LOCOMOTION IN SOME EAST AFRICAN VIVERRIDS

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ABSTRACT.—Twelve species representing nine genera of East African viverrids were studied in captivity and in their natural habitats. Filmed sequences of captive animals showing walking, trotting, running, galloping, jumping, climbing, swimming, and burrowing were studied and are described, and where possible gait formulae are given. The types of locomotion used by different species of viverrids reflect divergent habitats and food preferences.

The viverrids in East Africa show considerable diversification, both with regard to their habits and to their locomotion. Little work has been done on the family, and Howell (1944) mentioned that nothing is known of the locomotion of the Viverridae. Nothing has been published since, and this account is intended as an introduction to the locomotion in the family.

There are 13 species of viverrids in Kenya, three of which are rare (one species was completely unobtainable) and several more of which have a restricted distribution. The viverrids from Tanzania and Uganda include a few additional species that are rare and were not obtained. My use of generic names in this paper follows Simpson (1945).

METHODS

Examples of 12 species of Kenyan viverrids (see Table 1 for scientific and vernacular names, physical characters, and habitats) have been observed. Inasmuch as most of these animals are nocturnal or elusive, the bulk of the observations used in this work are based on the behavior of captive animals, but some have also been photographed in the wild.

The analysis of the locomotor types was made by using 8-millimeter cine film at 16 and 64 frames per second. I took 160 meters of film, which I edited to 100 meters for the purpose of this study. The cartoon figures were traced on a square viewing box with a ground glass top. A large plain mirror was mounted inside at 45° to the horizontal, and a hole was cut in the side of the box for the projector beam. The mirror reflected the beam onto the ground glass screen and obviated the reversal of image that would occur if a back projection technique had been used. An Eumig P8 projector with zoom lens was used. For drawing the cartoons the film was wound through manually, and the number of each frame was noted, so that the position of each limb could be related to the gait pattern at any particular phase of the stride. Where the image is blurred due to the speed of movement, other sequences were studied to elucidate the analysis. In cases where the position of the claws or feet could not be observed in the film, the animals were studied closely in captivity to obtain the necessary information. The mode of analysis follows that used by Hildebrand (1959 and 1961) on the locomotion of the cheetah, though Hildebrand's (1964) recommended filming technique could not be carried out to the full, due to the size of the cages used (about 3.7 by 4.6 meters) and the difficulty in filming some of the animals.

WALKING

The stride of mongooses walking is similar to that found in dogs, and can be divided into two parts, an elevation or protraction period and a contact or

TABLE 1.—*Comparisons of dimensions and habitats of East African Viverridae.*

Species	Common name	No. of speci-mens	Head and body length (mm)	Tail length (mm)	Weight (kg)	Habitat
Atilax paludinosus	Marsh mongoose	2	440–510	280–355	1.8–2.7	Near streams, rivers, and marshes.
Bdeogale crassicauda	Northern four-toed mongoose	7	420–470	200–245	1.0–1.5	Coastal forest, acacia woodland, rocky hills.
Civettictis civetta	African civet	2	710–790	380–450	10.0–11.3	Forest, thick acacia wood to open grassland.
Genetta genetta	Genet	11	410–520	410–500	1.0–2.0	Acacia bush, regions < 67 mm. rain per annum.
Genetta servalina	Genet	1	435	420	1.25	Forest and thick wood, > 160 mm. rain per annum.
Genetta tigrina	Genet	26	370–545	330–465	1.2–2.0	Most habitats, 67–160 mm. rain per annum.
Helogale parvula	Pygmy mongoose	2	228–280	152–180	0.25–0.34	Open bush and grassland.
Herpestes ichneumon	Gray mongoose	1	570	490	2.7	Most open habitats.
Herpestes sanguineus	Black-tipped mongoose	42	275–400	230–330	0.35–0.9	All habitats except thick forest.
Ichneumia albicauda	White-tailed mongoose	17	470–690	355–460	1.8–4.5	Light woodland to plains.
Mungos mungo	Banded mongoose	2	350–390	250–290	1.0–1.5	Dry acacia bush and plains.
Nandinia binotata	Palm civet	1	505	510	3.2	Forest only.

retraction period (Ottaway, 1961). The protraction period of the white-tailed mongoose, as in dogs, involves three phases. First there is a flexion of the foot followed by a bending of the elbow as the limb is retracted. The second phase involves the swinging forward of the limb and the third phase includes the complete extension of the limb so that it is ready to be placed on the ground. During retraction, the forefoot, which may be as much as 25° hyperextended, is placed on the ground. The second phase involves the thorax swinging over the extended limb, and the third phase, when the foot is thrust backward and fully extended, produces a certain amount of propulsion. The main propulsive thrust is produced by the hind limbs as in most terrestrial mammals, the fore-limbs acting more as struts.

The only form of locomotion common to all the East African Viverridae is walking. In all the terrestrial species, the head is carried low, and the shoulder is nearer the ground than the base of the tail (Fig. 1). The pygmy and banded mongooses have short legs in proportion to their body size, which may well be an adaptation to living in termite holes. The genets move along much closer to the surface of either branches or the ground than other viverrids, and their vertebral axis is kept horizontal. The palm civet (Fig. 2), hugs the branch or ground while walking and keeps its body low. It carries its body with the shoulders lower and the base of the tail higher in relation to the ground, as in the mongooses, but the center of gravity for the whole body is much lower. This indicates that the animal has better control of its movements on slippery branches

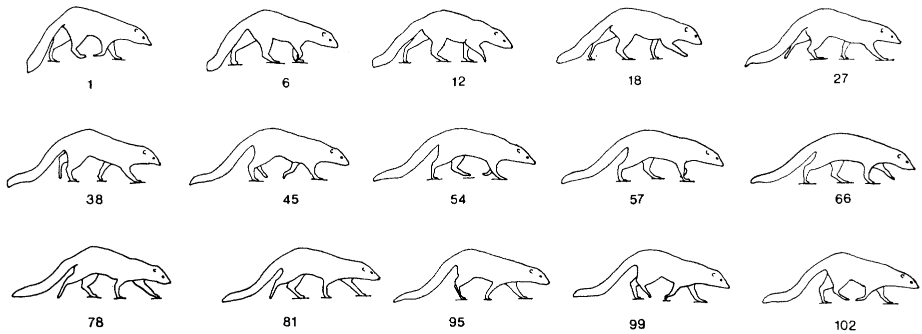

FIG. 1.—White-tailed mongoose (*Ichneumia albicauda*) walking at 4.4 kilometers per hour. The film speed was 64 frames per second and the frame numbers are indicated.

than it would if it had a higher center of gravity like that of the African civet. The tail of the palm civet is long and heavy and serves as a balancing organ. It is always held higher than the horizontal, and often vertically, whereas genets carry their tails straight out behind, and the mongooses generally drag theirs on the ground.

All species had the same type of gait pattern as the white-tailed mongoose, but three variations will be discussed. Some clear sequences were obtained for the white-tailed mongoose walking in front of 51-millimeter wire mesh. The animal has long legs, the top of the scapula being about 200 millimeters from the ground.

The white-tailed mongoose filmed did not change lead, probably due to the fact that the cage was only 3.75 meters wide. However I noted that when mongooses were put in a large cage they only used a small length for walking as do most other caged carnivores. Hildebrand (1965 and 1966) classified the theoretical and natural gait formulae, and I have used his terminology for describing the symmetrical gaits of viverrids. The sequence in Figs. 1 and 3a shows a slow single foot, lateral sequence walk with a gait formula of 73–20. The mongoose was walking at approximately 4.2 kilometers per hour, each stride taking approximately 1.7 seconds.

There are various differences in the postures of genets and the white-tailed mongoose when they are walking. Genets have a palmigrade forefoot and semidigitigrade hindfoot, whereas the mongooses studied are digitigrade. Genets have a scapula that is set higher on the rib cage, and allows a greater abduction of the forelimb than is possible in the white-tailed mongoose. When a genet is walking along a branch, besides keeping its legs in a more flexed position than mongooses, it swings its legs out in a lateral arc, which allows a faster correcting movement should it slip. Yalden (1966) referred to the abnormal gait of a sailor who is continually adjusting to the varing angle of the ship's deck by swinging his legs out in a lateral arc. The genets do this instead of the more usual system of protraction. Genets observed walked at a

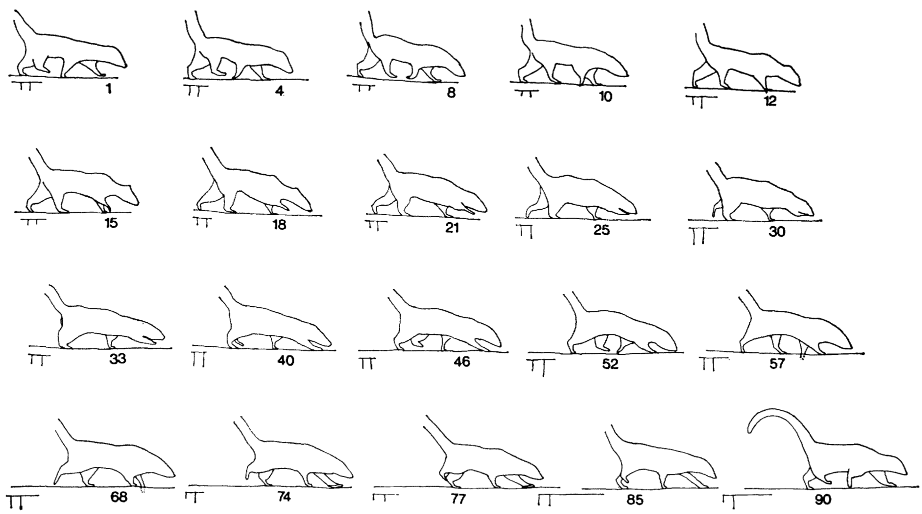

FIG. 2.—Palm civet (*Nandinia binotata*) walking along a horizontal branch. The tail is included only in the last frame due to its length. It was held in a similar position throughout the stride. The film speed was 64 frames per second and the frame numbers are indicated.

slower speed than the white-tailed mongoose and used a slow, single foot, lateral sequence walk. The time taken for a stride varied considerably but averaged about 3.5 seconds per stride.

The palm civet's method of walking is similar to that of genets, except for the posture of the animal and the position of the tail (Fig. 2). The forefeet when brought forward are usually supinated to a certain extent, and the forelegs are invariably moved to the side of the branch in a lateral arc. The sequence in Figs. 2 and 3b shows a moderate, single foot, lateral sequence walk (63–21), each stride taking about 1.5 seconds.

TROTTING

The trot of viverrids differs from that of the horse as described by Muybridge (1957). Referring to the horse, Muybridge stated: "The trot is a system of progress in which each pair of diagonal feet are alternately lifted with more or less synchronism, thrust forward, and again placed on the ground; the body making a transit, without support, twice during each stride." In the white-tailed mongoose (Fig. 3c) the trot involves diagonal pairs of limbs working together, as in the horse, yet there are no distinct transit phases when all the limbs are off the ground.

Few of the mongooses trot, this usually being restricted to the larger terrestrial forms in East Africa. A moderate walking trot (63–45) is the fastest method of locomotion so far observed in the white-tailed mongoose. The filmed strides show a diagonal sequence of footfalls, each stride taking about

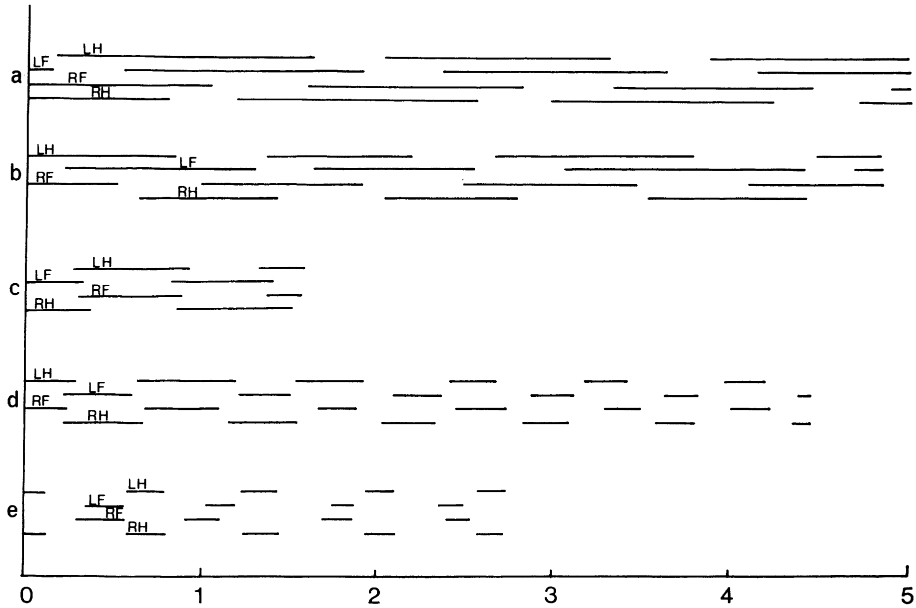

FIG. 3.—Gait patterns. Sequence of footfalls and phases of representative strides of: (a) white-tailed mongoose walking; (b) palm civet walking; (c) white-tailed mongoose trotting; (d) banded mongoose trotting for two strides and then running; (e) banded mongoose galloping, using the half-bound. The period that each foot is on the ground is shown by the length of the respective line. The letters L, R, H, and F mean left, right, hind foot, and forefoot, respectively. Time is in seconds.

1.1 seconds. The first complete stride in Fig. 3d shows a banded mongoose completing a fast walking trot stride (55–55) before breaking into a slow run.

RUNNING

The differences between running and trotting can be seen in Figs. 3c and d. The running pattern is distinct in that there are never more than two feet on the ground at any one time and they are always diagonal pairs. Also there are two distinct transit phases when all the feet are off the ground.

The best running sequence was obtained with a banded mongoose. The gait diagram shows this mongoose as it is accelerating from a fast walking trot, through a slow run to its maximum speed of a moderate, diagonal sequence, diagonal couplets run (35–60). While the animal is trotting, there is an overlap between the ipse-lateral forefoot and the hind foot of each side, but as it achieves its maximum running speed this overlap is lost. Initially the banded mongoose made one stride in 0.92 seconds, but two strides later it took only 0.75 seconds.

GALLOPING

The half-bound, a form of galloping, was observed and filmed in the banded mongoose (Fig. 4). As in all galloping carnivores, the main forward thrust

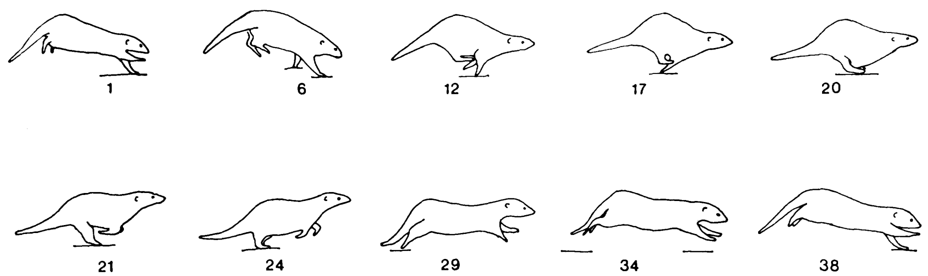

FIG. 4.—Banded mongoose (*Mungos mungo*) galloping, using the half-bound. The ground is indicated by horizontal lines. The film speed was 64 frames per second and the frame numbers are indicated.

is produced by the hind feet. The forefeet do not touch the ground simultaneously; one touches the ground first, and then the other is brought down in front of the first. At the beginning of this sequence, the right touches the ground first; later the lead is changed and the left touches first. The forefeet provide support while the hind feet are brought forward and the spine is flexed, and the forefeet leave the ground before the hindfeet touch. The body is flexed to about 60 per cent of the extended chest-rump length while the legs are brought forward. This is a pronounced flexion, and a similar one was observed only in the vertical looping of a palm civet and the threat posture of genets.

Since the forefeet touch the ground before the hind feet, there is no index for the percentage of the stride interval that the footfall of a forefoot lags behind the footfall of the hind foot on the same side of the body; therefore the gait formula for galloping cannot be calculated. However the forefeet are on the ground for about 24 per cent of the stride and the hind feet are on the ground for about 28 per cent of the stride. The time taken for one stride is 0.65 seconds.

JUMPING

Jumping occurs in most of the species of Viverridae under discussion, though it does not form an integral part of locomotion for the majority of them. The larger mongooses will jump to a height of about 90 centimeters to obtain food, but this is ungainly and apparently is not done often. In captivity the banded mongoose will rise to its hind feet to collect food and, standing on its hind legs, may jump vertically as much as 50 centimeters. It will also jump down where necessary, pushing off with its hind feet, absorbing the shock of landing with its forefeet. The genets that have been observed in captivity will jump up or down with equal facility, and, though they cannot jump much higher than a meter, they will usually jump down 1.8 meters without hesitation. Fig. 5 shows a genet (*G. tigrina*) jump a short distance (22 centimeters) up a branch.

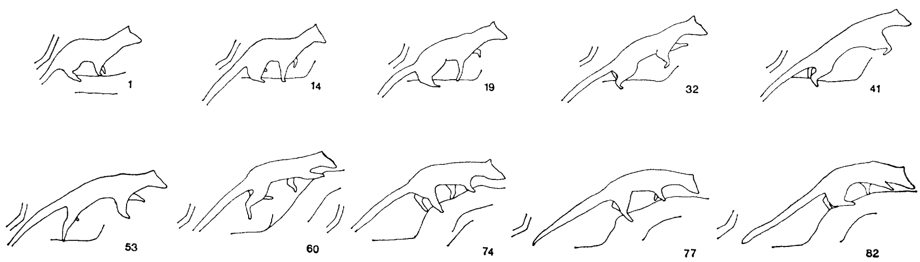

FIG. 5.—Genet (*Genetta tigrina*) jumping up a branch. The height of the jump was 22 centimeters. The film speed was 64 frames per second and the frame numbers are indicated.

During frames 1 to 14 (Fig. 5), this genet is adjusting its forefeet prior to jumping; it uses the left forefoot for the initial jump thrust. From the time the left foot has been raised, the right forefoot continues the thrust for about 0.07 seconds, during which time it helps lift the anterior end of the animal well clear of the branch. During this initial phase the hind legs remain flexed, but by frame 19 they have just begun to extend. Frame 32 shows the hind limbs at three quarters extension and by frame 41, the left hind foot is already being retracted. While the hind legs develop the thrust the vertebral column straightens out and the forelimbs are extended. The right forefoot lands first and absorbs the initial impact of landing. Due to the momentum of the body, it swings over the right forelimb and the left is brought ahead of the right and placed on the branch. The tail is used for balance during this sequence, and is held out straight. The whole jump takes about one second.

The palm civet is the most efficient viverrid at jumping, though it will rarely jump down, prefering to climb downwards. In captivity it often jumps up 1.8 meters without apparent difficulty and may carry as much as 850 grams of meat. It can also jump across gaps of about a meter, in some cases landing on a vertical pole with its body in a vertical plane and all its limbs outstretched.

CLIMBING

Only a few of the East African viverrids are capable climbers, the palm civet being the most proficient. The black-tipped mongoose is the only East African mongoose observed to show any skill in arboreal climbing, though Haines (1958) noted that the Indian mongoose, *Herpestes mungo* is an accomplished climber. The black-tipped mongoose can with agility run up and down wire netting, rough cut stone walls, and branches, but it does not seem to be a controlled climber, rushing up and usually falling down.

The palm civet is arboreal and its adaptations can best be seen when it is in its natural surroundings. Some good sequences of it climbing up and down poles and wire netting were obtained. On vertical and nearly vertical poles, up to 20 centimeters diameter, *Nandinia binotata* climbed in a specialized way. In the sequence shown in Fig. 6 it is climbing down a vertical corner post with wire netting on two sides. It always climbs down head first, and

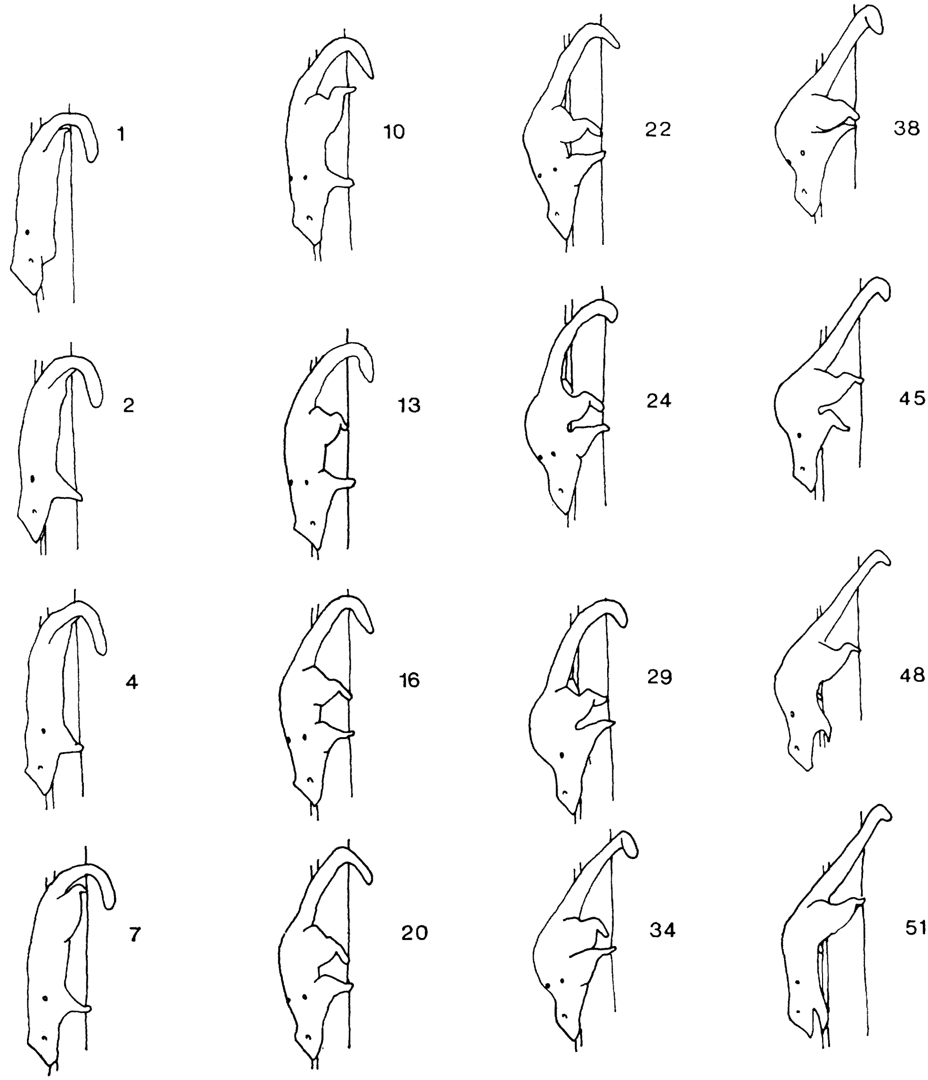

FIG. 6.—Palm civet (*Nandinia binotata*) climbing down a vertical post, using vertical looping mode of progression. In each stride it moves about 50 centimeters. The tail is foreshortened because the end was bent towards the camera. The film speed was 64 frames per second and the frame numbers are indicated.

progresses in a series of loops. It grips the post with its forefeet at a position just forward of the scapula so that it can exert the maximum lateral pressure on the post. It then brings both hind feet forward together until they touch the forefeet, and they then grip; the flexed chest-rump length is 68 per cent of the extended chest-rump length. As the animal brings the hind feet up, the whole animal may twist. This twisting can be seen from the two light colored spots that are symmetrically placed on either side of the back above the scapulae (Fig. 6). In the absence of any detailed reference to this kind of locomotion in the Viverridae, I term it "vertical looping." *N. binotata* will also climb up by this method.

On two occasions I have seen a genet, *G. tigrina*, use a rushed form of this locomotor pattern for climbing vertical poles; it was acting under considerable stress and was not particularly successful, having little control. It then jumped down. The domestic cat climbs trees by this method, but often gets stuck at the top, for it cannot move downwards by vertical looping.

A form of controlled climbing in the Paradoxurinae of the Himalayas was observed by Hodgson (1847), though no detailed description was given indicative of vertical looping. Haines (1958) mentioned briefly the pine marten, *Martes martes*, which is able to walk down tree trunks head first; he did not indicate whether it loops down, or walks down using its claws to grip fissures in the bark. Hurrell (1968) mentioned the climbing ability of pine martens and noted that they race up and down trees. This indicates a walking or running movement. Hurrell also stated (personal communication) that they do not climb down using a method of vertical looping. The downward vertical looping of the palm civet reflects its arboreal adaptations.

Swimming

The marsh mongoose is the only East African viverrid known to be a good swimmer. Other species known to swim occasionally are the gray mongoose (Haines, 1958), the white-tailed mongoose, and the genet, *G. tigrina*. The marsh mongoose eats fresh water crabs and fish in addition to carrion. It swims by lateral undulations of the body, with the back partly exposed, whereas most other aquatic mammals such as otters and the coypu swim completely submerged except for the head. The fur of the marsh mongoose becomes completely wet during swimming. I have observed captive specimens remaining submerged for 15 seconds. The toes can be spread widely due to a lack of skin joining the digits, and this is likely to be of functional use to an animal that has to cross soft mud without sinking.

Burrowing

The banded and pygmy mongooses spend much of their time underground. They live in old termite mounds in dry areas, and are gregarious. Their digging is limited to enlarging holes for nesting quarters and burrows, and they do this by scraping with their front claws. In both species the claws are long and well developed and the earth is thrown back between the hind feet. The South African meerkats (*Suricata* spp.) dig their own burrows in sandy soils (Ewer, 1963).

Discussion

In the larger species of viverrids that live in savannah and light woodland, trotting is the most common mode of progression and appears to be associated with larger feeding territories. From trapping results, I have found that viverrids have feeding territories varying from about 1 square kilometer for the black-tipped mongoose to about 8 square kilometers for the white-tailed mongoose. The running and galloping forms of locomotion are characteristic of the smaller viverrids such as the banded and pygmy mongooses.

Three or more species of viverrids usually coexist in a given locality. Black-tipped mongooses, white-tailed mongooses, and one species of genet often live in the same area but their foraging habits do not overlap much because black-tipped mongooses are diurnal, genets are crepuscular and hunt visually in the trees or on the ground, and white-tailed mongooses, which hunt mainly by scent, are completely nocturnal and terrestrial.

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