ANALYSIS OF POSTURE AND GAIT SELECTION DURING LOCOMOTION IN THE STRIPED SKUNK (*MEPHITIS MEPHITIS*)

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ABSTRACT.—The pelvic and hindlimb posture and the gaits of *Mephitis mephitis* are described using cinematography (to 64 f.p.s.) and cineradiography (to 200 f.p.s.) of captive adult animals. *M. mephitis* preferentially selects a symmetrical, single-foot gait within the lateral sequence, which apparently provides maximum stability and, on the basis of comparative studies (Hildebrand, 1976), is primitive. At speeds faster than the walk, the striped skunk seldom selects the trot; rather, it moves directly into a slow transverse gallop with little or no gathered suspension phase. This asymmetrical gait maximizes stability and is considered primitive. Several aspects of hindlimb posture of *M. mephitis* during walking reflect the pattern thought to be primitive for mammals (Jenkins, 1971; Jenkins and Camazine, 1977). In contrast to patterns of the more specialized carnivores, these aspects include: 1) upon contact of a foot the long axis of the femur intersects the sagittal plane at a relatively large angle (25° to 40°); 2) relatively greater adduction of the femur occurs just after foot contact (E^2) followed by abduction in the late stance phase (E^3) of the step cycle; and 3) the pelvis in E^3 experiences a relatively greater contralateral shift. These features confer a wide and stable stance. Unlike those mammals thought to be primitive, however, *M. mephitis* positions its femur such that the distal end is always below the level of the acetabulum. Either we have misinterpreted the primitive condition in this regard, or the depression of the entire femur relative to the acetabulum was an adaptation among carnivores and related to an ambulatory way of life. The evidence leads us to conclude that in its gait selection and posture, *M. mephitis* represents the primitive condition for the Order Carnivora.

In a review of limb structure as it relates to mammalian locomotion, Brown and Yalden (1973) emphasize the need for (1) studies of those species that are generalized in their locomotor postures and habits, and (2) integrative methods of study that incorporate behavior, anatomy, and physiology of select locomotor systems. The domestic dog and cat, two carnivores that have been extensively studied, possess many morphological features of the appendages that reflect a cursorial habit, characterized by marked digitigrade posture and rapid phasic movements during prey capture. Most mammals are not cursorial, however, and distinct differences exist between primitive and specialized mammals in their skeletal movements during locomotion (Jenkins, 1971).

In an effort to distinguish between specialized morphological features associated with running and generalized features of the Order Carnivora, and perhaps mammals in general, we have begun a series of studies relating to the posture and locomotion of the striped skunk (*Mephitis mephitis*) (Frederick and Goslow, 1976; Van De Graaff et al., 1977; Frederick et al., 1978; Goslow and Van De Graaff, in press). Skunks, which are comparable to cats and dogs in size, move relatively slowly and assume a more generalized locomotor posture than either cats or dogs. Footfall patterns and hindlimb postural changes during walking and galloping are described for *M. mephitis*, and its gait selection is compared to that of the domestic ferret (*Mustela putorius*) and domestic cat. Cinematography and cineradiography form the basis of the behavioral observations. Hildebrand (1976, 1977) presented some useful data on the gaits of *Mephitis* and *Spilogale*.

This report is a companion study to an analysis of the mechanical aspects of the hindlimb of *M. mephitis* (Goslow and Van De Graaff, in press). The two studies lead us to conclude that the posture, gait selection, and musculoskeletal structure of the striped skunk are primitive.

METHODS

The locomotion of four adult *M. mephitis*, weighing 2.0 to 3.3 kg, and six domestic adult ferrets (*M. putorius*), weighing 1.5–2.5 kg, was photographed with a 16-mm camera at 64 frames per second (F.P.S.;

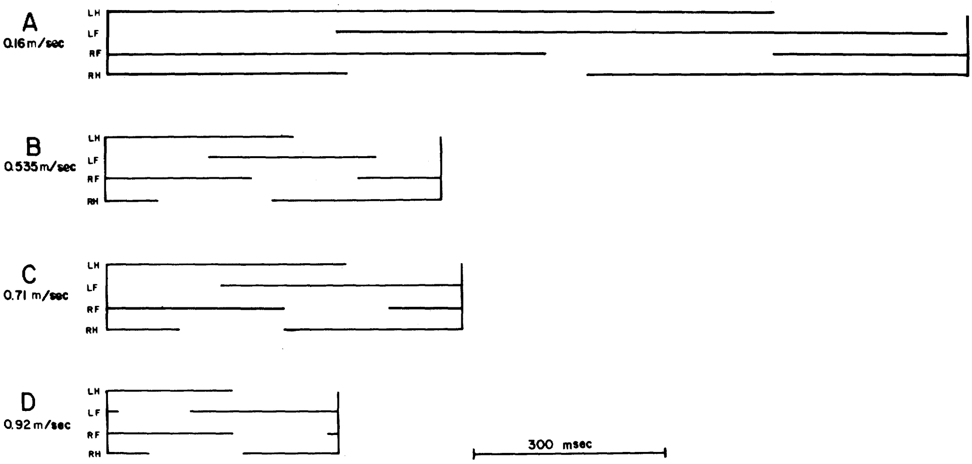

FIG. 1.—Gait diagrams (Hildebrand, 1966) for the walking skunk (*Mephitis mephitis*) moving at a variety of forward speeds. In this and some subsequent figures, the horizontal lines are assigned from top to bottom to the left hind—(LH), left fore—(LF), right fore—(RF), and right hind—(RH) limbs. Continuous horizontal lines indicate the duration of each limb's stance phase (foot on ground), and open spaces indicate the swing phase (foot off ground). The stride is begun and ended with LH limb placement as the animal moves from left to right. The A and B gaits were used by two different 2.5 kg skunks, and the C and D gaits were used by a third 3.3 kg animal. The skunk employs the walk to a far greater extent than any other gait.

2 msec exposure, each 15.6 msec). The walking sequences of both species and the gallop of *M. putorius* were filmed against a 30-m background of a ruled grid of 10-cm squares. To reduce parallax, the background was bowed into a semicircle with a radius of 64 m. The camera was mounted at the center of a circle on a tripod at the level of the moving animal, a 75-mm, F-1.5 lens was used, and locomotion was tracked and filmed from the center of the semicircle. To film the skunks' gallop, the camera was positioned 30 to 60 m from a flat background grid, and a 25-mm, F-1.4 lens was used.

Limb posture during locomotion was studied from cineradiographs of three adult skunks, two of which were filmed at the Veterans Hospital in St. Paul, Minnesota. The third, a 3.3-kg adult male, from which postural reconstructions were made, was filmed at the Museum of Comparative Zoology (MCZ), Harvard University. Lateral and dorsoventral projection films were made (not simultaneously).

Cineradiographs were taken of the animal walking in a clear plastic box suspended over a variable speed treadmill. The top of the box was open, the box length was about three times the head-tail length, and the box width was sufficient to allow the animal to walk freely without touching the sides. Treadmill speeds of 0.28 m/sec and 0.72 m/sec were used to facilitate slow and fast walks, respectively. Faster speeds failed to force the animal to break into a faster gait. Siemens cineradiographic apparatus, including a grid-controlled tube with 0.06-mm focal spot and a 27.94-cm Sirecon image intensification system, was positioned for radiography. An Eclair GV16 high speed cine camera, mounted on the image intensifier and operated at 200 F.P.S., recorded each sequence simultaneously with the monitoring of the image on a 43-cm television screen.

Six hundred feet of light film and 400 feet of cineradiographic film were studied with an L & W Optical Film Analyzer. Articulated skeletons of two animals previously filmed (one cineradiographically) were mounted in positions corresponding to filmed postures. Joint angles and changes in muscle lengths were measured on these skeletal mounts.

RESULTS

Footfall patterns and gaits adopted.—Symmetrical gaits are defined as those in which the two fore feet strike the ground successively at intervals of constant duration, and the same is true of the two hind feet. The walk, which is considered a symmetrical gait, is employed by skunks to a far greater extent than other gaits. We adopt Hildebrand's (1966) definition of a

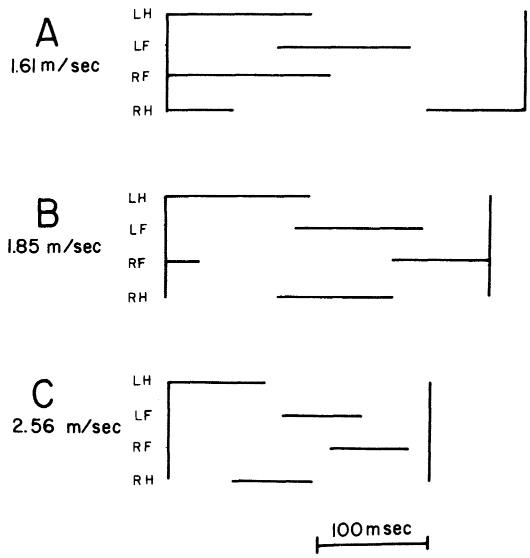

FIG. 2.—Different patterns of running for the skunk (*Mephitis mephitis*). These three gaits were used by the same 3.3-kg skunk at the indicated speeds. All are transverse gallops.

walk: a symmetrical gait in which the duration of contact of the foot is 50% or more that of the stride.

Figure 1 illustrates four individual gait diagrams of skunks walking at 0.16–0.92 m/sec. A and B were made by two individuals and C and D by a third. In this and subsequent gait diagrams a complete stride of the left hindfoot is figured, and the support patterns of the other feet are in relation to it. Continuous horizontal lines indicate the duration of each limb's stance phase (foot on ground), and open spaces indicate the swing phase (foot off ground).

Skunks characteristically vary the support pattern of the four limbs, even when walking over a surface free of obstruction. For example, in A (3,4,3,2,3,4,3,2), C (3,2,3,4,3,2,3), and D (4,3,2,3,1,2,3), support pattern variants are clear. In general, however, as the animal increases its forward speed, periods of diagonal support become more synchronized and the periods of three-legged support become shorter.

As forward speed increases, skunks seldom trot; rather, they break from a walk into an asymmetrical gallop. Transition trots were infrequently seen as the animals slowed from a gallop to a walk. In asymmetrical gaits, the footfalls of each pair of feet are unevenly spaced in time. If the lead foot (second of a pair to strike) is the same for front and back, the gait is a transverse gallop. If the leads are opposite, the gait is a rotary gallop. Fig. 2 provides gait diagrams for a single skunk galloping at 1.6, 1.85, and 2.56/m sec; all are transverse gallops. As the animal increases its speed, the hindlimbs tend to move more in synchrony with one another (short hind lead). Further, at the fastest speed, a period of gathered suspension (all four limbs off the ground; zero support) is illustrated. The laboratory situation may have prevented this species from attaining its maximum speed. Neither the rotary gallop nor a period of extended suspension was observed.

Select gait diagrams for the domestic ferret are illustrated in Fig. 3. Fig. 3A is the walking pattern and is similar to that of the skunk at a comparable speed (Fig. 1B). An alternate 3,2,3, etc., support pattern is shown. Fig. 3 B and C depict slow transverse gallops, which all ferrets in this study appeared to prefer. Unlike the skunk, the ferret exhibited periods of extended suspension at rapid forward speeds, but no gathered suspension.

In both species, the timing of the four footfalls within the symmetrical gaits varies consider-

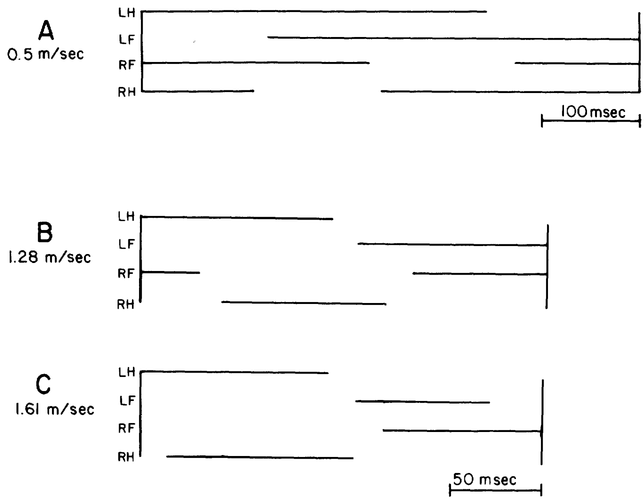

FIG. 3.—Different patterns of forward movement for the domestic ferret (*Mustela putorius*). The A gait was made by one animal and B and C gaits made by a second.

ably and can be plotted and compared with that of other species by employing the "gait formula" or "gait graph" technique of Hildebrand (1966, 1976). If, within a stride interval, the percent that a hindfoot is on the ground and the percent that the ipsilateral forefoot contact follows are determined, the important variables for a symmetrical gait are known and can be plotted on a gait graph. Fig. 4 illustrates the distribution on the gait graph of: 1) approximately 1,000 plots of symmetrical gaits for 156 genera of tetrapods (Hildebrand, 1976); 2) four skunks (●); 3) two ferrets (O); and 4) seven domestic cats (×) filmed for a previous study (Rasmussen et al., 1978). For footfall comparison, we adopt the terminology of Hildebrand (1966). If the strike of a hindfoot is followed by the strike of the ipsilateral forefoot, the gait is a lateral sequence gait. Fig. 4 shows that skunks, ferrets, and cats employ this gait. Within the lateral sequence gait, if the four feet strike evenly spaced in time, the gait is a single foot (between 18 and 31% on the ordinate). Finally, if the footfalls on the same side of the body are coupled in time, the gait has lateral couplets (between 6 and 18% on the ordinate). On the contrary, if footfalls on the opposite sides of the body are coupled in time, the gait has diagonal couplets (between 31 and 44% on the ordinate).

The walking gait formulae of the skunk occur within the single foot range with few diagonal couplet patterns. Walking cats use the lateral couplet and single foot gaits about equally. One cat, which appeared to be trotting normally, displayed the diagonal couplet slow run, centering around a gait formula of about 40, 40. Unlike both skunks and cats, ferrets employ a wide range of symmetrical gaits and this may relate to their extensive movements of the spine and relatively short legs.

The step cycle and hindlimb movements.—Pelvic and hindlimb postures of a 3.3 kg skunk, walking at 0.28 m/sec on a treadmill, correspond to joint angle settings most often given for the Philippson (1905) step cycle (Fig. 5). The flexion (F) phase begins as the foot is thrust off the ground and flexion begins at the hip, knee, and ankle joints. This phase ends as extension begins in the ankle. The movements of limb flexion and early extension (E^1) comprise the swing (foot off the ground) phase of the step cycle. The stance (foot on the ground) phase involves progressive extension of the hip at increasing speed. During the second extension phase (E^2), the knee, ankle, and metatarsophalangeal joints yield under the weight of the animal.

At the beginning of the F phase, the pelvis and lower spine rotate toward the limb (an average of 10°). The pelvis is tilted about the anteroposterior axis, bringing the acetabulum of the swing

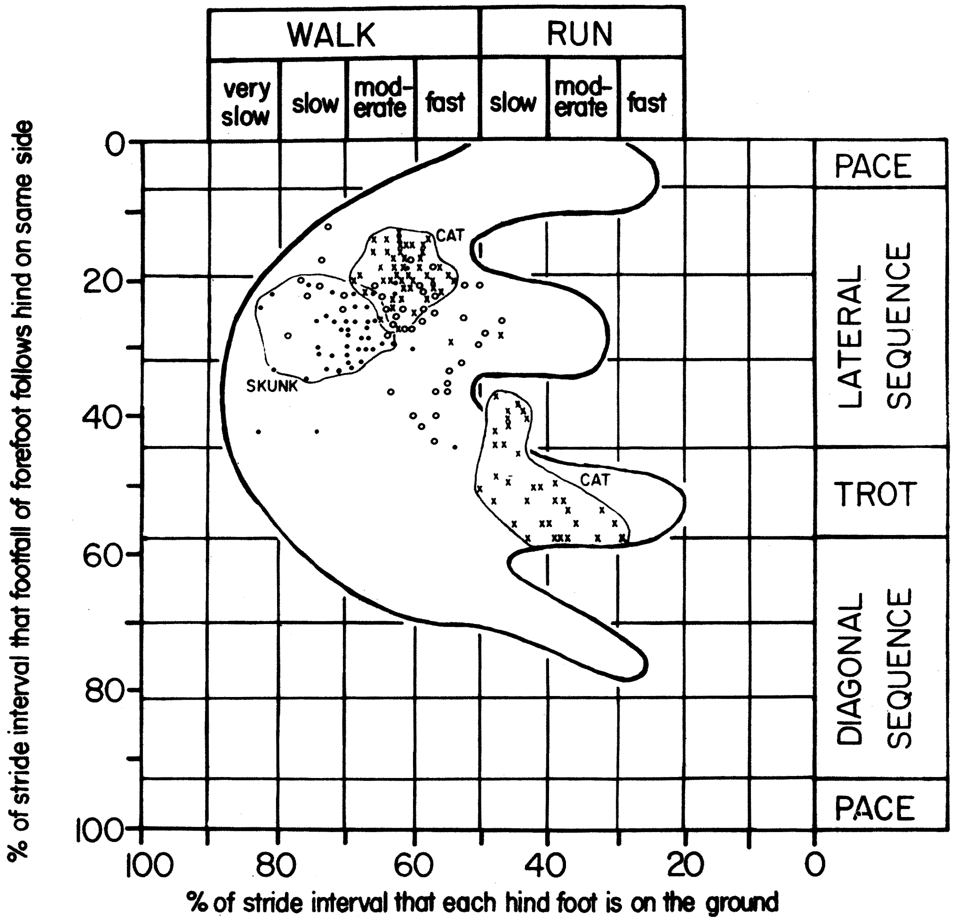

FIG. 4.—Gait graph for some symmetrical gaits of tetrapods having fore and hind contact intervals about equal. The thick-lined enclosed area represents the distribution of plots for 156 genera of tetrapods (Hildebrand, 1976). Superimposed are plots for seven domestic cats (×), three striped skunks (●), and two domestic ferrets (○). All three species use a lateral sequence gait (see text for explanation). The walking cat uses a lateral sequence, lateral couplet or lateral sequence, single-foot gait about equally while the skunk uses almost exclusively a lateral sequence, single-foot gait. Our limited data for the ferret suggest that this species moves slowly with either lateral sequence, single-foot or lateral sequence, diagonal couplet gaits.

phase limb slightly higher than that of the opposite limb. Throughout F and E^1 the pelvis rotates toward the midline and, at the end of E^1, is displaced maximally toward the opposite leg. As the swing phase progresses, the pelvis continually tilts downward until it reaches its lowest position relative to the contralateral acetabulum at the moment of foot contact. At about the F–E^1 transition the two acetabula are lined up on a horizontal plane. Pelvic movements opposite to those described for the swing phase occur in the stance phase. The amount of rotation about the vertical axis averages 20°. Lateromedial pelvic displacements also occur and are more easily considered with movements of the femur.

During stepping the femur undergoes not only flexion and extension movements but also abduction and adduction movements. Among carnivores, femoral movements and lateromedial movements of the pelvis are interrelated (Jenkins and Camazine, 1977). At the beginning of F, the long axis of the femur intersects the sagittal plane at about 25°. As the limb swings forward to contact, the femur remains abducted while the pelvis moves away from the suspended limb (contralateral shift) toward the support limb (ipsilateral shift). In E^2, after foot contact, the

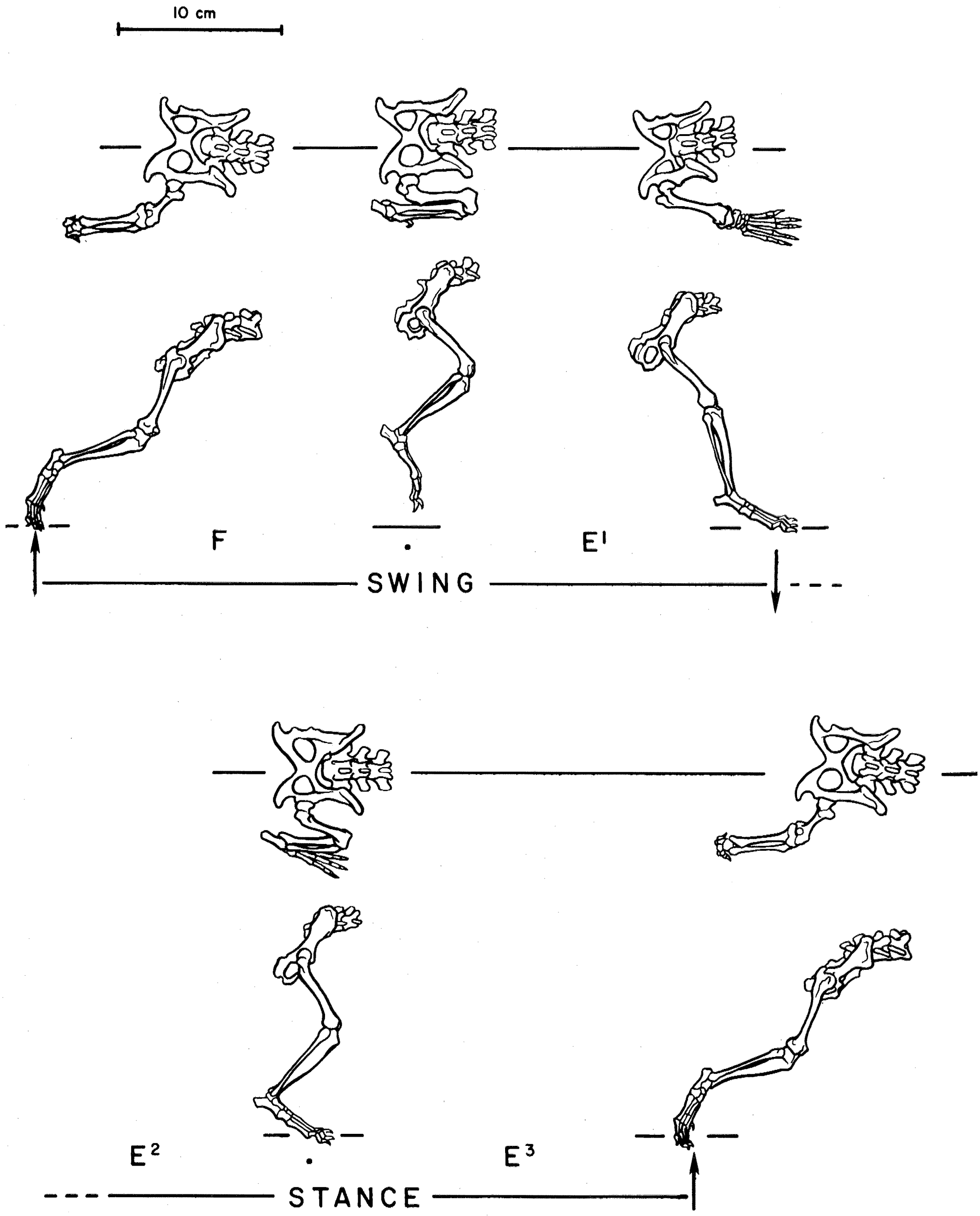

FIG. 5.—Pelvic and hindlimb postures of a 3.3 kg skunk (*Mephitis mephitis*) walking 0.28 m/sec on a treadmill. Dorsal and lateral skeletal reconstructions are as interpreted from cineradiography. Postures illustrated correspond to joint angle settings most often given for the Philippson (1905) step cycle. To simplify the figure, the four phases of the cycle have been given equal allotments of time. The flexion (F) phase begins as the foot is thrust off the ground, at which time flexion begins at the hip, knee, and ankle joint. This phase ends as extension begins in the ankle. These movements of the limb flexion and early extension (E^1) comprise the swing (foot off the ground) phase of the step cycle. The stance (foot on ground) phase involves progressive extension of the hip at increasing speed. During the second extension phase (E^2), the knee, ankle, and metatarsophalangeal joints yield under the animal. In this and subsequent figures note the use of arrows to separate swing and stance phases and the use of black dots to separate F from E^1 and E^2 from E^3.

lateral displacement of the pelvis toward the supporting limb facilitates an ipsilateral shift to this side; femur adduction (to about 15° to the sagittal plane), followed by gradual abduction in E^3, also occurs. At the beginning of F, the femur is extended beyond the acetabulum. The femur continually flexes through about a 30 to 40° iliofemoral angle during the swing. At E^2 the hip joint stabilizes, and in E^3 extension of the femur progresses.

Discussion

Vertebrate morphologists have long been interested in the primitive locomotor adaptations of early mammals (Huxley, 1880; Matthew, 1904; Gregory, 1951; Gambaryan, 1974; Jenkins, 1974). Of particular interest to the present study is the conclusion of Gambaryan (1974) that early mammals were semifossorial. Gambaryan supported his idea by analyses of two mammalian features that he believes to contrast sharply to the reptilian condition: 1) the mammalian hindlimb moves in a parasagittal plane independent of the lateral or segmental movements of the body; and 2) mammals possess asymmetrical gaits as well as symmetrical ones. Freeing the forelimbs for digging and foraging necessitated that mechanical support of the hindlimbs be improved. This resulted in movement of the knee into a forward and parasagittal plane, which further led to a neural uncoupling of fore and hindlimb movements. On the basis of extensive comparisons of the gaits and musculo-skeletal structure of the forelimb and vertebral column of selected carnivores, Gambaryan concluded that early members of the Order Carnivora were also semifossorial. Although specific data in support of this hypothesis are certainly limited (Cartmill, 1975), some of our results are consistent with Gambaryan's general thesis.

The phylogeny of the Mustelidae is difficult to interpret because of the wide and comparatively rapid adaptive radiation within the family. Early Oligocene mustelids were already weasel-like, and Gambaryan interprets this body plan as reflecting their predatory habits of chasing rodents in narrow burrows (Gambaryan, 1974). Gambaryan believed that selective pressure for increased size of these subterranean predators led to their need for burrow enlargement and subsequent fossorial adaptation. From such a form, the tree-dwelling and aquatic mustelids evolved. On the other hand, large size may have inhibited fossorial existence and restricted their evolution to surface terrestrial forms such as the skunks. If this latter hypothesis is true, aspects of locomotor morphology in skunks may be primitive. Van De Graaff (1969), in a detailed osteological study of the cranial and postcranial features of *Mephitis*, *Conepatus*, and *Spilogale*, concluded that *Mephitis* is the least specialized of the group; hence, our selection of this species for study.

Gait selection.—Sukhanov (1974) and Hildebrand (1976) concluded that symmetrical gaits are primitive because they encompass almost all of the forms of locomotion in the lower tetrapods as well as many mammalian gaits. Furthermore, the first terrestrial vertebrates were undoubtedly slow animals with a high demand for maintenance of equilibrium and maximum stability in all stages of the locomotory cycle. Gray (1944) illustrated that the lateral sequence of walking provides periods of three-limb support that are stable. Howell (1944) predicted that early forms probably avoided diagonal sequences and even the trot, as the two-limb support periods would prove too unstable.

The striped skunk prefers the use of the single-foot gait within the lateral sequence. In a summary of gait selection in tetrapods, Hildebrand (1980) illustrated that this gait is a preferred gait for maximum stability because support by four feet is maximum and the periods of two-limb support (bipod) are the more stable diagonal opposites (Fig. 1). Hildebrand (1976) proposed an evolutionary sequence of mammalian gaits and suggested that the single-foot in lateral sequence, as preferred by skunks, is a primitive mammalian pattern.

Hildebrand (1976) suggests that the single-foot in lateral sequence became modified by more specialized animals to the lateral couplet, lateral sequence gait, which is the gait preferred by the domestic cat. Dogs use a variety of footfall timings, which probably reflects the effects of man's selective breeding programs on their morphology and hence their gait preference (Hildebrand, 1968). However, gait graph distribution of the footfall patterns of the African hunting dog (*Lycaon*) and gray fox (*Urocyon*), which were selected to be representative for this group, fall into the lateral couplet, lateral sequence area, and substantially overlap that of the domestic cat (Hildebrand, 1976, fig. 14). Though the ferret may use the primitive, single-foot in lateral sequence pattern (Figs. 3A and 4), this species also uses lateral, as well as diagonal, couplet timings; this, we believe, relates to its degree of specialization.

Cats and dogs select the symmetrical trot at increased speeds, whereas the skunk does not. The skunk breaks directly from a fast walk into an asymmetrical gallop, avoiding the relatively unstable trot. Predictably, the gallop selected by the skunk reflects its lack of stability and noncursorial specialization. The phylogeny of asymmetrical gaits is not clear, but in light of footfall data for approximately 70 genera, Hildebrand (1977) critically reviews the schemes proposed to date. He concludes that half bounds and gallops in both lead sequences are all very old and may have evolved almost simultaneously. Hildebrand (1980) believes the transverse gallop to be more stable than the rotary gallop for two reasons: 1) all but the fastest speeds include one or two phases of support by three feet (tripods), which encompass a larger area in the transverse than the rotary gallop; and 2) the bipods that combine support by a fore and hindfoot are usually the contralaterals (Fig. 2B, C). Economy of effort of the transverse gallop compared with the rotary gallop is also suggested. It is not surprising that when pressed to run, *M. mephitis* selects a slow transverse gallop with only a brief, if any, gathered suspension phase. This contrasts sharply with the versatility of asymmetrical gait selection shown by more specialized cursors—domestic cats, dogs, and even ferrets. Cats may half-bound, bound, gallop with either lead, and use both extended and gathered phase suspension (Stuart et al., 1976; Fig. 4). Dogs also use both gallops and two periods of suspension (Hildebrand, 1977). Ferrets select the transverse gallop and half-bound when running fast and often show an extended phase suspension. *M. mephitis* appears to use a basic asymmetrical gait, which maximizes stability and does not reflect cursorial specialization.

Hindlimb posture.—Several aspects of hindlimb posture during stepping further reflect the primitive nature of *M. mephitis*. Cineradiographic studies of select noncursors and cursors reveal primitive and specialized features characteristic to each group (Jenkins, 1971; Jenkins and Camazine, 1977). For example, at foot contact, the long axis of the femur may intersect the parasagittal plane at a relatively large angle (25°–40°) in *M. mephitis* as well as in other noncursors, such as opossums (*Didelphis*), tree shrews (*Tupaia*), and raccoons (*Procyon*). For cats and dogs, however, the axis lies much closer to the parasagittal plane (10°–15°). The stance phase of *M. mephitis* and raccoons may be further contrasted to the more specialized carnivores by: 1) greater femoral adduction in E^2 followed by abduction in E^3; and 2) greater contralateral shift of the pelvis in E^3. These features relate to a wide stance and a distinct capacity for femur abduction.

Jenkins (1971) reported that in the noncursorial mammals he studied, the distal end of the femur was characteristically held level with, or above, the acetabulum during standing and in the early stance phase of stepping. He concluded this to be the primitive mammalian condition, but it is not characteristic for either skunks or raccoons (Jenkins and Camazine, 1977). It is, however, typical of ferrets (Jenkins, 1971). We conclude from our data that in its gait selection and general hind limb posture, *M. mephitis* represents the primitive condition for the Order Carnivora. It is unclear if the position of the femur relative to the acetabulum is an important structural consideration in determining which carnivores are primitive or advanced. Seemingly, those carnivores with an elevated femur are adapted to pursue rodents through a burrow system, whereas those which have a depressed femur relative to the acetabulum are adapted to an ambulatory way of life.

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