (1953) who took daily vaginal smears from caged wild-caught females.

MATERNAL BEHAVIOUR

As pregnancy progresses in captive animals, the female does not become hostile to the young of the previous litter. We have left the previous litter in the cage until the onset of labour, and the mother has not shown any unusual aggression. However, females show strong antagonism towards adult males in the later stages of pregnancy. This antagonism continues until the young are well-developed and self-sufficient. The mongoose gives birth in a slightly squatting position with the rear legs spread, and she eats the afterbirth. Of six pregnancies in which close observation was possible, three birth episodes were recorded between 19:30 and 21:00 h. A fourth episode took place between 20:00 and 23:00 h, and two others took place between 19:00 h and dawn. It would thus seem that mongooses may control their time of parturition, and that they wait until dusk. Although the mother gives birth in the open, she carries the baby to the dark, secluded nestbox immediately after the post-partum cleaning is com-

pleted. Giving birth in the open may be an artifact of captivity resulting from the mother's pacing back and forth in her cage during labour and the early stages of birth. The nestbox provided is too small to allow this type of exercise.

Young mongooses have been found in rock piles (SEAMAN, 1952), and during radio-telemetry studies mongooses were found to take refuge in simple burrows. From local accounts and the above evidence it seems that mongooses will raise their young in any protected spot available.

Neither wild captive females nor our tame animals used the various bedding materials provided for the nestbox. The captive tame animal occasionally moved her young into an ingeniously contrived tent-like structure made from a piece of folded newspaper which is normally provided on the floor of the cage as litter. It is our belief that mongooses will use any available dark, secluded area for a nest. The young are altricial, being born partially haired and blind. If transportation is necessary at a very young age, the baby is usually carried with its entire head in the mother's mouth, but the mother may occasionally grasp the baby around the rib cage. As the youngster grows larger the mother carries it, when necessary, by a grip on the side or back of the neck.

The first vocalizations of the baby are mewling sounds about 10 minutes post-partum. The mother is very attentive and leaves the baby for only a few minutes at a time, not even leaving her cage for her usual exercise period. The young are periodically thoroughly licked over the entire body surface by the mother. Licking on the head and neck region is also used as a gesture to reassure the young in a strange or stressful situation. Hand-raised mongooses react favourably to being stroked with a damp paper towel and seem to derive particular pleasure from having their head and ears rubbed at any time. As the baby develops, the mother becomes somewhat less attentive but rapidly returns to the baby if it vocalizes.

The mother mongoose nurses her young while lying on her side curled about them. Mongooses have three pairs of teats. The posterior pair are more frequently sucked, although it is not uncommon for the middle and posterior teat on the same side to be used. Although evidence of nursing from the anterior teats has been seen only once in over 400 female mongooses examined, when lactating females are stimulated with oxytocin, milk can be expressed from the anterior teats; the teats are therefore functional, even if not normally used.

Weaning is gradual, taking place in captive animals at 6 to 8 weeks of age. As the young begin to take solid food, behaviour similar to that described by EWER (1963a) for *Suricata suricatta* begins to take place. Mongooses typically show a great envy of others in the possession of food. The mother uses this trait in teaching the young to eat. She will pick up a piece of food and carry it back and forth near the young, allowing them to snatch it from her when they begin to show interest. This behaviour continues until the young can no longer be enticed to take food, and only then will the mother eat. The digestive system of the young is able to handle solid food at a very early age. Young destined for domestication at home were weaned just after the eyes opened on a diet of raw, finely-chopped meat, hard-boiled eggs, papaya or mango pulp, and gruel. They were handled as frequently as possible and brought up individually, as two or more young weaned together are always far more independent than those brought up singly. Young mongooses which were to be kept in the laboratory were weaned 21 to 28 days after birth, and in addition to the above diet were provided with suckling white mice (in Trinidad) and a vitamin supplement. *H. a. auropunctatus* is not particularly amenable to domestication, though it does show the characteristic mongoose trait of extreme curiosity provided that fear of humans has been overcome at an early age.

A tame mother mongoose would allow NELLIS to handle her baby for weighing and measuring, but if the baby vocalized the mother would jump to his arms, grasp the baby firmly, and try to take it away from him. If he let her have it she would run about carrying the baby, then jump 70 cm to the table which supported her cage and return the baby to the nestbox. If the baby is separated from the mother when it vocalizes, she becomes very excited and vocalizes with weeps, honks, and squawks. The mother's vocalization incites the baby to further vocalization. When the mother and offspring are re-united, many quiet sounds of contentment and encouragement are exchanged. The playback of recorded distress calls of a 5-week-old infant caused much excitement and vocalization in a mother mongoose who was with her own 13-week-old offspring. By 5 days of age the young mongoose spits when handled or disturbed. At 10 days of age weeps are given, and by 18 days barks and growls are added to the vocabulary.

The first tentative excursions from the nest take place at about 25 days of age. When travelling with the mother, young mongooses show a very

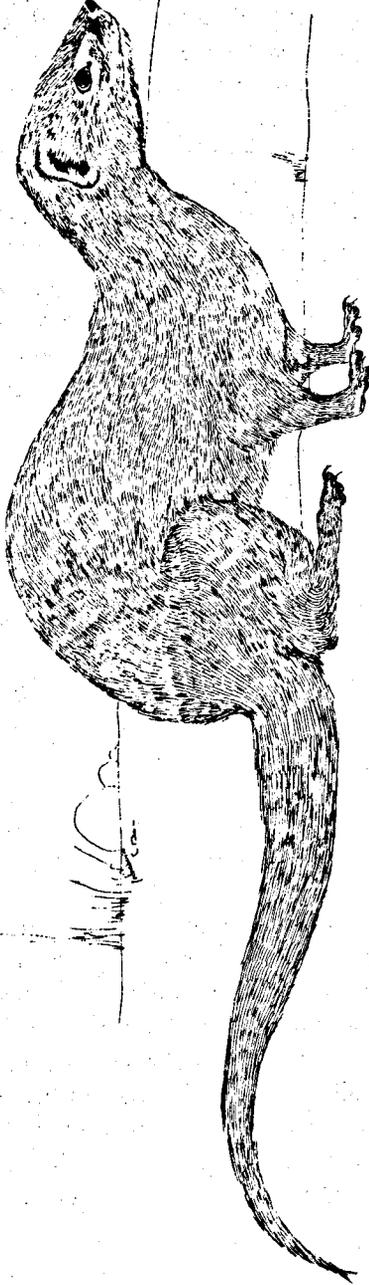


Fig. 31. Mongoose marking a horizontal object.

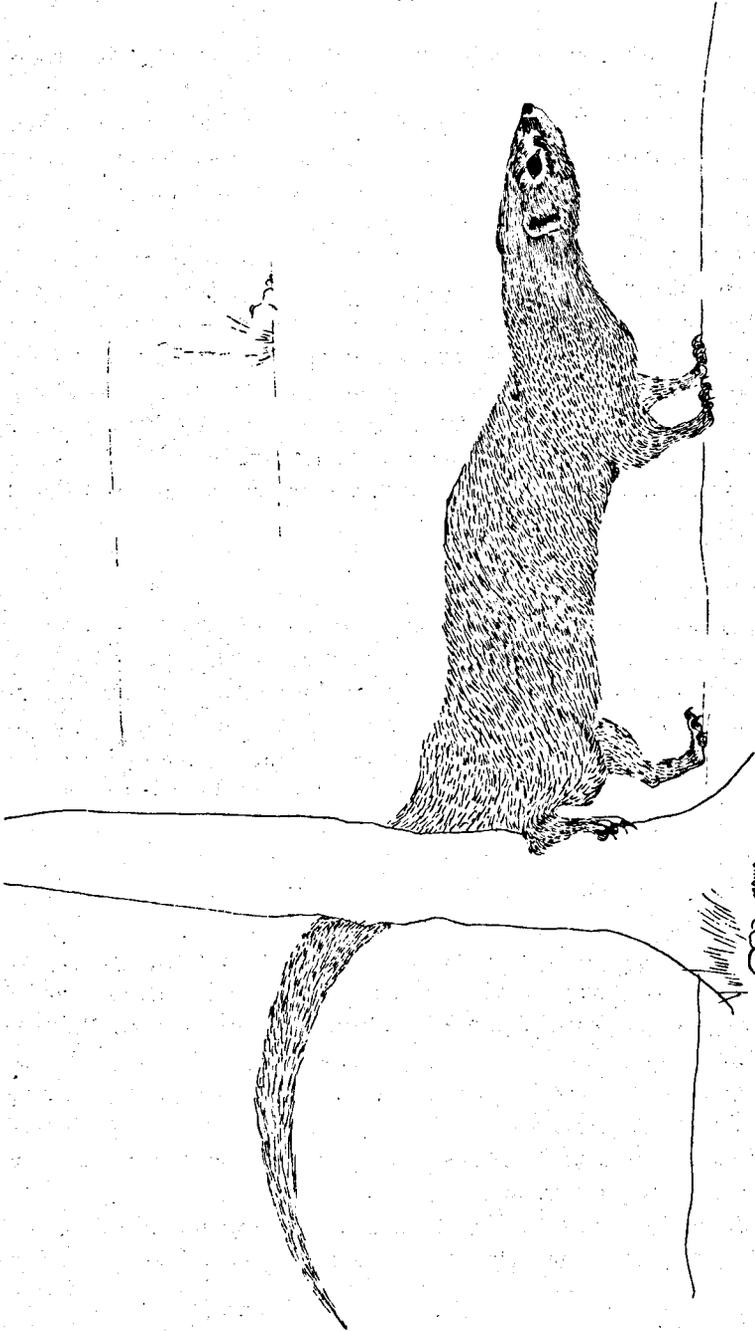


Fig. 32. Mongoose marking a vertical object.

strong following response. When mother and young are observed in the wild they are always in very close proximity, the young seldom venturing more than one body length away from her. This has resulted in mother and young (on one occasion two young) being caught together in the same trap. This strong following response is transferred to humans in hand-raised animals, but it is not a case of imprinting, since other mongooses can evoke the response, which declines gradually until it disappears at puberty.

The mother mongoose is very protective of her offspring, and if one youngster of a litter is caught in a live-trap the mother will usually stay in the vicinity for several days. If the youngster gives a distress scream while being handled in the trap, the mother is prone to attack. While handling a wild-caught youngster in a live-trap, NELLIS had a wild mother mongoose bite and hang on to his trouser leg in a very determined manner. The young seem to remain with the mother until they reach sexual maturity, or until she gives birth to another litter.

MARKING

Mongoose have paired ducted glands opening into an extensible pouch which surrounds the anus. When marking, the pouch is expanded to form a flat pad, and as the pouch is wiped on the object to be marked the glands extrude a buttery substance whose odour is not readily detectable to humans. Horizontal substrates are marked by dragging the anal pad over them (Fig. 31), and one tame mongoose regularly marked its owner's bare feet. Vertical objects are marked by lifting the tail and one hind leg and applying the anal pad to the object with a downwards stroke (Fig. 32).

With tame animals, certain objects become traditional marking spots. A particular chair leg may be marked regularly by all mongooses, while an adjacent one is seldom or never marked. An object marked by one mongoose may or may not be sniffed before the second mongoose applies its mark. RASA (1974) has described similar marking behaviour in *Helogale undulata*.

A female in heat shows a great increase in marking behaviour, marking many different objects with a greater frequency than usual, both with anal gland exudate and urine. Males find the marks placed by a female in oestrus to be very interesting.

Marking also occurs as a displacement activity during agonistic encounters, the vanquished animal being more inclined to mark than the victor. A

characteristic marking sequence often takes place after an animal has been dominated in an agonistic encounter. A vertical object (such as a table leg) is approached, and the head and neck are rubbed up and down several times on opposite sides of it. Then, with the mongoose standing on its hind legs, the chest is rubbed on the same site. The mongoose then drops to all fours, and, as it moves forward, strokes the side of the body on the same site. A small bare patch of skin anterior to the eye suggests that this behaviour may be associated with marking by a suborbital gland. As the hindquarters pass the object, the appropriate hind leg is lifted and a deliberate anal mark is applied.

GORMAN *et al.* (1974) have shown that the contents of the anal pockets include a series of volatile, short-chain carboxylic acids (acetic, propionic, n-butyric, n-valeric, and iso-valeric) produced from sebum and apocrine secretions by bacterial action. GORMAN (1976a) found the relative concentrations of the acids to vary from one individual to another, giving each a different odour. In free-choice experiments GORMAN found that mongooses can discriminate between the anal pocket contents of conspecifics and also between synthetic odours made from combinations of pure acids.

The fact that mongooses mark with urine, anal glands and suborbital cheek glands is of unknown significance in the wild. The marking behaviour of these animals linked with their generally solitary nature and the apparent random overlapping of their home ranges provides a fertile field for future investigation.

PLAY

As with many carnivores, mongoose play is composed of many of the required adult behaviour patterns performed in an extravagant manner. The play of captive *Herpestes edwardsi* and *H. ichneumon*, described by RENSCH & DÜCKER (1959), seems to be very similar to that of *H. a. auropunctatus*.

In the wild, the form of play most commonly observed is an undirected dashing about with rapid starts, stops, and radical changes in direction. The head may be tossed with the mouth open before a sham attack is made. Both young and adults seem to enjoy dashing under a light object that provides cover, such as newsprint or plastic sheeting. A tail flick is a playful gesture and is frequently regarded by a conspecific as an invitation to chase.

HOME RANGE AND MOVEMENT

Local folklore and early investigators maintained that mongooses had no specific home range (SPENCER, 1950), but this was disproved by later investigation. PIMENTEL (1955a) in Puerto Rico, using a 30-metre separation of traps on a 10 × 10 grid, found an average home range diameter of 98 metres for an area of 0.75 ha. Males had larger home ranges than females.

TOMICH (1969) set live-traps at 161-metre intervals along intersecting roads and found an adjusted range length of 666 metres for males and 324 metres for females. Because mongooses have a propensity for travelling along ecotones, we feel that these range lengths, while valid, are an artifact of the narrow strip of preferred habitat along the roadside. TOMICH and other investigators who used live-traps have found that mongooses rapidly become trap-shy, making multiple recaptures difficult. However, even considering this trap-shyness and other limitations of mark-and-recapture, we considered this to be the most practical technique on a limited budget.

The movement and population densities of mongooses were studied by mark-and-release on several grids see pages 12–25. Although some of the grids were of different sizes and used different trap-spacing, all of them, except Grid II in Trinidad, were marked out from a baseline by means of an accurate prismatic compass and tape measure. Grid II was very large (104 ha), and the system of parallel roads at the old airbase was therefore used. Here, the positions of the traps were plotted on a 1:2,500 airphotograph, and the distance between them measured from the photographic scale. On all grids the traps were numbered. On Trinidad and Grenada they were baited with chicken heads at the beginning of each week, and rebaited at mid-week except when a mongoose was caught, in which event the bait was replaced immediately. On St. Croix, traps were rebaited daily. Trapping commenced on Mondays and closed on Fridays on Trinidad and Grenada, but operated continuously on St. Croix except when unforeseen difficulties intervened. Whenever possible, each trap was sited in the shade since direct exposure to sunlight will cause heat prostration and kill a mongoose in a short period of time.

Mongooses were marked with size 1, Monel Metal 4-1005 ear tags (National Band and Tag Co., 721 New York Street, Newport, Ky.,

U.S.A.) punched directly into the ear. The date, trap number, ear tag number, sex, weight, length, and adult or juvenile status were recorded before the animal was released at the site of capture.

Where possible, the range of mongoose movement within a defined area was calculated by the exclusive and inclusive boundary strip method of STICKEL (1954). The use of distance between captures as an index of range is discussed by DAVIS (1953). TOMICH (1969) used the average distance between captures as one method of expressing mongoose movement, and we have used a similar assessment for comparison. Trapping continued on the grids until few new animals were caught and numbers of recaptures had diminished through trap-shyness.

On ST. CROIX, Grid 1 in the mahogany was found to be too small for a home range study when recaptures were made within hours on opposite sides of the grid.

On Grid 2, in the shrubby grassland, males had a mean home range of 1.1 ha (range 0.4–1.6). Females had a mean of 1.2 ha (range 0.5–1.8). One female with a calculated home range of 3.4 ha was excluded from the mean because a grass fire was the probable cause of shift in home range. There is no statistical difference in the home ranges of males and females. While these values are in general agreement with those reported by PIMENTEL (1955a), several possible sources of bias exist: the borders of the study area were irregular, and the spacing between traps and the study area boundary was not uniform. Also, the open lawn and sea boundaries of the area may have restricted movements. The mean distance between recapture sites was 90.4 metres.

On Grid 3, in the pasture, too few recaptures were recorded to accurately portray home range. The mean distance between recapture sites was 193 metres, with a maximum of 375 metres. The trapping records for the pasture show that the only successful traps in the grid were those set along fence-lines or a wooded ravine, thus demonstrating the mongoose's preference for ecotones which we have regularly observed.

On GRENADA, Grid B (30.1 ha) was the only one large enough for the assessment of movement (Fig. 7), but it is possible that even this grid with a diagonal of 777 metres was too small and produced an underestimate of home range size.

TABLE 16
 DISTANCES IN METRES BETWEEN SUCCESSIVE RECAPTURES ON GRID B,
 GRENADA
 (Trap numbers in parentheses)

Mongoose No. and sex	Recaptures				
	1st	2nd	3rd	4th	5th
M 145 (42)	(76) 305	(45) 192			
F 202 (72)	(101) 195	(36) 527			
M 226 (57)	(36) 134				
F 227 (60)	(12) 329	(29) 433			
M 228 (95)	(24) 433	(22) 122	(50) 223	(12) 274	
F 229 (45)	(10) 357	(34) 274	(46) 137	(93) 358	
M 231 (85)	(12) 466				
F 232 (41)	(73) 219	(20) 357			
M 234 (33)	(22) 88				
M 238 (41)	(100) 373				
F 240 (92)	(78) 387	(68) 61			
M 242 (31)	(13) 172				
F 250 (50)	(62) 136	(24) 274	(52) 274		
M 310 (77)	(93) 274	(94) 61	(65) 195		
M 311 (96)	(62) 305				
F 313 (97)	(78) 137	(105) 259	(67) 274		
M 314 (42)	(27) 274				
F 329 (60)	(41) 137				
F 330 (40)	(30) 61	(63) 259	(34) 195	(52) 174	
F 334 (22)	(12) 61				
M 335 (59)	(69) 61	(43) 387	(58) 314	(89) 195	
F 336 (30)	(69) 579				
M 337 (57)	(78) 134	(76) 122	(86) 61	(84) 122	(58) 305
M 341 (26)	(45) 137	(21) 274	(43) 171		
M 344 (45)	(54) 85				
M 346 (12)	(63) 311				
M 354 (21)	(21) 0	(17) 372	(83) 491		
M 381 (63)	(77) 253	(67) 61	(77) 61	(84) 192	(66) 174*
F 383 (68)	(87) 137	(65) 171	(56) 85		
F 384 (69)	(74) 314	(45) 195			
F 386 (105)	(94) 85				
F 388 (30)	(14) 274	(105) 549			
M 390 (50)	(23) 259	(52) 195	(34) 177		
F 392 (12)	(28) 375				
F 393 (85)	(82) 183	(86) 244			
M 396 (31)	(51) 122				
F 397 (13)	(46) 259	(44) 122			
F 399 (66)	(49) 223				
M 601 (79)	(29) 305	(87) 387			

M 611 (109)	(103) 366	(108) 305			
F 614 (50)	(75) 332				
M 617 (108)	(100) 488	(105) 305			
M 618 (88)	(96) 137	(105) 85			
F 620 (49)	(69) 122	(67) 122	(87) 122		
M 622 (35)	(12) 223				
Sub-totals**	45	27	14	6	2

* To be continued as follows: 6th (65) 61, 7th (77) 137, 8th (64) 195, 9th (64) 0, 10th (58) 253, 11th (82) 412, 12th (53) 195.

** Total 101.

The distances travelled by 45 mongooses on Grid B between successive recaptures are shown in Table 16. The mean distances travelled were 220 metres for males and 241 metres for females, which is not a statistically significant difference. The mean distance travelled between successive recapture sites by both sexes combined was 229 metres, with a maximum of 579 metres. For recaptures on successive days, the mean distance travelled was 210 metres (maximum, 387 metres); and for recaptures within 1 week the mean distance was 213 metres (maximum, 488 metres). There is no significant difference between these three means. For animal 381 (a male which moved over Grid B for several weeks in succession), the mean distance travelled between each of 12 recaptures was 166 metres. This mean does not differ significantly from the mean for recaptures on the following day (210 metres), $t = 0.76$; nor does it differ from the female mean (241 metres) at the 5% level ($t = 1.81$).

The area used by mongoose 381 was calculated as 5.7 ha by the exclusive boundary strip method and 8.5 ha by the inclusive boundary strip (STICKEL, 1954). The movements of this mongoose and the boundaries are shown in Fig. 33. Figure 34 shows the movements of five other animals which were recaptured on four or more occasions on Grid B. Mongoose 330 (female) ranged over 3.4 ha (exclusive boundary strip) and 5.7 ha (inclusive boundary strip), while animal 337 (male) ranged over 5.4 ha (inclusive boundary strip). These figures almost certainly represent the minimum range, as many of the other mongooses moved much greater distances between recaptures.

In TRINIDAD, there were too few recaptures to assess home range, but the mean distance travelled between recaptures was 462 metres, with a max-

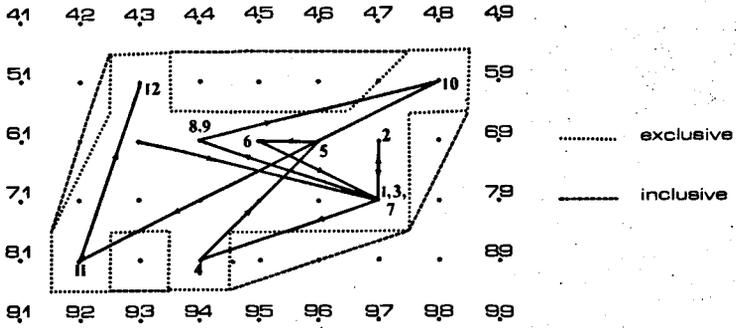


Fig. 33. Movements of mongoose 381 on Grid B, Grenada.

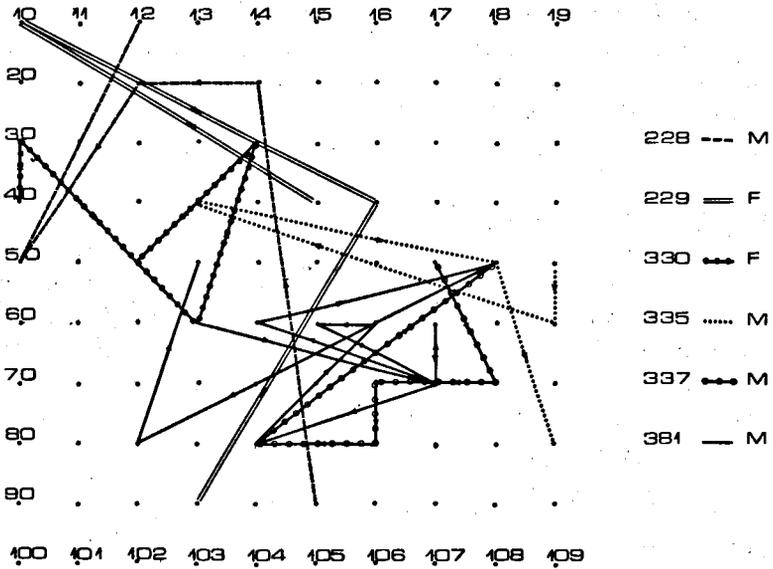


Fig. 34. Movements of six mongooses each caught more than four times on Grid B.

imum of 1333 metres. For recapture on successive days the mean distance travelled was 216 metres with a maximum of 381 metres.

Though mongooses seem to have compact home ranges in homogeneous territory, these may become extremely linear in situations such as forest edges, fence-lines, roadsides, or proximity to human habitations. As an example, a 1-ha home range along a roadside which provides a 5-metre width of desirable habitat would be 2 km long. Thus a distinction should be made between animals found in populated areas or linearly-arranged heterogeneous habitats and those in homogeneous open country.

Over long periods of time mongooses may be found at some distance from the original point of marking. On St. Croix a mongoose was killed by a dog 1800 metres from its original capture site across open brushy pasture, and another was killed by a farmer 1930 metres away across pasture-land 5 months after tagging. Another mongoose was found dead 2290 metres from its original capture site across an intervening habitat of dense thorny scrub. In Grenada two marked mongooses which were inadvertently caught in a removal-trapping effort had travelled at least 1520 and 1740 metres. Another Grenadian mongoose was captured on both Grids A and B before it was finally killed by a dog 26 months after its original capture. Although it was found to be rabid, it had moved 2100 metres from its original capture site.

While all the above studies gave tantalizing indications of the home range and movements of mongooses, the many limitations of the techniques used frustrated our attempts to learn about the daily activities of an undisturbed mongoose. Eventually funds became available for radio-telemetry on St. Croix.

Radio-telemetry equipment was purchased from Wildlife Materials Inc., Carbondale, Illinois. The transmitters provided a pulsed signal and were mounted on integral collar antennae. The entire unit with battery weighed between 17 and 20 g. The receiver was an AVM Model 12 with crystal controlled channels in the 150.8 to 151.15 range. The receiving antenna was a model 28 Hy-Gain, with an eight-element 4.2-metre-long directional yagi mounted on a mast in the rear of a pickup truck. For occasional use and to closely approach a mongoose on foot, a 1-metre-long three-element yagi was used.

The study area was a homogeneous savannah composed of *Acacia tortuosa* and *Panicum maximum* which was traversed by a dirt track with a north-south orientation. Tracking stations were marked at 100-metre intervals along the road. Radio collars were attached to 13 mongooses under ether anaesthesia. After full recovery the animals were released at the exact site of capture. Compass bearings for the radio signal were then determined from two or more

tracking stations, and the point of intersection of the bearings was considered to be the location of the animal. No allowance was made for the possible movement of the animal in the approximate 3-minute interval between successive bearings.

As with many complex but potentially rewarding field techniques, the telemetry studies did not proceed as planned. Two mongooses disappeared upon release and were never heard from again. Three mongooses managed to extricate themselves from their collars, and one animal took up residence near an electric transformer installation which provided too much radio interference to allow direction-finding.

Of the animals successfully tracked, two were adult females and five were adult males. The home range was determined by mapping all the radio fixes, then connecting the outermost points. The area of the resulting polygon was then determined with a compensating polar planimeter.

The data from the seven successfully tracked animals are shown in Table 17. The mean home range was found to be 3.7 ha for all animals. The females had a consistently smaller home range than males, the means being 2.2 for females and 4.2 for males. While the home range of most animals was homogeneous, male number 4 included a linear stretch of rocky seashore in his home range. The resulting shape produced a considerable upward bias in the calculated home range. Excluding this animal from the calculations probably results in a more realistic mean of 3.1 ha overall and 3.6 ha for males.

Home ranges of males were found to extensively overlap the ranges of other males and females. The home range of the two females did not overlap, but no significance is attached to this since the home ranges of females determined by mark-and-recapture at Estate Slob and in Grenada regularly overlapped. In Fiji, GORMAN (1979) also found all home range combinations overlapped.

Much of the daily activity tended to occur in a smaller core area than the entire home range, with only occasional excursions accounting for much of the calculated home range size. It seems likely that with long-term continuous radio-tracking, the recorded or calculated home range would gradually continue to increase. The difference between the values for the home range obtained from trapping and telemetry on St. Croix may have resulted because the former measured the core area and was limited by grid size, whereas the latter included all the short-term peripheral wanderings.

It appears that between St. Croix, Grenada and Trinidad, in that order,

TABLE 17
 THE HOME RANGE OF *Herpestes* ON ST. CROIX
 determined by radio-telemetry

Mongoose number	Sex	Home range (hectares)	Number of fixes	Number of days followed
1	Female	1.7	48	9
2	Female	2.85	24	4
3	Male	3.3	32	8
4	Male	6.8	10	3
5	Male	5.1	39	5
6	Male	2.9	39	5
7	Male	3.1	25	3

there may be a progressive increase in the land area used by mongooses, but standardized and more accurate methods of assessment would be needed to confirm this.

Probably differences in population density, numbers of competitors, and availability of food, create differences in patterns of movement within one species. As a general observation, as one proceeds from a simple to a more diverse ecosystem, as from a small island to a continental land mass, the numbers of competitive species increase and one could expect a larger home range.

Due to sparse resources, specialized competitors, and little if any unused niche space, we would predict a home range in excess of 10 ha if mongooses become established in the xeric shrublands of continental North or South America. Even larger home ranges might be expected in the native Asian habitats of the mongoose where predators, prey and parasites have all evolved in the presence of mongooses.

POPULATION STRUCTURE AND DENSITY

AGE STRUCTURE

The age structure of the mongoose population on St. Croix was investigated by calculating age from the weights of eye lenses of animals collected over a three-year period. In compiling data from specimens over time, population structure was assumed to be stable. Fig. 35a shows the age of 243 mongooses under one year of age, while Fig. 35b shows the age distribution of a sample of 474 mongooses up to 5 years of age. The data are probably biased by an under-representation of animals under six months of age, especially the altricial young, since weaning does not normally take place until the young are about two months of age. It appears that at least 88 percent of all mongooses in the wild are under two years of age.

The sex ratios of mongoose populations are discussed in detail on pages 42–45. Briefly, until seven months of age, females on St. Croix outnumbered males (Figs. 35a and 35b), while from eight months onwards males were more numerous. We attribute the change in sex ratio at seven months to the attainment of sexual maturity. At this stage there is possibly an increase in mortality from transmissible diseases; there is also likely to be an increase in the activity of post-pubertal males when searching for sexually-receptive females, and post-pubertal females are likely to be more stressed than immature specimens. If the sex ratio of the population is modified only by a higher mortality rate in females, a trapping sample could represent the true sex ratio. However, if increased male activity significantly modifies the catch ratio, the ratio would not be a true one. From a sample of 924 mongooses on St. Croix, the sex ratio of females to males was 1:1.28. This is comparable to the ratio of 1:1.87 found by PEARSON & BALDWIN (1953) in Hawaii, and to the ratio of 1:1.06 found by PIMENTEL (1955a) in Puerto Rico.

Omitting the biased sample of animals under 6 months and taking both sexes together, a survival curve was constructed from the data in Fig. 35 (Fig. 36). This curve indicates that the maximum life-span of 6 years, 7 months and 10 days reported by FLOWER (1931) for a captive zoo animal is rare, although exceeded recently by a zoo specimen in India which survived 9 years and 8 months (ACHARJYO & MOHAPATRA, 1976). Two animals raised by NELLIS to 8 years 6 months and 9 years 3 months died of acute infection and showed no signs of age-related deterioration.

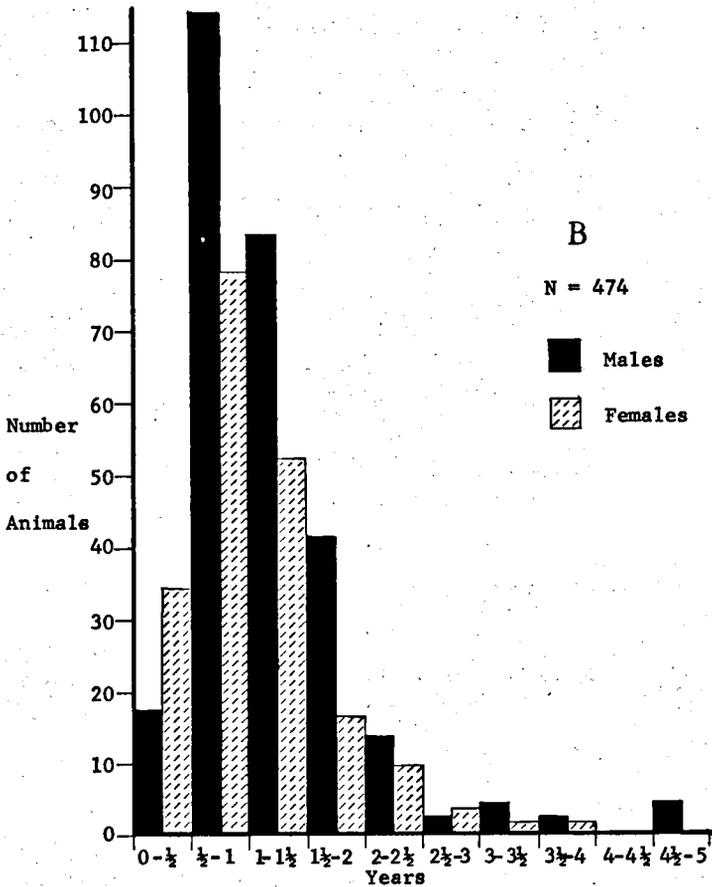
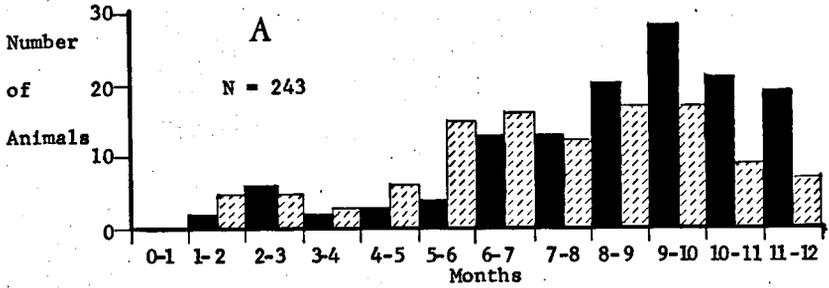


Fig. 35. Age structure of the mongoose population on St. Croix: A - Animals under one year. B - Total population.

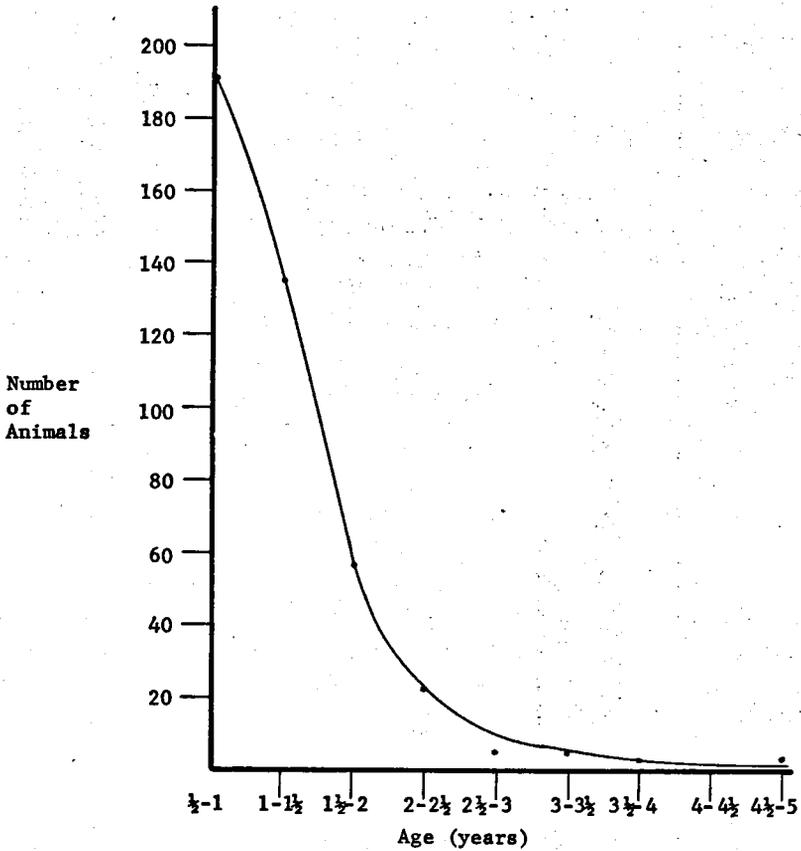


Fig. 36. Survival of mongooses in the wild after six months of age.

The factors causing early mortality in wild populations are at present unknown, but diseases and, to a lesser extent, parasites must be contributing factors.

POPULATION DENSITY

The traditional mark-and-recapture techniques which lead to an estimate of population size by the Lincoln index or its variations, such as the Schnabel, are not completely valid for mongooses. Our data indicate that although *Herpestes a. auropunctatus* is not basically trap-shy, some indivi-

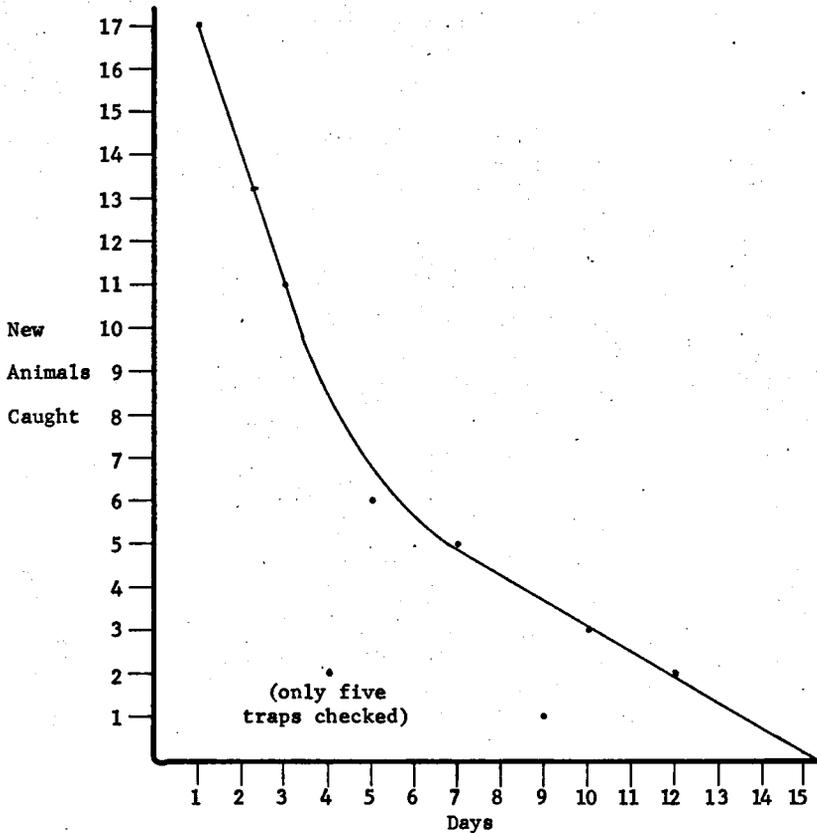


Fig. 37. New mongooses caught per day on Grid 2 (Estate Slob).

duals may not venture into a trap again for some time after capture. Thus, all animals may not be equally susceptible to marking. Trap-shy and occasional trap-prone animals invalidate the required assumption that marking does not influence the future catch probability.

In Puerto Rico, PIMENTEL (1955a) found a population density of about 2.5 mongoose per ha after an 18-day mark-and-recapture study. He observed that "There was a definite indication of trap-shyness after an animal had once been taken and released."

TABLE 18
TIME INTERVALS IN DAYS BETWEEN SUCCESSIVE RECAPTURES OF MONGOOSES
ON GRID A, GRENADA

Animal Number	Recaptures						
	1st	2nd	3rd	4th	5th	6th	7th
106	5	21	14				
107	17	211					
111	7	13					
117	1	5	37				
119	81						
121	31	12	7				
122	17						
123	37						
125	8						
127	7						
130	16						
131	21	23	43				
132	7	15	36	22			
135	7	9	7	21	71	70	23
136	31						
139	43	153					
140	37	58	51	29			
141	9	1	4	2			
143	14	162					
*145	13	112	37	4	36	32	21
146	25	15					
148	166	2					
149	22						
153	1						
154	11	22	8				
155	1	34					
158	126						
160	14						
161	14						
162	63						
164	7						
165	35	41	7	16			
167	28						
168	35	4	17				
*202	50						
204	1	7					
206	1						
208	49						
210	4						
212	36						
214	39						
216	52	21					
218	13						
Total (88)	43	21	12	6	2	2	2

* Subsequently recaptured on Grid B.

On ST. CROIX trapping on Grid 1 at Estate Prosperity resulted in the capture of 47 animals. This accumulated total indicates the great number of animals which may utilize a small area over a period of time. In a later three-day trapping period on this same area in October 1970, 14 animals were captured, indicating a minimum of 6.4 animals per ha using the area at a given time. It is unlikely that all these animals confined their activities exclusively to the study area.

On Grid 2 at Estate Slob, 54 mongooses were caught, indicating a minimum population density of 3.2 animals per ha. If the 15-day duration of this mark-and-release study is treated as a trap-out effort, and the numbers of new captures are plotted against the days of trapping, the resulting line indicates an almost complete census (Fig. 37).

In the central area of St. Croix (Grid 3), 44 new animals were captured in the first 12 days of the study, and a single additional new animal was caught on the final eighteenth day. The total of 45 mongooses indicates a minimum population density of 3.4 animals per ha. An analysis of capture locations shows a distribution closely related to habitat which is suitable for *Anolis* lizards and to thick cover. Thirty-one of the mongooses were caught in 11 of the traps which were set along the ravine area or near cover on a fence-line. Nine of the traps set among shrubs in the central areas of the pasture caught no animals.

On GRENADA, a study of trapping effectiveness was made. Forty-three of 80 marked animals on Grid A (54 percent) were recaptured on one or more occasions, as were 45 of 84 (54 percent) on Grid B. On Grid C, 31 of 60 marked mongooses (52 percent) were recaptured, as were 24 of 41 (59 percent) on Grid D. For Grid E 25 of 47 (53 percent) were recaptured, while at Piedmont/Florida (Grid F) only 22 of 63 (35 percent) were recaptured. Thus, altogether 190 of 375 mongooses were recaptured during grid-trapping. Except for Grid F, this is a remarkably uniform series of recaptures at the different grids.

Time interval studies were undertaken only on Grenada on Grids A and B. Tables 18 and 19 show the time intervals in days between successive recaptures on Grids A and B, respectively, while Table 20 shows the percentages of these recaptures in successive days and weeks. Nearly one-third of all recaptures (range, 24.1 to 38.3 percent) took place within one week of the previous capture, over 56 percent (range, 49.0 to 64.2 percent)

614	23										
617	6	42									
618	10	12									
620	14	4	2								
622	34										
Total (101)	45	27	14	6	2	1	1	1	1	1	1

* Previously captured on Grid A.

within three weeks, and two-thirds (range, 58.4 to 74.9 percent) within four weeks. Over 90 percent of recaptures were made within 10 weeks.

The Schumacher-Eschmeyer procedure was used to estimate the mongoose populations from the mark-and-recapture data (DAVIS, 1963). The results are shown in Table 21. The population estimate of 10.4 per ha for Grid A during 1970 appears to be consistent with the large number of animals removal-trapped (8.62 per 100 trap-days) in this southwest dry zone (EVERARD, 1975a). The lower population estimate of 3.2 per ha in 1971/72 from the larger Grid B, also in this dry zone, also appears valid when compared to the smaller catch (5.34 per 100 trap-days) in the dry zone removal-trapping programme in 1971 (EVERARD, 1975a).

In TRINIDAD population estimates of mongooses on Grids I and II fall in the range of only 1 to 4 per ha (Table 22). Grid II (first part) covers the period before the fire, while Grid II (second part) covers the period after the vegetation had recovered. On Grids I and II (first and second parts) together with the line of 45 traps, 149 mongooses were marked and released, of which only 32 (21.5 percent) were recaptured. The percentages recaptured on the subsequent 2nd, 3rd, 4th and 5th recaptures were 6.0 (9/149), 2.7 (4/149), 2.0 (3/149) and 0.7 (1/149), respectively. Using data from both parts of Grid II and the trapline, the percentages of mongooses recaptured within a given time interval were as follows:

Within 1 week – 21.6 percent

Within 3 weeks – 29.7 percent

Within 6 weeks – 48.6 percent

Within 10 weeks – 64.9 percent

TABLE 20
 TIME INTERVALS IN DAYS AND WEEKS BETWEEN SUCCESSIVE RECAPTURES OF MONGOOSES ON GRIDS A AND B,
 GRENADA

Weeks Days	1 1-7	2 8-14	3 15-21	4 22-28	5 29-35	6 36-42	7 43-49	8 50-56	9 57-63	10 64-70	>10 ≥71	Total
Grid A. Mongoose recaptures	23	13	12	7	7	9	3	3	2	1	8	88
Grid B. Mongoose recaptures	36	17	6	12	8	6	3	3	1	1	8	101
Both Grids - Total	59	30	18	19	15	15	6	6	3	2	16	189
Percentage recaptures	31.2	15.9	9.5	10.0	7.9	7.9	3.2	3.2	1.6	1.1	8.5	100.0
Accumulative percentage recaptures	31.2	47.1	56.6	66.6	74.5	82.4	85.6	88.8	90.4	91.5	100.0	-

TABLE 21

MONGOOSE POPULATIONS ON GRIDS A-F IN GRENADA

calculated by the Schumacher - Eschmeyer procedure

Zone	Grid	Grid area (ha) and habitat	Area (ha) used for population estimate	Period of trapping	Number of weeks trapping achieved	Number of mongooses marked and released	Number of recaptures	Population estimate (plus standard error)	Population estimate per ha	Population range per ha from standard error
I	Mt. Hartman Grid A.	6.7 dry zone scrub and woodland	9.3	20 July 1970 to 26 March 1971 (36 weeks)	28	80	88	96.1 (10.4)	10.4	8.2-12.6
I	Mt. Hartman Grid B.	30.1 dry zone scrub and woodland	30.1	24 May 1971 to 4 Feb. 1972 (37 weeks)	25	84	101	97.5 (11.7)	3.2	2.5- 4.0
II	Annandale Grid C.	7.5 forest and cocoa cultivation	11.3	13 March 1972 to 9 June 1972 (13 weeks)	13	60	65	67.8 (6.2)	5.9	4.9- 7.2
II	Les Avocats Grid D.	7.5 forest reserve and natural forest	11.3	1 Aug. 1972 to 27 Oct. 1972 (13 weeks)	11	41	55	43.7 (7.0)	4.0	2.7- 5.2
III	Grand Etang Grid E.	7.5 rain-forest and palm brake	11.3	12 Dec. 1972 to 27 Feb. 1973 (11 weeks)	8	47	51	52.8 (3.8)	4.7	4.0- 5.4
III	Piedmont/ Florida Grid F.	5.0 cocoa, savannah and rain-forest	8.5	13 March 1973 to 8 June 1973 (13 weeks)	9	63	44	83.6 (9.4)	9.9	7.7-12.1
					Total	375	404			

TABLE 22
MONGOOSE POPULATIONS ON GRIDS I AND II IN TRINIDAD
calculated by the Schumacher-Eschmeyer procedure

Grid	Grid area (ha) and habitat	Area (ha) used for population estimate	Period of trapping	Number of weeks trapping achieved	Number of mongooses marked and released	Number of recaptures	Population estimate (plus standard error)	Population estimate per ha	Population range per ha from standard error
Waller Field Grid I.	10.4 savannah and secondary scrub woodland	14.9	1 June 1970 to 11 Sept. 1970 (15 weeks)	15	29	11	57.8 (11.7)	4.0	2.2-5.4
Waller Field Grid II. (1st part)	104 savannah and secondary scrub woodland	82.0	19 Oct. 1970 to 26 March 1971 (23 weeks)	21	47	25	79.8 (16.6)	1.0	0.7-1.5
Waller Field Grid II. (2nd part)	104 savannah and secondary scrub woodland	82.0	6 Sept. 1971 to 14 April 1972 (32 weeks)	27	35	9	111.5* (28.9)	1.5*	0.7-2.0*
Total					111	45			

* These figures are disproportionate due to the small number of recaptures.

Comparison of population density on various islands and in various habitats indicates that there may be considerable local variation in density due to both natural and man-induced factors. There is little doubt that under natural conditions the dry zones are preferred. These areas are comparable with the indigenous habitat of the mongoose in parts of northern India as typified by the Ridge area near Delhi examined by both authors and described by MAHESHWARI (1963).

This does not in any way imply that mongooses do not range into other types of habitat either in India or the Caribbean, Grenada itself providing ample proof of the adaptability of these animals. In Puerto Rico there are many diversified habitats including arid south and humid north, sea coasts, mountains, grasslands, forests, cultivation, urban and suburban areas, all of which, except the forests and urban areas, are inhabited by mongooses (PIMENTEL, 1955a). In Hawaii, forest, grasslands, desert, scrub, sea coast, cultivated tracts of sugarcane, pineapple and coffee, and settled suburban areas are all occupied by mongooses, and even steep wet slopes and rocky cliffs are also visited (BALDWIN *et al.*, 1952). According to these authors: "The best habitat seems to be in the lowlands below 2000 feet elevation. Favored areas have a warm humid climate, mixed natural vegetation, and the diversity of cover and substrate afforded by clearings, rock fences, and paths which go with small-scale country farming. The humid, warm coastal forest in the Puna District of windward Hawaii harbors the heaviest mongoose population encountered in the trapping work; however, high populations also live in some portions of the Kau and Kona districts of this island where cactus and shrub-covered lava fields occur under arid conditions... Rarely are the animals found in the interior of virgin forests, as at Kipahulu Valley, Maui, where moss on the trees is perpetually wet and rainfall reaches 300 inches annually."

SEAMAN (1952), writing mainly of the Virgin Islands, states that: "While highly adaptable to the tropical environment, the preferred habitat of the mongoose is dry, brush country. Humid forested areas are generally avoided." Our results confirm these conclusions from other countries and islands, though we have not found that, as BALDWIN *et al.* (1952) put it, "The humid, warm coastal forest ... harbors the heaviest mongoose population...". On the contrary, dry bush terrain supports the highest density of mongooses recorded in the Grenada study. During the course of arbovirus studies in Trinidad, it was found that mongooses were not present in pure stands of rain-forest either in the north or south of the island.

In comparing mongoose populations, both removal- and grid-trapping indicate a much lower density of mongooses on Trinidad savannahs than on Grenada and St. Croix. It is possible that overcrowding and the consequent shortage of food and territory in the favoured habitats on Grenada and St. Croix have forced mongooses to spread into the less preferred wet, forested areas. These areas on Trinidad are occupied by competitors from the more diverse fauna. ALLEE *et al.* (1949) point out that crowding of animals within a restricted environment elicits diverse responses in natality, mortality, and dispersion within individual communities. It would indeed seem that mongooses in Grenada and St. Croix have responded to overcrowding by dispersion, though this is not a necessity or such a widespread phenomenon in Trinidad or the mainland of South America. ALLEE *et al.* consider a number of examples of successfully introduced species. They state that, "the introduced form may become established in the simple natural community but be unable to invade a more complex community. Islands and island-like habitats do not have such strong biotic barriers as may be present on the edges of continental communities.

For example, the mongoose was introduced on Caribbean islands and South American shores where it has reached pest proportions, but it has been unable to invade the continental rain-forest a few miles inland from the region of its marked success along the shore." Thus it seems that the majority of the Caribbean islands into which the mongoose was introduced are functioning as simple communities and afford few barriers to dispersion.

In Grenada, and more so on St. Croix, predation plays little or no part in population dynamics as mongooses have few enemies other than man and his domestic dogs. Small mammals are few on the islands even in the forests, and the opossum (*Didelphis marsupialis*) on Grenada cannot be considered a serious competitor for the food available. Similarly, on Trinidad very few mammals are found in the open derived savannahs frequented by mongooses. Throughout the period of trapping there, other than mongooses only a few *Didelphis* were taken, and the only animals that coexist with the mongooses are a few snakes and the large carnivorous ground lizard, *Tupinambis nigropunctatus*. GREENHALL (1959) has suggested that adult lizards may be able to catch and overpower immature mongooses; the converse would also be true. *Boa constrictor* and other

mammal-eating snakes in Trinidad, including the poisonous fer-de-lance (*Bothrops atrox*) and bushmaster (*Lachesis muta*), are not generally found in the same areas as the mongoose. It appears, therefore, that despite the fact that most rodents are nocturnal, mongooses and possibly *Tupinambis* may have been responsible for the removal of any small mammals which previously inhabited the savannah areas. However, small mammals including numerous rodents are commonly trapped in forests adjacent to the savannahs (EVERARD & TIKASINGH, 1973a and 1973b). The general absence of mongooses in the forest areas of Trinidad, where an abundant food supply would be available, is consistent with the concept that the low density of the mongoose population in the savannah does not give rise to those overpopulation pressures which in Grenada and St. Croix initiated dispersal to the less characteristic environments of forest.

That the mongoose was a serious pest in Trinidad in the past as a consequence of enormous population expansion after its introduction, has already been mentioned, but no certain reason is known for the comparative decline in numbers which, from current findings, appears to have occurred. Present density figures may indicate a condition of equilibrium a century after introduction or a period of population depression as part of a natural fluctuation in numbers not uncommon in mammal populations. However, the periodic heavy and prolonged flooding of parts of the central plain, particularly in the Caroni area, may be responsible for sudden drops in the mongoose population, as might be the frequent fires in the grasslands and canefields during the dry season. The relatively large size of Trinidad (which is more than 15 times the size of Grenada) and the presence of a fauna of South American origin may have contributed factors of "biotic complexity" of the kind implied by ALLEE *et al.* (1949) which have stabilized or limited both mongoose population expansion and distribution.

The situation appears to be that over-population in Trinidad has not forced mongooses to establish extensive permanent residence in atypical habitats, such as forests and tree cultivations. This is, in contrast, what prevails in Grenada and St. Croix where individuals have also been observed to scavenge near dustbins and rubbish heaps in urban areas. It is suggested that in Grenada and St. Croix usually not less than 2.5 mongooses utilize a hectare of land, and the figure may be as high as ten or more. As

already mentioned, PIMENTEL (1955a) also found a density of 2.5 mongooses per ha in Puerto Rico.

In conclusion, the depauperate Caribbean islands with no significant mongoose predators or competitors maintain much higher densities of mongooses than do Trinidad or the South American mainland where there is greater faunal diversity.

PARASITES AND DISEASES

Our discussion of the mongoose to this point has related to the considerable ecological effects of this small, aggressive and voracious carnivore on the neotropical island ecosystems. Although it has acquired a reputation as a cunning pest, the present-day major issues involving the mongoose are not its failure to control rodents or its sporadic nuisance value but its status as a known and potential carrier of parasites and disease, the consequences of which are already being felt on some of the Caribbean islands.

PARASITES

Immediately after death, and before being weighed and measured, removal-trapped mongooses from Trinidad and Grenada were examined for ectoparasites. The fur was combed onto a paper towel, to which was added hair and parasites found on the paper lining of the glass etherizing jar when this had been used. The fur litter was funnelled into standard petri dishes, covered with ethyl alcohol, and screened under a binocular microscope. The ectoparasites of each mongoose were kept separately and sorted into major groups in 70 percent alcohol, before representative samples were sent away for identification.

Mongooses from all three islands were examined for endoparasites. The stomach, rectum, and portions of the intestine were removed and placed separately in normal saline. These organs were then split open and the contents brushed out into the dish and examined for helminths. Other viscera and organs were checked for gross signs of parasitic infection or disease. Lungs were also removed and cut open in saline. Nematodes were isolated, transferred to cavity slides containing saline, and gently heated over a spirit lamp until they relaxed and elongated. They were stored in alcohol-formalin-acetic acid before being sent away for identification. The kidneys of some mongooses were removed aseptically and cultured for leptospire.

Blood was taken from immobilized animals by cardiac puncture and transferred to a cotton-plugged sterile glass tube; the last few drops of blood in the syringe were used to make a thick and thin film blood slide. Only 1 ml of blood was withdrawn from caged animals or those due to be released, but from those that were being killed over 5 ml were taken when they were moribund. The blood was allowed to clot at room temperature before being rimmed and centrifuged. The pipetted serum was stored frozen at -20°C until it was tested for leptospiral and/or rabies serum neutralizing (SN) antibodies. The thick and thin blood films were air-dried, fixed in methyl alcohol, stained with Giemsa, and examined for haemoparasites. Alternatively, the haemoglobin was removed from some smears with distilled water, and the slides were then stained.

ECTOPARASITES

Fleas

In Grenada, 178 fleas were taken from 117 of 1,068 mongooses examined (11.0 percent infested). A sample of 151 fleas from 101 of these animals were all identified as *Ctenocephalides felis felis* (cat flea); the ratio of male to female fleas was 1:3.4. In Trinidad, 14 fleas were found on 8 of 86 animals examined (9.3 percent infested). All of these were *C. felis felis*.

SEAMAN (1963) found 106 of 129 mongooses in St. Croix infested with *C. felis*, with a maximum of 21 and an average of 8.6 per mongoose. WEBB (1972) found an average of 2.7 cat fleas on 51 of 100 mongooses on St. Croix. Males carried more fleas on average than females (1.96:1). In Puerto Rico, PIMENTEL (1955a) found only 1 of 210 mongooses infested with these fleas.

During a 1934 survey in Hawaii, from 157 mongooses COLE & KOEPKE (1947) found 6 lice, 24 mites, and 1,063 fleas of which 78.9 percent were *Ctenocephalides felis*; the remaining fleas were *Echidnophaga gallinacea* and a few individuals of *Xenopsylla cheopis*. In addition to these species ESKEY (1934), in a study of plague on the Hawaiian Islands, found a few *X. hawaiiensis*, *Nosopsyllus fasciatus* and *Leptopsylla segnis*, and one *Pulex irritans*, on mongooses. HAAS (1966) presents data to show that *H. a. auropunctatus* is a true natural host of *C. felis* in Hawaii; this is probably also true in Grenada, Trinidad and St. Croix, where *C. felis felis* is the only flea found so far on mongooses.

Ticks

Of 1,068 mongooses examined in Grenada, 80 (7.5 percent) were harbouring 195 ticks. A representative sample of ticks from 22 of these 80 animals was found to consist entirely of nymphs or larvae of *Amblyomma* and *Ornithodoros*. Where species identification was possible, these proved to be *A. ovale* and *O. puertoricensis*. In Trinidad, ticks were found on 3 of 80 animals (3.8 percent) examined; these were identified as larvae or nymphs of *Amblyomma* sp. and *Rhipicephalus sanguineus*.

SEAMAN (1963) reports *Ornithodoros puertoricensis* on 17 percent of 23 mongooses from St. Croix, with not more than five ticks on any one animal. WEBB (1972) found only *O. puertoricensis* present on 15 percent of mongooses from St. Croix. The average number on infested mongooses

was two per animal with a maximum of seven; adult ticks were found on only two specimens. Nymphs of the African Bont Tick, *Amblyomma variegatum*, have been found twice on mongooses from St. Croix (SHULTERBRANDT, 1970).

THOMPSON (1950) believes that much of what has been written about the mongoose/tick relationship in Jamaica is based on little evidence. He refutes much of STEIN's popular article in *Baily's Magazine* in 1903 (page 321), which claims that the increase in ticks during the preceding quarter century could be directly traced to the influence of the mongoose. THOMPSON found mongooses to be singularly free of ticks, and the only specimens found by him from "six examples" were larvae of *Ornithodoros*. He reports that in 1941 TATE found only one unengorged larva of *Boophilus annulatus microplus* from 15 mongooses in Puerto Rico.

The absence of adult ticks on mongooses from Trinidad and Grenada, and the very few found on specimens from St. Croix, suggests that *H. a. auropunctatus* may not be the normal host for the tick species found on the islands, which is not surprising since mongooses are introduced animals. However, it is possible that larger ticks are removed by the host. Tick host preference during the life history may also account for the absence of adults. EVERARD & TIKASINGH (1973a) found mostly immature stages of the ticks *Amblyomma longirostre*, *A. ovale*, *A. humerale*, and *Ixodes luciae* on the forest rodents *Proechimys guyannensis trinitatis* and *Oryzomys capito velutinus* in Trinidad. FAIRCHILD *et al.* (1966) in Panamá suggest that rodents may be the preferred hosts of the earlier stages of *Ixodes luciae* and possibly other tick genera as well.

HOOGSTRAAL *et al.* (1968) found the ixodide ticks *Aponomma pattori*, *Haemaphysalis histricus*, and *H. larangei* on mongooses in Danang, Vietnam. *A. pattori* are commonly found on snakes, and it is suggested that the mongooses acquired the ticks while eating snakes. HOOGSTRAAL (1970) found mongooses to be the preferred hosts of *Haemaphysalis indica* which have a distribution in West Pakistan, India and Ceylon.

Mites

Mites were found on 107 of 1,068 Grenadian mongooses examined, or almost exactly 10 percent. A representative sample of mites from 26 animals is listed in Table 23. All but one were found to be free-living forms, so that presumably they accidentally adhered to the fur of the hosts as they

TABLE 23
FREE-LIVING MITES FROM *Herpestes* ON GRENADA

	Family	Number of mongooses infested
<i>Uroactinia anchor</i>	Uroactiniidae	1
<i>Archezogetes</i> sp.	Trhypochthoniidae	5
<i>Oppia</i> sp.	Oppiidae	6
<i>Oribatula</i> sp.	Oribatulidae	2
<i>Dynatozetes</i> sp.	Mochlozetidae	*
<i>Eutrachytes</i> sp.	Eutrachytidae	9
<i>Gamasiphis</i> sp.	Rhodacaridae	1
<i>Parasitus</i> sp.	Parasitidae	1
<i>Liodes</i> sp.	Neolioididae	**
<i>Mochlozetes</i> sp.	Mochlozetidae	1

* Found on a mongoose with *Oppia*.

** Found on the mongoose with *Mochlozetes*.

passed through vegetation. *Eutrachytes* was found to be the most prevalent mite (21 percent) of the total collection. The parasitic specimen was identified as *Androlaelaps*: Laelaptidae.

Mites from 5 of 86 Trinidadian mongooses (5.8 percent infested) were identified as *Eutrombicula goeldii*, *Ornithonyssus bacoti*, and *Glypholaspis americana*. There were no free-living forms. BRENNAN & JONES (1960) also recorded *E. goeldii* and *Euschöngastia downsi* from Trinidadian *Herpestes*.

Mange mites of the genus *Notoedres* were reported from one mongoose on St. Croix by SEAMAN (1953), and WEBB (1972) identified the mange mite, *Notoedres cati*, from one mongoose on St. Croix. It is assumed that *N. cati* is the agent responsible for the advanced cases of mange which we have observed in areas of unusually high mongoose density, such as garbage dumps on St. Croix. LOOMIS (pers. comm.) and GARRETT & HARAMOTA (1967) report *N. cati* on mongooses from Hawaii, but COLE & KOEPKE (1947) do not identify the 24 mites they found on mongooses there.

Other ectoparasites

Robust bot flies (Cuterebridae) have not been found on Grenadian mongooses, but *Cuterebra* spp. have been found on mongooses from Trinidad (EVERARD & AITKEN, 1972). Cuterebrids cause a characteristic

and easily discernible bot lesion on the posterior flank or inguinal region of mongooses and other small mammals. Three of 207 (1.4 percent) Trinidadian mongooses examined were infested; in all three cases the larvae dropped from the dermal pocket in the usual way prior to pupation, but they were eaten by the host before eclosion could take place. Species identification was therefore not possible. EVERARD & AITKEN (1972) also record the species of *Cuterebra* so far identified from other small mammals in Trinidad. In South Africa, ZUMPT (1971) has found the yellow mongoose (*Cynictis penicillata*) infested with a similar fly, *Cordylobia anthropophaga*. This author also records the work of BLACKLOCK & THOMPSON who found "a mongoose" in Sierra Leone infested with the same parasite in 1923.

We did not observe any Mallophaga (biting or bird lice) on mongooses from Trinidad, Grenada or St. Croix, but AITKEN (pers. comm.) has recorded *Oxylipurus dentatus* (3), *Goniocotes gallinae* (2) and *Goniodes dissimilis* (4) from a single mongoose caught at Arima, Trinidad, in 1953. He has also found *Menopon gallinae* on a Trinidadian mongoose, but the locality record has been lost. HOPKINS (1949) records lice species of the genus *Felicola* from several different mongooses, including seven species of *Herpestes*, but he does not include *H. a. auropunctatus*. However, *Felicola rohani* was collected from *H. auropunctatus* in Katmandu (EMERSON, 1971). COLE & KOEPKE (1947) do not name the six lice they found on mongooses in Hawaii.

ENDOPARASITES

Blood from more than 2,300 mongooses from Trinidad and Grenada was screened microscopically for microfilariae, trypanosomes, haemogregarines and haemosporidia, but no evidence of these was found. EVERARD (1975b) has frequently found representatives from the above groups in reptiles and small forest-dwelling mammals in Trinidad. GREWAL (1955) found two new trypanosomes in the African mongoose and the Egyptian mongoose (ichneumon). The natural vector was not known, but development could be followed completely in *Rhodnius prolixus*.

Only two juvenile acanthocephala were found in a mongoose from Trinidad, one in the intestinal tract and the other in the dermis. In St. Croix several acanthocephala were found embedded in the muscle of one mon-

goose. Specimens from both islands were identified as members of the Family Oligacanthorhynchidae, probably *Oligacanthorhynchus* or *Oncicola*. There are no records of acanthocephala from mongooses elsewhere, as far as we are aware.

Only three genera of small intestinal nematodes, *Physaloptera* (Spiruroidea), *Capillaria* (Trichuroidea), and *Skrjabinocapillaria* (Trichuroidea), were found in 55 of 1,117 (4.9 percent) Grenadian mongooses examined, and in 10 of 80 (12.5 percent) Trinidadian specimens. The worm burden was generally small. There were no cestodes or trematodes, nor have any been reported by other workers in the Caribbean. KHALIL (1977) described specimens of *Skrjabinocapillaria* collected by us in St. Croix and Trinidad as a new species, *S. caballeroi*. In St. Croix, WEBB (1972) has noted at least two species of *Capillaria* in 21 of 100 mongooses examined, and *Strongyloides* (Rhabdiasoidea) in six of them; in Puerto Rico PIMENTEL (1955a) found no intestinal parasites in 210 mongooses examined. HUIZINGA *et al.* (1976) recovered a species of *Capillaria* from the kidneys of 28 of 30 (93.3 percent) mongooses from St. Lucia, W.I. SLONKA *et al.* (1976) found no *Trichinella spiralis* in 38 mongooses on St. Croix.

It appears that there are relatively few species of macro-endoparasites in *H. a. auropunctatus* from the Caribbean area, and there are only a few records from elsewhere. These are given here for the sake of completeness.

BALDWIN *et al.* (1952) reported the absence of intestinal parasites in mongooses in Hawaii, though ALICATA in BALDWIN *et al.* (1952) found *Trichinella spiralis* in 15 of 70 mongooses on the Island of Hawaii, and in 2 of 22 mongooses in Maui. STEMMERMANN & HAYASHI (1970) found 8 of 57 Hawaiian mongooses infested with parasites resembling *Strongyloides*. LIANG-SHENG (1958) gives a redescription of the nematode *Pulmostrongylus herpestis* (Metastrongylidae) obtained from the lung of a mongoose, *Herpestes* sp. (probably *H. auropunctatus* or *H. javanicus*), on Fiji. *Pulmostrongylus fengi* is the only other species in the genus described from the mongoose, *H. urva*, from Indo-China. LIANG-SHENG shows that the genus *Herpestostrongylus* Khera is untenable and should be regarded as a synonym for *Pulmostrongylus* Hsu. WOOD (1965) recovered *Angiostrongylus cantonensis* (Strongyloidea) from the heart and pulmonary arteries of *Herpestes urva* (Formosan crab-eating mongoose) following experimental infection. LIM (1970) found *Pulmostrongylus herpestis*, dicrocoelid trematodes, and filarioid worms in *H. auropunctatus* from West Malaysia, but his experimental observations indicate that this animal is not a suitable host for *Angiostrongylus cantonensis*. CROSS *et al.* (1970) also consider that the mongoose (in this case *H. urva* on Formosa) is not a suitable host for *A. cantonensis*. *A. cantonensis* from the Indo-Pacific area is regarded as the cause of eosinophilic meningitis in man and has been found in adult form in the pulmonary vessels of murine rodents which are considered to be the natural vertebrate hosts. Larval stages are found in snails such as *Australorbis glabratus* and *Subulina octona*. CORNIOU (pers. comm.) examined 200 peridomestic *Rattus* from Port-of-Spain (Trinidad) wharfs but did not en-

counter *Angiostrongylus* in the pulmonary vessels. KANNANGARA & KARUNARATNE (1969) record the lung fluke, *Paragonimus siamensis*, for the first time in Sri Lanka from a naturally-infected grey mongoose, *Herpestes lanka* (syn. *H. edwardsi*, HINTON & DUNN, 1967). According to these Sinhalese authors, their species most closely resembles *P. compactus* described by VEVERS from the mongoose in India. The cestodes *Oochoristica amphisbeteta* and *Sparganum* sp. have been taken from *H. auro-punctatus* (called *H. albopunctatus* Hodgson, 1853) in Burma (MEGGITT, 1924). JOHRI (1961) described a new species of the cestode genus *Mathevo-taenia* as *M. hardioensis* from *Herpestes javanicus auro-punctatus* in India.

No search was made for protozoans in the alimentary tract of Grenadian and Trinidadian mongooses, but six mongooses from St. Croix contained assorted protozoa, including unidentified amoebae and *Entamoeba*-like cysts, coccidians, *Chilomastix*-like cysts and *Giardia*. There is no reason to suppose that similar protozoa would not be found in mongooses from Trinidad and Grenada.

NAVARATHNAM (1970) describes a new species of Trichomonad, *Pentatrichomonas smithi*, from the caecum of *Herpestes smithi* taken at Hyderabad, India. *Isospora* (Coccidia) was found to be a common parasite of the yellow mongoose *Cynictis penicillata* from Western Transvaal, South Africa (MARKUS, 1972). KNOWLES & DAS GUPTA (1931) record *Isospora* (possibly *I. rivolta*) and typical *Trichomonas*-like organisms from the caecum of *H. auro-punctatus* near Calcutta. VAN PEENEN *et al.* (1968) collected *Babesia* sp. from *H. javanicus* in South Vietnam.

When the carnivorous/omnivorous diet of *H. a. auro-punctatus* is considered, it is surprising that a greater assortment of intestinal parasites is not found in this animal, not only in the Western Hemisphere but elsewhere. It appears that the general trend of a host to have a greater parasitic burden in its indigenous habitat than in an area to which it has been introduced holds well for *H. a. auro-punctatus*. Parasites with a direct transfer mechanism between hosts of the same species probably survive better than those with one or more intermediate hosts.

DISEASES

RABIES

The most important communicable disease transmitted by mongooses in the Americas, Africa and Asia is rabies. BISSERU (1972) records mongoose rabies from Botswana, Kenya, Nigeria, Rhodesia, and South Africa. In Africa, the most commonly involved species are the yellow mongoose, *Cynictis penicillata*, and the meerkat or suricate, *Suricata suricatta*; other

mongooses such as *Atilax* and *Herpestes*, and the striped weasel, *Poecilogale*, may also be involved. Additional information on mongoose rabies in South Africa is provided by SNYMAN (1940), ZUMPT (1969), and BISSERU (1972). In Asia, BISSERU reports mongoose-transmitted rabies from Sri Lanka and India. WEST (1972) states that, in Israel, wildlife rabies has involved the mongoose *Herpestes ichneumon*.

TIERKEL *et al.* (1952) reported the first major outbreak of mongoose rabies in the Western Hemisphere from Puerto Rico in 1950 associated with *Herpestes javanicus* (see section on nomenclature), though it should be noted that rabies in Puerto Rico dates back to at least 1841, over 30 years before the introduction of the mongoose (COLON, 1930). However, until the 1950 outbreak Puerto Rico had been considered free from rabies, as no cases had been confirmed since 1933. Elsewhere in the Caribbean, mongoose rabies has been recorded in Grenada, Cuba and the Dominican Republic. It may also be present in Haiti. The history of rabies in Grenada is given by EVERARD *et al.* (1972), while EVERARD *et al.* (1974) give an account of the epidemiology of the disease in the island and describe the behaviour of rabid mongooses. EVERARD *et al.* (1979a) report on 10 years of surveillance of mongoose rabies on Grenada, and EVERARD *et al.* (1981) report the results of studies on rabies SN antibodies in mongooses. From the *Weekly Epidemiological Record* (1976), reported cases of rabies (including mongooses) in 1974 in Cuba, the Dominican Republic, Puerto Rico and Haiti numbered 177, 107, 57 and 27, respectively. On the remaining Caribbean islands, rabies is known only in Trinidad, where the vampire bat, *Desmodus rotundus*, is the principal vector; mongooses are not known to be involved in the epidemiology of the disease on that island. The Virgin Islands are at present free of rabies. WEST (1972) claims that the mongoose now acts as a major reservoir in Panamá, but we have found no supporting evidence of this.

Because the mongoose is the major reservoir of rabies on Grenada and this disease has achieved economic and public health significance, it is felt that a discussion of the ecology of the mongoose would not be complete without a brief account of the epidemiology of rabies on the island, even though most of this information is published in detail elsewhere.

Rabies was first seriously suspected in Grenada in the late nineteen-forties; because of the known involvement of vampire bats in rabies

epizootics in Trinidad (HURST & PAWAN, 1931 and 1932), bat rabies was suspected, but a survey found no evidence of bat bites on cattle or of the presence of the vampire, *Desmodus*. The first laboratory-confirmed case of rabies (in a cow) was reported in 1952, and in the following year a cow known to have been bitten by a mongoose died of rabies. The first laboratory confirmation of rabies in a dog was in 1955, and that of rabies in a mongoose in early 1956, when an animal was killed after it had bitten a person. The first rabies control programme (under the Pan American Sanitary Bureau) commenced in early 1956, and a preliminary report on this was made by the Veterinary Officer (COCOZZA, 1956) in June of that year. Mongoose poisoning and compulsory dog vaccination were put into effect, and it was adjudged that 10,000 mongooses had been poisoned. The accidental poisoning of dogs put this part of the programme into disrepute, causing it to be suspended (MURRAY, 1968). The whole programme was gradually discontinued, though the vaccination of dogs was continued on a voluntary basis. In 1959, a bounty system was introduced for a short while.

The death of three people from rabies in the years 1962 to 1963 and the increase in the numbers of cases of animal rabies prompted a reappraisal of the situation and the initiation of a further control programme in 1965. This is reported in some detail by PRESNALL (1965), TAYLOR (1965), and PRESNALL (1966). During 1966, 1967 and early 1968, the programme was markedly reduced, and in 1967 there was no poisoning. SIKES *et al.* (1968) reported success in controlling the disease in humans and dogs but no substantial reduction in the number of mongooses. An enhanced programme was undertaken in 1968, and this was reviewed by PRESNALL (1969).

The increase in the number of people receiving antirabies prophylaxis during 1970 as a consequence of bites, and the death of a child in November of that year, prompted a further appraisal of the rabies control programme early in the next year (WINKLER, 1971). A major dog vaccination programme was conducted by the Grenada Government in 1971. In early 1973 the Grenada Government and Pan American Health Organization initiated a mongoose poisoning campaign and programmes for the vaccination of livestock and domestic animals. This work was terminated abruptly in early 1974 because of difficulties in Grenada at that time.

The dog vaccination programmes on Grenada are reported by EVERARD

et al. (1972) and EVERARD *et al.* (1979a). During the six major campaigns undertaken between 1965 and 1976 42,622 doses of vaccine were used on dogs; an additional 2,903 doses were used in the interim years to include those animals that had been too young or had missed vaccination previously. The number of dogs considered rabid by clinical assessment and/or laboratory testing during the period 1955 to 1967 was 88, while the number of rabid cats was only 3 (EVERARD *et al.*, 1972). The total numbers of cases between 1952 (when records were first kept) and 1976 were 115 and 15 for dogs and cats, respectively. There were 6.8 rabid dogs per year between 1955 and 1967 (88/13) and 3.0 per year between 1968 and 1976 (27/9), indicating the reduction in numbers of dog rabies cases in years following vaccination. However, the five cases of dog rabies in 1976 were disquieting, especially when it was realized that one of the rabid dogs bit 3 persons.

Livestock reported rabid during the 10-year period of 1968 to 1977 totalled 113 animals, including one unknown (Table 24). The observed range in the number of bovines recorded rabid per year during the period was 2 to 13, mean 6; the range in numbers of all categories of livestock together recorded rabid per year in the same period was 6 to 30, mean 12.

The number of rabid mongooses recorded on Grenada between 1952 and 1967 was 142 (EVERARD *et al.*, 1972). The results of tests on samples of trapped and attacking mongooses sent to TRVL between 1965 and March 1968 are reported by JONKERS *et al.* (1969); 2 of 75 (2.7 percent), 8 of 191 (4.2 percent) and 12 of 262 (4.6 percent) trapped mongooses were diagnosed as rabid in the years 1965, 1966 and 1967, respectively. The total number of rabid mongooses that had been found on Grenada by 1977 was 142 + 541 = 683 (Table 24). The recorded range per year was 31 to 107, mean 54. Of importance is the fact that there was a highly significant difference ($p < 0.001$) between the ratios of rabies-positive trapped mongooses to the total number of trapped mongooses for each of the 10 years, 1968 to 1977. This suggests that a natural fluctuation of wildlife rabies occurs in the mongoose population, which is reflected in the decrease from 3.7 percent trapped rabid mongooses in 1968 to 0.5 percent in 1970, and the subsequent increase to 3.5 percent in 1971 with the corresponding more gradual decline to 0.14 percent by 1977 (EVERARD *et al.*, 1979a). Mongoose rabies occurs throughout the island.

Rabies SN antibodies at a titre greater than 1:5 were found in 498 of

TABLE 24
RECORDED CASES OF RABIES ON GRENADA BETWEEN 1968 AND 1977

Host	Number	Percentage
Human	1	0.1
Opossum, <i>Didelphis</i>	1	0.1
Bat	2	0.1
Mongoose	541	77.4
Dog	29	4.1
Cat	12	1.7
Bovine	60	8.6
Goat	19	2.7
Sheep	14	2.0
Pig	11	1.6
Equine	8	1.2
Unknown	1	0.1
Total	699	100

1,675 (29.7 percent) mongooses tested between 1971 and 1974. The lowest and highest proportions of antibody-protected mongooses from selected localities were 9.1 percent (3 of 33) in northern Grenada and 54.5 percent (30 of 55) on the central west coast (EVERARD *et al.*, 1981). From a sample of 127 mongooses, 7.1 percent had a SN antibody titre of >1:1,000; the highest titre recorded was 1:5,900 (EVERARD *et al.*, 1974).

Rabies in wildlife other than mongooses has also been documented in Grenada. A *Molossus* bat bit a woman in 1961; what must almost certainly be a spurious case in an opossum (*Didelphis*) was recorded in 1969 (EVERARD *et al.*, 1972); and two cases were recorded from bats in 1974, one of which (*Artibeus*) was confirmed in the laboratory (PRICE & EVERARD, 1977). The 699 cases of rabies reported in Grenada between 1968 to 1977 are recorded in Table 24.

The isolation of rabies virus from a frugivorous bat, *Artibeus jamaicensis*, in 1974 led to the investigation of additional bat specimens, but none was found to be rabies-positive. Rabies SN antibody studies, however, showed that antibody was present in 27 of 353 (7.6 percent) bats involving the following 6 species: *Anoura geoffroyi*, *Artibeus jamaicensis*, *Artibeus cinereus*, *Glossophaga longirostris*, *Molossus molossus* (formerly *M. major*), and *Sturnira lilium*. The highest proportion of antibody was

found in 17 of 42 (40.5 percent) *Artibeus jamaicensis* from the west coast of Grenada (PRICE & EVERARD, 1977). However, bats are not thought to play a significant role in the transmission of rabies to other hosts in Grenada.

Only four humans have died of rabies on Grenada as far as is known, three in the period 1962 to 1963 (2 of which were attributable to dog bites and one to a cat bite) and one in 1970 from an unknown source of exposure (EVERARD *et al.*, 1972). Post-exposure antirabies treatment in humans averaged 20.8 cases per year (range 5 to 45) during the period 1968 to 1977; no records of treatment are available prior to 1968. The contacts of the cases requiring treatment are recorded by EVERARD *et al.* (1979a). Between 1968 and 1977, bites from attacking mongooses precipitated 57 percent of all treatments, and the average number of mongooses biting humans per year was 11.9, observed range 5 to 22. Two incidents exemplifying unprovoked mongoose attacks are reported: on November 24 1973 in Clozier, St. John's, a 22-year-old woman was taking clothes from the line in the yard of her farm when she was suddenly bitten on the right side of her right foot. Not being able to kill the attacking mongoose, she ran into the house for protection, from where she observed the animal frantically attacking a tannia bush; the mongoose escaped. On 26 January 1974 in Maran, St. John's, at 7 p.m. a distraught one-year-old child was found inside the house with a mongoose attached to her nose. The animal was killed, and the child was taken to the hospital. The mongoose was found to be rabid on examination at the laboratory.

LEPTOSPIROSIS

From the standpoint of public health, leptospirosis is probably the second most important disease of which mongooses are known carriers and perhaps disseminators. We investigated the presence of leptospiral antibodies in mongooses by the microscopic agglutination (MA) test described by GALTON *et al.* (1962) and SULZER & JONES (1976), and we isolated the organisms from kidney tissue according to the methods described by TURNER (1970) and SULZER & JONES (1976).

The presence of antibodies to *Leptospira* in Grenadian mongooses is reported by EVERARD *et al.* (1976). Leptospiral infection was found in 35 percent (152 of 432) of those examined. Seropositive titres ranged from 1:100 to 1:12,800, with most at 1:400. At least three serogroups were

present. They were Icterohaemorrhagiae in 57 mongooses (37 percent of the positive sample), Pomona in 32 (21 percent) and Canicola in 10 (7 percent). The remaining 53 cases (35 percent) showed evidence of more than one infection, with Icterohaemorrhagiae most frequently showing the highest titre of those recorded present. The fact that more than one serogroup was detected in some of the mongooses suggests previous or multiple infection in addition to any serological cross-reactions. No geographical distinction of serogroups within the island could be discerned.

The proportion of seropositive mongooses in Trinidad ranged from 33 to 51 percent of those examined. Serogroup Canicola predominated, but Icterohaemorrhagiae and Pomona were also encountered. Titres from 1:100 to 1:12,800 were also recorded for these animals.

In Grenada, *Leptospira* isolates were made from 10 mongooses. They were identified as: Icterohaemorrhagiae *copenhageni* (4), *Bataviae brasiliensis* (5) and *Tarassovi atchafalaya* (1) (EVERARD *et al.*, 1980). Serovar *canicola* in the Canicola serogroup was isolated from the kidneys of 5 of 106 mongooses in Trinidad (EVERARD *et al.*, 1976). Isolates from two of a further nine mongooses examined were shown to be *Canicola canicola* and *Panama mangus*. GREEN *et al.* (1978) report this *mangus* isolate as a new serovar. This is the first isolate of serogroup Panama in Trinidad, and the first record of this serogroup in the mongoose. All 100 *Leptospira* isolates obtained from humans and animals on Trinidad and Grenada are reported by EVERARD *et al.* (1980).

Leptospirosis has not been previously reported from wildlife on St. Croix. In a sample of 21 mongooses, 14 were seropositive to *Hebdomadis wolffi* antigen at titres between 1:100 and 1:12,800. One of these was also positive to *Hebdomadis georgia* antigen. A second sample of 21 mongooses consisted of seven animals (4 of which were positive to *H. wolffi*) trapped in a remote area without resident dogs, and 14 animals which were taken within areas containing both feral and domestic dogs at high density. Seven of this latter group of 14 were also seropositive to *H. wolffi*. Thus, leptospirosis can be maintained in mongooses independently of dogs, but interspecific cross infection may also occur. Dogs on Trinidad have been found infected mainly with serogroups Canicola and Icterohaemorrhagiae (EVERARD *et al.*, 1979c), as is the case with mongooses.

Early reports of leptospirosis in the Caribbean are those of DOWNS *et al.* (1962) and cyclostyled documents listed in the bibliography as REPORT I and II (1968). From REPORT I, covering the period January 1967 to December 1968 in Jamaica, nine isolates were made from 40 mongooses (23 percent). The two main serogroups involved were Icterohaemorrhagiae and Hebdomadis (*jules*). URQUHART (pers. comm.) also found that Icterohaemorrhagiae was the predominant serogroup in mongooses from Jamaica between 1967 and 1971, with reactions to serovar *jules* from the Hebdomadis serogroup also recorded; 32 percent of those examined were seropositive. DAMUDE *et al.* (1979) report the isolation of *Autumnalis fortbragg* from a mongoose in Barbados. Reports by ALEXANDER *et al.* (1963) and YEAGER in PIMENTEL (1955a) (both from Puerto Rico), and SPENCE *et al.* (1972) in Trinidad also form part of the bibliographical background to the disease in the Caribbean.

In Hawaii, ALICATA & BREAKS (1943), ALICATA (1958) and MINETTE (1964) are among those who have reported on the disease in the mongoose. MINETTE (1964) reports serogroup Icterohaemorrhagiae predominant in *H. auropunctatus* from Hawaii, with *Canicola* and Hebdomadis (*sejroe*), but not Ballum, also present; 33 percent of the mongooses examined were positive by serological or isolation techniques. More recent work in Hawaii (Oahu) by HIGA & FUJINAKA (1976) showed that 22 percent of mongooses examined (53 of 241) were serologically positive, with 12 percent reactive to serovar *sejroe* in the Hebdomadis serogroup, 7 percent to Icterohaemorrhagiae, <2 percent to Ballum and <1 percent to *Canicola*. Further, 23 percent (65 of 282) mongooses examined in Hawaii were culture-positive; of 60 cultures identified, 85 percent (51) were Hebdomadis *sejroe*, 13 percent (8) were Icterohaemorrhagiae, and 2 percent (1) were *Canicola*.

ROTH (1970) mentions that the three most important serogroups from a public health and domestic animal standpoint are Icterohaemorrhagiae, *Canicola* and *Pomona*, which are those found in Grenada. The percentages of seropositive mongooses from Jamaica, Trinidad, Grenada and Hawaii are remarkably consistent.

OTHER DISEASES AND PATHOGENS

1. Canine distemper

Goss (1948) found no susceptibility to canine distemper in *Herpestes nyula* [sic] (probably *H. edwardsi*) but observed typical inclusion bodies in another viverrid, the binturong (*Arctictis binturong*), which died after

showing signs of the disease. WINKLER, at the Centers for Disease Control (pers. comm.), has injected canine distemper virus intramuscularly and intranasally into *H. auro-punctatus*, causing death by viral pneumonia in 19 days. Sera from 63 wild mongooses from St. Croix were examined at Cornell University Veterinary Virus Laboratory using methods described by DAVIS *et al.* (1973), DAVIS *et al.* (1970) and SIEGMUND (1973). One animal was found to have a titre of 1:310 for canine distemper virus.

2. Canine hepatitis

Four of the 63 mongooses examined at Cornell University were found to have positive titres ranging from 1:500 to 1:25,000 for infectious canine hepatitis. Six mongooses injected with standardized suspensions of the virus failed to show any clinical signs of disease.

3. Feline panleukopenia

One ml of feline panleukopenia virus provided by the Pittman-Moore Drug Co. with a titre of $10^{4.3}$ TCID₅₀/ml was injected intraperitoneally into 10 mongooses from St. Croix. No signs of disease were apparent after 20 days. Civets, the only viverrids noted by Goss (1948), were considered by him to be non-susceptible. Much remains to be learned about the susceptibility of the Viverridae in general and *Herpestes* in particular to carnivore diseases.

4. Pulmonary virus

Mongooses exposed to rain and damp in traps were observed to be more susceptible to illness and death than were those exposed for an equivalent period in fine weather, suggesting the possibility of a latent pulmonary infection. Also, a virus capable of producing consolidation in Jamaican mongooses was isolated from human patients in the United States with a clinical syndrome termed acute pneumonitis (WEIR & HORSFALL, 1940). An attempt was therefore made to recover a viral agent from the lung tissues of 58 mongooses on Grenada. Fresh or frozen lung tissue was inoculated into human embryonic kidney (HEK) and monkey kidney (MK) cell cultures according to the method described by SCHMIDT (1969),

but no viruses were isolated. HAYASHI & STEMMERMANN (1972) found a lipid pneumonia in 30 of 57 Hawaiian mongooses.

5. *Toxoplasma*

Because more than 56 percent of human sera tested in Trinidad were found to have antibodies to *Toxoplasma* (LUNDE & JACOBS, 1958), 12 mongoose sera from Trinidad were subjected to the agglutination test of FULTON (1965) in 1970; two had titres of 1:16. In 1973, 287 mongoose sera from Grenada were examined by the indirect immunofluorescence test described by GOLDMAN (1957) and GARIN *et al.* (1967). All of them were negative. *Toxoplasma* may well be absent in Grenadian mongooses, but further studies on *Herpestes* from Trinidad are indicated.

6. *Streptococcus*

Discrete white pustular lesions observed on the lung and liver of two trapped mongooses from Grenada were excised aseptically and teased out. Some of the teased material was cultured on Sabouraud's agar, and the remainder was stained in Giemsa and examined under a microscope. Micrococci which were observed on the agar after 4 days were sub-cultured on blood-agar plates and sent to Rockefeller University for typing. The micrococci were identified as "Group D" *Streptococcus*. This group is found in other animals as an intestinal pathogen, so that the foci on the lungs may be considered unusual.

7. *Salmonella*

Examination and culture of the intestinal contents of 23 mongooses caught in Trinidad resulted in the isolation of *Salmonella* from 3 of them. The isolates were identified as *S. corvallis* (1) and *S. johannesburg* (2). On Grenada, 6 *Salmonella* isolates were obtained from 11 mongooses examined; they were identified as *S. agona* (1), *S. corvallis* (2), *S. panama* (1) and *S. wernigerode* (2) (EVERARD *et al.*, 1979b).

Elsewhere, plague bacillus (*Yersinia pestis*) is reported for three mongoose species, *Suricata suricatta* and *Cynictis penicillata* of Southern Africa (MEYER, 1963), and *Herpestes* in Hawaii (MEYER *et al.*, 1965). Rickettsial complement fixation (CF) antibodies at low titres

were found in the mongooses *Herpestes sanguineus*, *Bdeogale crassicauda* and *Ichneumia albicauda* in Kenya (HEISCH *et al.*, 1962). HOTCHIN & BENSON (1970) report on lymphocytic choriomeningitis virus from several animals, including *Herpestes ichneumon numidicus*, in Morocco. Mongooses are known to harbour encephalomyocarditis virus (HULL, 1963). HINSLEY & YOKOYAMA (1970) report on serologic studies involving isoagglutinogens from mongooses on Hawaii and note a variety of pathological conditions reported by other authors. Further accounts of pathological findings are given by STEMERMANN & HAYASHI (1970), and the diseases of different mongoose genera are partially reviewed by HINTON & DUNN (1967).

CONCLUSION

Just over a century has elapsed since the mongoose was established in the Carribean, and from a handful of animals has grown a population which in places rivals the black rat as a pest. Personal communications from Antigua, Haiti and Barbados indicate that the mongoose may still be a considerable nuisance, as it is in St. Croix, particularly during periods of population increase. However, because economic change and the diversification of agricultural practices have removed the sugarcane industry from its position of dominance on the majority of the islands, little attention is now given to the problem of rodent damage in canefields, and this has become a forgotten issue at Government level. It also appears that the mongoose-rat association has adjusted to a natural balance of predator and prey in most areas. Ironically, those islands, chiefly Jamaica and Trinidad, which formerly suffered the heaviest damage are now the least affected by the mongoose, while Grenada, whose report to a Commission of Enquiry in 1890 (ANONYMOUS, 1918) stated that the mongoose was not a serious pest, now pays a price which, seen against the overall budget for the island, it can ill afford. In 1973 the Government of Grenada budgeted more than 0.4 percent of its entire revenue for that year for mongoose control, and this figure does not include the cost of equipment, pre-exposure vaccination, or staff provided by the Pan American Health Organization and the MRC; nor does it take into account the loss of livestock through rabies, or the cost of human antirabies treatment.

WILLIAMS (1918) found that the mongoose was neither entirely harmful nor entirely beneficial. He drew up a balance sheet for the mongoose in Trinidad in which over a period of 3 months he debited one animal with 26 birds, 17 lizards, 29 frogs and toads, 44 useful insects and 44 spiders; and he listed 28 rats, 600 injurious insects and 3 crabs to its credit. While there is no reason to suppose that this balance has shifted in Trinidad from the point of view of pest status, the incrimination in the 1950's of the mongoose in Puerto Rico and Grenada as a carrier of rabies, and its potential as such on Trinidad and other islands, have brought new factors into consideration. Further, *Herpestes* may play nearly as significant a role in the dissemination of leptospirosis to man and animals in the Caribbean and Hawaii as that attributed to peridomestic rodents.

Certainly in Grenada the mongoose has very little to its credit. Between

1968 and 1977, 57 percent (119 of 208) of human exposures in Grenada resulted directly from mongoose bites; in this same period there were nearly 700 recorded cases of rabies. Mongooses alone accounted for 541 of them. All the known sources of livestock rabies on the island have been mongooses and not dogs or cats.

The transmission of rabies by Vampire bats (*Desmodus* or *Diaemus*) to man and livestock is well documented (BAER, 1975a), but the ecological relationships between non-haematophagous bats and livestock, domestic pets, and terrestrial wildlife, including carnivores, are little known. BAER (1975a and b) points out, and observations on St. Croix confirm, that there is much evidence that predators regularly consume bats in cave roosts; there is, therefore, occasion for carnivores to be exposed to rabies virus by aerosol (CONSTANTINE, 1967), ingestion of sick bats, or bites from moribund bats. The magnitude of the problem can be seen from the fact that in the United States rabies continues to be more widely distributed in bats than in any other single wildlife host. Here, it is of interest that the geographic distribution of cases in bats appears to be largely independent of the cases reported from terrestrial animals (ZONOSSES SURVEILLANCE, 1976). In Trinidad, rabies is known from several genera of bats, including haematophagous and non-haematophagous types, with involvement of livestock through transmission by vampire species; mongooses, other wildlife and domestic pets have not been involved as far as is known. Rabies can therefore exist in bats without transmission to other available hosts; it can also exist in different species of bats independently of each other. However, any attempt to control rabies in a mongoose population would have to take into account the possibility that a coexisting population of rabid bats may well reintroduce the disease.

If no attempt was made to control the mongoose on Grenada, it could be predicted that a continuous threshold of wildlife rabies would be maintained, with a limited observable fluctuation. Using data on mongooses trapped between 1968 and 1977, EVERARD *et al.* (1979a) found 156 of 11,917 examined to be positive for rabies. The 99 percent confidence limits for the mean of 1.3 percent would range from 1.0 to 1.6 percent of the mongoose population rabid in any 10-year period. The population density calculated from the six different population samples on Grenada ranged between not less than 2.5 or more than 12.2 mongooses per ha. Our data indicate that 3.1 to 10 (mean, 6.2) animals may be utilizing a hectare of

land at any one time, so that the hypothetical island-wide population on Grenada (31,080 ha) may approximate to nearly 200,000 mongooses and probably not fewer than 77,000. Estimating further, 29.7 percent (see page 135) of the lower figure of 77,000 would give 22,870 mongooses with rabies SN antibodies; and when the mean of 1.3 percent rabid mongooses in the population is used, 1,000 could be rabid at any one time (range 3.68 percent or 2,834 to 0.14 percent or 108). If the mean figure of 6.2 mongooses per ha were used instead, the estimated numbers of diseased and immune animals would be considerably higher. Viewed against the total mongoose population, the trapping of less than 1,800 mongooses per year for the surveillance programme can only be regarded as negligible as a control measure.

Ineffectual control campaigns succeed only in reducing populations to a level which encourages a rapid build-up to the original density. Since there is also a possibility that the presence of rabies and conceivably that of leptospirosis in the mongoose population achieves this effect naturally, mongoose numbers on Grenada are more likely to fluctuate than to maintain a constant level. Population increases are more noticeable on smaller islands where animals have been forced to occupy most available habitats and areas, and where density variation between these areas is more marked. Provided that land utilization does not change significantly, the existing pattern of mongoose activity on Grenada will probably remain much as it is now, and natural fluctuations in the mongoose population are likely to continue in years to come.

ALLEE *et al.*, (1949) state that if the host population consists largely or entirely of susceptibles, the probability of cross-infection by chance contact is high, and the disease spreads rapidly. As the number of susceptibles is reduced through conversion to actual cases, fatalities and immune animals, the probability diminishes and the epidemic subsides. It seems likely that the fluctuation in the proportions of trapped rabid mongooses on Grenada can be accounted for in this way, especially when the island's oceanic barrier and limited size are considered. Partial population control may well bring about a reduction in the prevalence of rabies by reducing the contact rate, but it will almost certainly result in a rapid build-up of the population and a resurgence of the disease. It is presumed that this is what has been happening in Grenada ever since control programmes were first instigated.

Up to the present time the only method available for the control of wildlife rabies has been the drastic reduction of the reservoir species, and this is only practicable in suitable, limited areas. It has long been evident that present measures against the mongoose are inadequate. Until the early 1950's, control of the mongoose in the Caribbean was undertaken (to reduce agricultural losses) mainly by bounty hunting and organized trapping. However, it is unwise for governments to offer bounty in areas where rabies (and arguably leptospirosis) exist, and the use of trapping alone to control mongoose populations can only be regarded as ineffectual. Small island economy imposes a limit on resources, particularly the availability of traps, employees and transport; the heavy and bulky traps cannot be moved more than a limited distance from the nearest track or trace, especially in difficult, hilly country; and thus precipitous tracts of forest must go untrapped. The "cleared" area is left open to reinvasion from adjacent land, and the residual population, which may be substantial, is able to build up again before trapping starts once more in the same area. Trapping is best used to study the effectiveness of poisoning campaigns, to sample populations for rabies surveillance, and to control mongooses in those places in which it would be impracticable to place poison, such as urban areas, farms and small-holdings where cattle and other livestock graze. However, there is no reason why individuals should not set out traps simply to remove an excess of mongooses which may be a nuisance for agricultural or domestic reasons, though it should be recognized that such effort can provide only temporary relief.

The aim of recent control programmes, as yet unattained, has been to reduce the population density to a level at which contact between rabid and susceptible mongooses is so rare that transmission of the disease becomes unlikely. This objective can be achieved only with a continuous and thorough poisoning campaign in all areas over a number of years, treating adjacent areas in succession, and planning the campaign to take advantage of natural barriers, thus limiting invasion from areas not yet reached by the poisoning teams. Each area should be baited at least twice, and this would take a minimum of three years in Grenada. However, because poisoning will indiscriminately remove both immune and susceptible animals, there is a strong possibility that drastic population reduction will result in the eventual build-up of a succeeding non-immune population. Efficient poisoning may therefore defeat its own objective in

rabies control, and it must be stressed that it is futile to attempt prevention of rabies transmission by mongoose control unless maximum attention has been given to the prior immunization of all domestic animals and livestock, and unless suspect animals are immediately impounded and slaughtered. At the present time, continuous and effective vaccination and mongoose control programmes, with their necessary high level of planning, implementation and efficiency, are beyond the physical and economic capabilities of Grenada.

It is unlikely that the mongoose will ever be eradicated on any large Caribbean island, nor will rabies be eliminated from Grenada in the near future. *Herpestes* will probably never be eradicated by the efforts of man, nor will its numbers be substantially reduced by the trapping efforts of rural communities, especially as humans are averse to eating it and its pelt is of no present commercial value. In Grenada, the vaccination of domestic animals and livestock, the elimination of stray dogs, routine surveillance, and the ready availability of post-exposure vaccine are of immediate importance, and no member of the public nor any visitor should be left unaware of the danger of animal bites. The fact that rabies is present on Trinidad without mongoose involvement is no guarantee that mongoose populations on other islands would remain uninfected were rabies to be introduced; nor is it a surety that mongoose rabies will not develop on Trinidad in the foreseeable future.

The Virgin Islands are at present rabies-free and support large populations of feral dogs and cats in addition to mongooses. With no quarantine of imported carnivores and only limited vaccination of domestic pets, the introduction of rabies could set off an epidemic of crisis proportions. Contingency plans to be followed in the event of an outbreak of rabies (or even the detection of a single case of the disease) should be formulated now and revised regularly.

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