Suricata suricatta. By Moira J. van Staaden

Suricata Desmarest, 1804

Suricata Desmarest, 1804:15. Type species *Suricata capensis.*
Ryzaena Illiger, 1811:134. (Not *Rizaena* Blainville, 1817:339; *Rysaena* Lesson, 1827:178; or *Rhyzaena* Wagner, 1841: 330). Type species *Viverra tetradactyla* Pallas and *Viverra zenik* Gmelin.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Feloidea (=Aeluroidea), Family Herpestidae, Subfamily Herpestinae, Genus *Suricata* is monospecific (Wozencraft, 1993).

Suricata suricatta (Schreber, 1776)

Suricate

Viverra suricatta Schreber, 1776:pl. 117. Type locality, Cape of Good Hope. Restricted to Deelfontein, north of Richmond, Cape Province, South Africa, by Thomas and Schwann (1905:133).
Viverra tetradactyla Pallas, 1777:434. Type locality "das Südliche Afrika . . . Vorgebirge der guten Hofnung," Cape of Good Hope.
Mus zenik Scopoli, 1786:84. Type locality "In terra Hottentotarum" (=western Cape Province, South Africa).
Suricata capensis Desmarest, 1804:15. Type locality, Cape of Good Hope.
Surikata viverrina Desmarest, 1819:297. Type locality, Cape of Good Hope.
Suricata suricatta Thomas and Schwann, 1905:133. First use of current name combination.
Suricata majoriae Bradfield, 1936:131. Type locality "Saltpan, 10 miles north of Swakopmund," Namibia. Privately printed and dated Benoni 26 September 1935.

CONTEXT AND CONTENT. Context noted in generic description above. Three subspecies, differentiated predominantly on color and size, are recognized as follows (Coetzee, 1977; Meester et al., 1986):

S. s. iona Cabral, 1971:65. Type locality Gobabis, eastern Namibia.
S. s. majoriae Bradfield, 1936:131. See above.
S. s. suricatta (Schreber, 1776:pl. 117), see above. Includes *tetradactyla* Pallas, 1777, *zenik* Scopoli, 1786, *capensis* Desmarest, 1804, *viverrina* Desmarest, 1819, and subspecies *hamiltoni* (Thomas and Schwann, 1905:133), *lophurus* (Thomas and Schwann, 1905:133), *namaquensis* (Thomas and Schwann, 1905:134), and *hahni* (Thomas, 1927:376) as recognized by Ellerman et al. (1953).

DIAGNOSIS. *Suricata suricatta* is smaller than most other Herpestidae, except *Helogale* (condylo-incisive length, <53 mm; body mass, 200-300 g) and perhaps *Galerella* (condylobasal length, <70 mm; body mass, 500-1,200 g—Meester et al., 1986; Skinner and Smithers, 1990). In the field, *S. suricatta* can be distinguished from the yellow mongoose, *Cynictis*, by ear size (usually >9% head and body length in the mongoose; smaller in suricates), and number of digits on manus and pes (five and four, respectively, in *Cynictis*; four on all appendages in *S. suricatta*—Skinner and Smithers, 1990). In suricates the dorsal pelage is indistinctly transversely banded, foreclaws are enlarged, and the tail appears slender not bushy. Most other mongooses are not banded, foreclaws are not enlarged, and tails are bushy. *S. suricatta* can be distinguished from all other Herpestinae, except *Helogale* and *Mungos*, on the basis of dental characteristics; suricates have only three premolars in each tooth row (36 teeth) whereas *Paracynictis* and *Bdeogale* have four upper, and three or four lower premolars (38-40 teeth), and *Cynictis* has four premolars. Other cranial characteristics differentiating

Paracynictis and *Bdeogale* from suricates include orbits that are not closed posteriorly, and an interorbital space greater than or equal to the postorbital constriction, in contrast to closed orbits and interorbital space less than two thirds of postorbital constriction in *S. suricatta.*

GENERAL CHARACTERISTICS. *Suricata suricatta* (Fig. 1) is a small-sized viverrid (head and body length, 245-290 mm; tail length, 190-240 mm—Smithers, 1971) with males averaging 731 g (626-797) and females 720 g (620-969—Smithers, 1971). The body is slender with long thin legs, and a characteristic slim, tapering tail. The face is pointed with a rounded forehead and small crescent-shaped ears. Pelage color varies considerably throughout the distributional range; animals from the southern portion of the range are darker than those from the arid west and northwest. The coat is soft and closely adpressed to the body, with long guard hairs (15-20 mm over most of body; 30-40 mm on the flanks—Skinner and Smithers, 1990). The underparts are sparsely haired. Overall coloration is typically a light grizzled gray, tan, or silvery-brown. Individual guard hairs are light colored at the base, have two dark annulations separated by a light colored one, and a silvery-white or black tip. The underfur is dark rufous in color. The head is almost

FIG. 1. A group of *Suricata suricatta* at a burrow entrance in the Kalahari Gemsbok National Park, South Africa. Photograph by J. Rood.
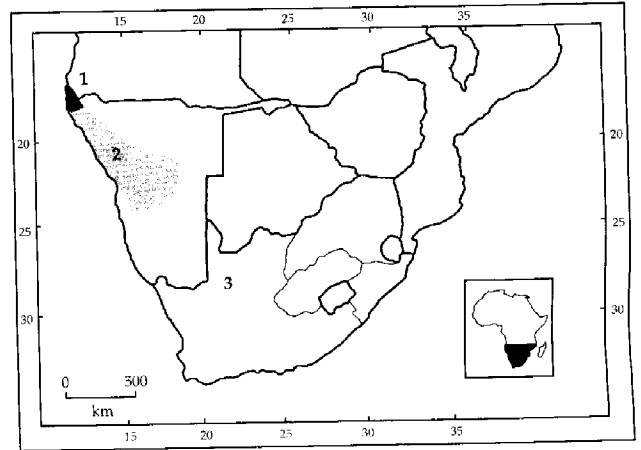
FIG. 3. Geographic distribution of *Suricata suricatta* in southern Africa (modified from Skinner and Smithers, 1990). Subspecies ranges are indicated by numbers: 1, *S. s. iona*; 2, *S. s. majoriae*; 3, *S. s. suricatta*.

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of lower jaw of *Suricata suricatta* (Museum of Comparative Zoology, Harvard University, 17913, adult male) from Hanover, Cape Province, South Africa. The greatest length of skull is 62.2 mm. Photograph by R. Huber.

white, with distinctive black eye patches. The nose is brown with short white or mixed brown/white hair above it, and the ears are black with white or black surrounds, in the northern and southern parts of the range, respectively. The tail is yellowish with a characteristic black tip. Darker mottling on the upper parts extends from the shoulders to the base of the tail, sometimes forming into distinct transverse bars, particularly in the lumbar region. The underparts are buff to yellow. Cranial characteristics of *S. suricatta* include large eye sockets (>20% total skull length) and a lightly built, high, and rounded skull (Fig. 2), which represents the most specialized form among the Herpestinae (Gregory and Hellman, 1939). No sagittal crest is evident, but the supraoccipital crest may be represented by a low, narrow ridge. The zygomatic arch is thin and the coronoid process is medium in height. The dental formula is i 3/3, c 1/1, p 3/3, m 2/2, total 36; the incisor rows are slightly curved and the molar teeth are broad with sharp cusps (Petter, 1969).

Selected morphometric characters for seven size categories of *S. suricatta* (Orange Free State, South Africa, $n = 3, 3, 8, 16, 43, 62, 57$ respectively—Lynch, 1980) identified by discriminant function analysis of skull and body measurements are (in mm; mean followed by range in parentheses): infraorbital foramen, 14.4 (13.9–14.8), 14.6 (13.2–16.0), 14.5 (13.4–16.2), 14.6 (13.5–15.6), 14.5 (13.0–16.0), 14.5 (12.2–15.8), 14.8 (12.0–16.7); minimum postorbital constriction, 20.3 (19.4–21.0), 21.1 (20.5–21.7), 20.7 (20.0–21.4), 20.7 (19.3–22.7), 20.8 (18.0–23.0), 20.5 (17.7–24.0), 20.6 (18.6–28.9); zygomatic width, 41.5 (39.6–42.8), 37.7 (33.6–40.9), 36.8 (29.7–43.1), 40.2 (36.6–43.7), 41.1 (28.9–44.6), 41.6 (26.3–47.2), 42.7 (25.8–49.0); incisor–palate length, 34.1 (33.6–35.0), 31.6 (29.1–34.0), 30.1 (20.5–35.4), 33.1 (29.3–34.8), 33.0 (20.8–35.5), 33.0 (18.2–36.3), 34.0 (17.7–37.2); height of mandible at molar 1, 6.7 (6.4–7.0), 5.4 (4.0–6.5), 5.3 (4.3–7.3), 6.4 (5.1–8.0), 6.6 (4.2–8.3), 6.8 (3.8–8.5), 7.0 (3.5–8.8); total length, 240 (232–252), 303 (293–310), 388 (368–417), 440 (407–490), 466 (438–500), 487 (453–513), 503 (472–545); length of tail, 91 (84–99), 122 (113–128), 164 (153–182), 170 (145–188), 188 (151–216), 197 (169–221), 211 (182–235); length of hindfoot, 37 (35–39), 46 (46–47), 57 (51–61), 59 (51–62), 61 (56–68), 63 (59–68), 65 (60–68); length of ear, 11 (11–12), 13 (12–14), 16 (14–17), 17 (12–18), 18 (15–20), 19 (16–22), 19 (17–21); mass of carcass (g), 113 (105–119), 189 (162–206), 323 (286–360), 467 (357–683), 585 (405–773), 659 (503–886), 709 (560–915). There was no significant difference in size between adult males and females from the Orange Free State.

DISTRIBUTION. Although *S. suricatta* is predominantly adapted for arid areas, occurring throughout the South West Arid biotic zone, its distribution extends eastward into the adjacent southern savanna and grasslands of the Highveld. It is widely distributed within the southern part of Africa (Fig. 3), occurring from southwestern Angola, then south and eastward through Namibia and much of Botswana and South Africa. *S. s. iona* is largely confined to the extreme southwestern part of Angola (Iona National Park). *S. s.*

majoriae occurs from Gobabis and southern Damaraland, Namibia, to about 100 km from the Kunene River. *S. s. suricatta* occupies the rest of the species range, occurring throughout the southwestern part of Botswana, north to about 21°S, and east to the Makgadikgadi Pan, but not in the eastern parts of the country. In South Africa, it is confined to the southern part of the Transvaal, is widespread throughout the Orange Free State but more common in the west than east (Lynch, 1980), occurs only marginally in the northwestern part of Natal, and is widespread in the Cape Province, except for the coastal belt (Lynch, 1975; Rautenbach, 1978; Smithers, 1971; Stuart, 1975).

FOSSIL RECORD. Details of viverrid history are meager, in part because the family developed in tropical regions of the Old World where the fossil record is inadequate (Dawson and Krishtalka, 1984). Fossil *S. suricatta* have been recorded from the Cave of Hearths in the Transvaal (Mason, 1962), and from the Quaternary limestone quarries at Hoedjiesbaai near Saldanha (Cooke, 1955). *Suricata major* n. sp., an early member of the suricate lineage that is intermediate between *S. suricatta* and *Mungos mungo gothneh* and not readily referable to any single modern species, has been recorded from the Cornelian deposits from Elandsfontein (Hendey, 1974). *S. major* resembles modern *S. suricatta* in the morphology of the tympanic region, relative development of inflated parts of the bulla, and the nature of the transverse slot of the ecotympanic. However, it is appreciably larger, the post-orbital process is not as well developed, and its dentition is significantly different (has p1, hence 4 premolars and 2 molars; larger upper cheekteeth; and different relative size of cusps on p4). Such differences do not warrant a distinct species designation (Hendey, 1974).

FORM AND FUNCTION. *Suricata suricatta* is noted as a proficient and avid digger; its claws are more advanced than other Feloidea and are adapted for digging. The foot is very narrow, with the first digit absent in both manus and pes, and the remaining digits closely bound together. Hallucal and pollical lobes of pads are missing, metapodial lobes are small and indistinct, and there is little development of hair (Ewer, 1973). However, the guard coat on the flanks contains a sparse admixture of 40-mm-long hairs which Skinner and Smithers (1990) speculate may have a tactile function. When burrowing the ears are closed by a forward and downwards movement of the posterior and superior ridges that prevents the entry of dust and debris.

Although well designed for digging, moving through tunnels, sitting, and standing erect, suricates are unable to run or climb well (Ewer, 1963b). *S. suricatta* is digitigrade with two usual gaits, a walk and a jump-run. The walking posture, with head low, tail trailing and hindquarters higher than forequarters, is distinctive (Smithers, 1971). Most of the seated and lying postures adopted by suricates enable heat loss by ensuring contact between the thinly haired underside and cool air or ground (Ewer, 1963b).

Suricates are excellent thermoregulators in hot environments, maintaining body temperature at or below ambient (T_a) when exposed to 40°C for 5 h (Müller and Lojewski, 1986). Body temperature exhibits a marked diurnal rhythm (mean ± *SD*; night, $\bar{X}$ = 36.3 ± 0.6°C; day, $\bar{X}$ = 38.3 ± 0.5°C). Oxygen consumption is lowest at T_a = 30–32.5°C ($\bar{X}$ = 0.365 ± 0.022 ml O_2 $g^{-1}h^{-1}$), but rises rapidly at temperatures below the thermoneutral zone. Lowest heart rates occur at T_a = 30°C ($\bar{X}$ = 109.6 ± 9.8 beats min^{-1}), and oxygen pulse is minimal at T_a = 30–35°C with 40–45 μl O_2 $beat^{-1}$. At T_a = 15–32.5°C, total evaporative water loss is from 0.46 to 0.63 ml H_2O $kg^{-1}h^{-1}$, increasing markedly during heat stress to $\bar{X}$ = 5.35 ml H_2O $kg^{-1}h^{-1}$ at T_a = 40°C because of the onset of panting at T_a > 35°C. The basal metabolic rate is unusually low for a carnivore (58% of theoretical), enabling reduced internal heat production, reduced water loss from the respiratory pathway, and longer periods of foraging at greater ambient temperatures. The suricate thermoneutral zone (30–32.5°C) is higher than that of other viverrids and desert canids, and thermal conductance (0.04 ml O_2 $g^{-1}h^{-1}$) is 18% higher than the theoretical mass-specific level. Nothing is known of seasonal changes in thermal conductance because of deposition of subcutaneous fat or growth of thicker fur. In cold environments (e.g., mean daily temperature in winter in Namibia is 6–10°C—Schultze and McGee, 1978), suricates counter rapid heat loss by increased metabolic heat production, but also extensively utilize behavioral mechanisms (e.g., sunbathing, huddling, sleeping densely packed in burrows at night) to reduce the energetic costs of thermoregulation.

Suricates have an excellent sense of smell, but their hearing and ability to locate sounds may be no better than that of humans (Ewer, 1963b). Flehman has been observed in *S. suricatta* but there is no information about the condition of Jacobson's organ (Ewer, 1973).

Visual capabilities of suricates are largely explicable by their lack of a tapetum (Walls, 1942) and the fact that retinal receptors are predominantly cones with only a few rods (Bernau, 1969). Behavioral observations indicate that vision is sufficiently acute to identify hawks at long distances, but is less acute than that of humans in dim light (Dücker, 1962; Ewer, 1973). Moran et al. (1983) estimate the threshold of visual acuity to be 6.3 cycles $degree^{-1}$. Although the ability to discriminate between 29 shades of gray is weakly developed, suricates can distinguish red, yellow, green, and blue (Bernau, 1969). The horizontally elongated, oval pupil, which extends the visual field in a horizontal plane, is advantageous in the open environments favored by *S. suricatta* (Ewer, 1973). Stereopsis is present in suricates, and predicates the occurrence of disparity tuned neurons in the visual cortex (Moran et al., 1983).

Röhrs et al. (1989) reported a cephalization index of 165 for *S. suricatta* (n = 2; body mass, $\bar{X}$ = 567 g; brain mass, $\bar{X}$ = 11.55 g), which is higher than both the mean for Herpestinae (n = 4 species; $\bar{X}$ = 150 g; range 113–177) and values reported for the Viverrinae (140 g; 145 g) and Paradoxurinae (120 g).

Suricata suricatta has sharply cusped, interlocking teeth, and a poorly developed carnassial shear, indicating a dependence on relatively soft insect food. Development of the temporalis and masseter muscles, thin zygomatic arches and coronoid processes of medium height likewise indicate a soft diet (Skinner and Smithers, 1990). By repeatedly puncturing the same spot with their sharp teeth, suricates can, however, eat prey which are so large or resistant that the jaws cannot be closed in a single bite (Ewer, 1973).

Cheek glands are absent in suricates, but both sexes have anal scent glands (Moran and Sorenson, 1986; Pocock, 1916). Skin glands around the anus are invaginated to form a pouch, closing to form a transverse line. The pouch lining is folded into a series of subsidiary pockets, presumably for storage of secretion from accessory glands (Ewer, 1973). Ducts of anal glands open into the pouch, which is everted to expose the openings when secretion is to be applied.

ONTOGENY AND REPRODUCTION. *Suricata suricatta* has an extended breeding season with no sychronized estrus, copulation, or parturition. Females with ripe (>1.40-mm) Graafian follicles are found year-round, but individual adult females exhibit significant seasonality. Forty-two percent of female suricates collected throughout the year were reproductively active (Lynch, 1980). In captive animals, mating or parturition have been recorded in all months of the year except April (Brand, 1963; Ewer, 1963b; Zuckerman, 1953). In the wild, births occurred during the warm, wet seasons (August through November, January, and March), with no evident peak (n = 12 females—Lynch, 1980). This pattern is supported by records of juveniles in October and March in the Kalahari Gemsbok Park (Lynch, 1980) and juveniles running with parents outside burrows in April in Botswana (Smithers, 1971). Captive suricates under controlled temperature regimes gave birth to 11 litters in 31 months, leading Lynch (1980) to speculate that the lengthy active reproductive period may be due to the buffering effect of the burrow microenvironment against external climatic extremes.

Thirty-four percent (n = 32) of reproductively active *S. suricatta* females examined in the wild were found to have two estrus cycles per season, but there was no indication that more than a single litter per year was produced (Lynch, 1980). Among captive suricates, mean intervals between successive births were 136 days (range 75–197) and 115 days (range 58–172), and three females exhibited postpartum ovulation, coming into estrus 4, 7, and 22 days after having given birth (Lynch, 1980; Wemmer and Fleming, 1974). Lynch (1980) found 5 of 84 females to be pseudopregnant, indicating that *S. suricatta* may be an induced ovulator.

Most fecundity losses in suricates occur prenatally up to the embryo/fetus stage. Average preimplantation loss was 0.2 and average postimplantation loss was 0.8, yielding a potential loss of 1.0 ovum or embryo or fetus/female. The mean number of embryos or fetuses/female was 3.0 and the mean number of young/litter was 2.9, giving an actual loss of 0.1 and a total loss from ovulation until after parturition of 1.1 ova, embryos, fetuses, or young/female

(Dücker, 1962; Ewer, 1973; Lynch, 1980; Shortridge, 1934; Smithers, 1971).

The gestation period is approximately 11 weeks, during which the teats increase in size and prominence, particularly in the last month (Ewer, 1963a), but there is no correlation between mammary gland size and stage of fetal development (Lynch, 1980). No differences in the number of embryos or fetuses/female were noted in nine wild-caught animals (Lynch, 1980). In pregnant *S. suricatta*, diameters of corpora lutea ($\bar{X} = 2.74$ mm; range, 2.25–3.18) were inversely related to fetal development (Lynch, 1980). Measurements (in mm; mean followed by range of means for individual litters; *n* = 12) of embryos and fetuses is as follows: length of head, 15.5 (5.9–34.2); crown/rump length, 33.2 (11.2–78.6); length of hind foot, 7.9 (1.6–22.0); length of tail, 16.9 (3.7–54.0); dorsal curvature length, 62.9 (23.7–120.0); body mass (g), 7.6 (0.3–36.6—Lynch, 1980).

Females in the wild are rarely seen with more than four young; estimates of litter size range from two to five in the wild (Ewer, 1973; Fitzsimons, 1919) and from two to seven for captive litters (Brand, 1963; Ewer, 1963a; Zuckerman, 1953). Females with four fetuses were recorded from Namibia in November (Shortridge, 1934), and from Botswana in February (Smithers, 1971). The mean number of fetuses/female in the Orange Free State was 2.9 (*n* = 34), with no significant variation in litter size between months (Lynch, 1980).

Neonates are born with eyes and ears closed, sparse, short hair, and weighing 25–36 g each at birth (Dücker, 1962; Ewer, 1963a). They are incapable of micturition or defecation without external stimulation by the female (Ewer, 1963a). Ears open after 10 days, and eyes after 10–14 days (Dücker, 1962). Solids are eaten at 23–30 days, and weaning occurs at 49–63 days (Ewer, 1973).

Sexual maturity is attained by 1 year of age (Grzimek, 1990). Quantitative characteristics of the reproductive tract and ovaries (in mm unless otherwise indicated; mean ± *SD*) for prepubertal, pubertal, and adult females (*n* = 7, 6, 5–13), respectively, are: mass of reproductive tract (g), 0.26 ± 0.15, 0.81 ± 0.29, 1.90 ± 0.75; length of uterine horn, 14.8 ± 4.0, 18.7 ± 7.4, 42.3 ± 6.42; diameter of uterine horn, 2.3 ± 0.50, 3.7 ± 0.89, 5.1 ± 1.28; length of vagina, 11.0 ± 3.56, 12.2 ± 3.70, 17.2 ± 3.8; diameter of vagina, 2.5 ± 0.28, 4.1 ± 1.34, 4.9 ± 0.64; ovary mass (g), <0.01, 0.01 ± 0.01, 0.13 ± 0.04; size of ovary, 3.4 ± 0.59 by 2.8 ± 0.4, 4.5 ± 0.72 by 3.6 ± 0.48, 8.7 ± 2.69 by 5.7 ± 1.33; number of corpora lutea/corpora albicantia, 0, 0, 4.4; diameter of corpora lutea/corpora albicantia, 0, 0, 3.35 ± 0.71; ameter of graafian follicles, 0, 15 ± 12, 19 ± 13; maximum number of graafian follicles, 0, 0.87 ± 0.24, 1.75 ± 0.34; number diameter of graafian follicles, 0, 14 ± 11, 16 ± 17; number of corpora of secondary follicles, 0, 53 ± 29, 82 ± 75 (Lynch, 1980). altretica lutea, 0, 53 ± 29, 82 ± 75 (Lynch, 1980).

Body condition appears to be influenced by reproductive activity and diet. Significant differences in kidney fat indices, ranging from a mean of 31 g in pubertal females to 130 g in pseudopregnant females, have been reported for adults (*n* = 63). There is also significant annual variation in kidney fat indices (*n* = 87), with means ranging from 139 g in March to 33 g in January. No significant differences have been reported for mass of thyroid gland (*n* = 56; mean ± *SD*; $\bar{X}$ = 0.03 g ± 0.02–0.1 ± 0.03) or mass of anal gland (*n* = 63; $\bar{X}$ = 0.41 g ± 0.02–1.59 ± 0.36) among females in various developmental categories, but pseudopregnant females have significantly greater mass of adrenal gland ($\bar{X}$ = 0.04 g ± 0.02–0.19 ± 0.06) and width of cortex ($\bar{X}$ = 0.60 mm ± 0.01–1.20 ± 0.44—Lynch, 1980).

Breeding in male suricates is not synchronized and there is no seasonal reproductive periodicity (Lynch, 1980). The apparent breeding cycle seems to be regulated by the cycle of the females. Mass of testes and epididymides increases in March/April, reaches a maximum in July/August, and decreases to a minimum in January/February. Numbers of spermatozoa in testes and epididymides increase in March/April and July/August, respectively, reaching a maximum in September/October. There is no increase in size of endocrine glands but mass of anal gland increases discernibly during the reproductively active period. Sperm counts ranged from 61–185 × 10⁶/epididymis, and 84% of adults had sperm in the testes. Some subadult males may be physiologically capable of reproducing; 27% of prepubertal males (*n* = 15) and 42% of pubertal males (*n* = 12) had spermatozoa in the testes or epididymides. Quantitative characteristics of the reproductive tract (in g unless otherwise indicated; mean followed by range in parentheses) for prepubertal,

pubertal, and adult males (*n* = 14, 8, 31–108) respectively are: size of testis (mm), 5.7 by 4.4, 9.4 by 7.7, 11.9 by 9.6; mass of testis, 0.11 (0.01–0.38), 0.29 (0.08–0.4), 0.60 (0.19–1.12); diameter of seminiferous tubule (µm), 99.6 (50.0–197.0), 195.7 (142.0–215.0), 253.8 (156.0–282.0); mass of epididymis, 0.05 (0.02–0.12), 0.07 (0.02–0.12), 0.14 (0.05–0.27); mass of bulbourethral gland, 0.16 (0.04–0.49), 0.57 (0.29–0.86), 0.78 (0.1–1.93); mass of prostate, 0.10 (0.03–0.21), 0.29 (0.20–0.39), 0.38 (0.16–0.67); mass of adrenal gland, 0.04 (0.02–0.09), 0.08 (0.05–0.17), 0.11 (0.06–0.17); width of adrenal cortex (mm), 0.8 (0.4–1.1), 0.8 (0.5–1.0), 0.9 (0.4–1.4); mass of thyroid gland, 0.05 (0.02–0.09), 0.07 (0.05–0.11), 0.09 (0.04–0.18); mass of anal gland, 0.55 (0.06–1.46), 0.87 (0.64–1.10), 3.45 (0.49–12.41—Lynch, 1980).

ECOLOGY. This herpestid inhabits the driest and most open country of all mongooses and is found in a variety of habitats, including savanna and open plains, alkaline pans, and the stony banks of dry water courses (Estes, 1991; Smithers, 1971). They prefer open ground with Karoo scrub or short grass and are associated with a variety of veld types: Botswana—*Acacia* scrub; Namibia—Camelthorn, Mixed Tree and Shrub, Thornbush, Highland, and Semi-desert Savannas, Savanna Transition, and infrequently, Mopane Savanna; Cape Province—Karoo and Karroid Bushveld, False Karoo veld; Orange Free State—Karroid veld, Kalahari thornveld, open Dry *Cymbopogon-Themeda* veld; Transvaal—Pure Grassveld, False Grassveld, Kalahari Thornveld (Acocks, 1975; Giess, 1971). The distribution of *S. suricatta* is largely governed by soil type. Suricates occur on Desert, Kalahari, and Sandy soils, but are also found in areas of less friable soils, namely Solonetzic soils (Orange Free State and Cape Province), Ferruginous lateritic soils, and Gleylike podsolic soils (Transvaal—Coetzee, 1977; Rautenbach, 1978; Smithers, 1971).

Colonies in stony areas live in crevices among the rocks (Michaelis, 1972). Those on the plains inhabit burrow systems that they may excavate themselves, but more usually they occupy existing burrows prepared by other small mammals. *Suricata suricatta* is regularly found in association with the social ground squirrel, *Xerus inauris*, and the solitary yellow mongoose, *Cynictis penicillata*. Lynch (1980) found joint burrow occupation in 85% of warren systems in the Orange Free State, with the relative proportion of suricates to associates averaging 6:1. Interspecific cooperation among migrant burrowing species saves time and energy. Suricate occupation of *Xerus* burrows is usually without aggression (Herzig-Straschil, 1978) and there is no competition for food or space (Smithers, 1971). The potential competition for food between insectivorous *S. suricatta* and *Cynictis* is lessened because the latter range more widely and eat murids, birds, and frogs more readily than will suricates (Skinner and Smithers, 1990). Other mammal species recorded in burrow systems of suricates include *Pedetes capensis, Rhabdomys pumilo, Mus minutoides, Mystromys albicaudatus, Tatera brantsii, Procavia capensis, Herpestes pulverulentus,* and *H. sanguineus* (Lynch, 1980).

Burrow sites are slightly elevated because of accumulation of excavated soil. On average, they measure 5 m in diameter with approximately 15 entrance holes (Lynch, 1980), although Snyman (1940) reported a system 25 by 32 m with 90 openings. Suricate dens may be simple, or extensive and complex labyrinths. Entrance holes, 15 cm in diameter, are dug at 40° angle to the soil surface. Tunnels 7.5-cm high and slightly broader descend from 1–1.5 m, end at 2–3 different levels, and are interconnected by chambers 30-cm high by 15–45 cm long which lack straw bedding (Lynch, 1980). Tunnels excavated by Snyman (1940) descended to a depth of 60–90 cm and ended at a single level. Temperatures in underground burrows are moderated; mean air temperatures showed an annual range of 43°C (summer, 21–39°C; winter, −4–26°C), whereas daily temperature variation in the deeper tunnels was <1°C (summer, 22.6–23.2°C; winter, 10.0–10.8°C), with an annual range of 13.2°C. A persistent temperature gradient in soil and burrows results from temperature penetration of soil with an 8-h lag; hence burrows are coolest during the day and warmest at night. Underground burrows enable suricates to avoid climatic extremes and create a microclimate which minimizes individual thermoregulation. The importance of this difference is indicated by the proportion of time the animals spend in the burrow system (summer, 66%; winter, 50%) and the increase in burrow usage with temperature extremes (Lynch, 1980).

Lynch (1980) listed the helminths *Pseudandrya suricattae, Ascaris suricattae, Vigisospirura whitei, Dipetalonema setariosum, Toxocara suricattae, Oxynema suricattae, Travassospirura dentata, Microfilaria sp., Physaloptera sp.,* and *Diplopylidium sp.* as endoparasites of *S. suricatta.* Ectoparasites include fleas (*Chiastopsyla numae, C. rossi, Ctenocephalides canis, C. connatus, C. felis, Dinopsyllus ellobius, Echidnophaga bradyta, E. gallinacea, E. larina, Listropsylla chelura, Pulex irritans, Synosternus caffer, Xenopsylla cryptonella*) and ticks (*Amblyomma sp., A. hebraeum, Haemaphysalis zumpti, H. l. leachii, H. l. müsami, Ixodes pilosus, Nuttalliella namaqua, Rhipicephalus appendiculatus, R. evertsi* and *R. theileri*—Haeselbarth et al., 1966; Lynch, 1980).

Pack size ranges from 2 to 30 individuals (Skinner and Smithers, 1990), with selection by predators and interpack competition favoring larger over smaller packs. Mean pack sizes of 15 ($n = 10$; range, 8–30) and 14.9 ± 6.5 *SD* ($n = 10$), were recorded in Botswana (Macdonald, 1984; Smithers, 1971). In the Orange Free State, average pack size was 10.6 ± 3.1 *SD* individuals ($n = 16$; range, 2–17—Lynch, 1980). Mean pack composition (range in parentheses) of eight complete social groups was: 5.4 adult males (2–9), 4 adult females (0–7), 0.75 juveniles (0–2), and 1.1 subadults (0–4). A sex ratio of 1:0.84 ($n = 90$) in favor of males was found. Suricates in captivity have lived 12.5 years (Jones, 1982), and potential longevity in the wild is estimated at 5–15 years (Nowak, 1991). Raptors, martial eagles, and jackals are the chief predators of suricates (Skinner and Smithers, 1990).

Migration by entire packs is related to food availability, population density, flooding, and predators (Grzimek, 1990), and generally entails rotational usage of multiple burrow systems within the home range. Home range may be relatively large (e.g., a pack of 12 animals ranged over an area of 15.5 km²) and may contain up to five burrow systems spaced from 50–100 m apart. Some packs are migratory and may occupy several burrow systems within a short time, but there is evidence of a pack inhabiting a single burrow system for many generations over 15 years (Snyman, 1940). Occasionally a single pack may split and occupy two adjacent burrow systems (Lynch, 1980). Suricate males routinely emigrate from their natal pack and attempt to join or take over another pack (Rood, 1986). There is anecdotal evidence of infrequent female emigration (Skinner and Smithers, 1990).

Suricata suricatta has a primarily insectivorous diet, but will readily kill small vertebrates and take eggs and plant food. Zumpt (1968) reported that three of 18 stomachs contained plants and seeds only. Suricates are not opportunistic feeders, but actively forage near the burrow, turning over stones and rooting in crevices. In waterless areas, suricates may obtain water by chewing tsamma melons and digging up roots and tubers (Ewer, 1973). The diet, in order of relative importance, includes the following classes (Lynch, 1980): Insecta, 82%; Arachnida, 7%; Chilopoda, 3%; Diplopoda, 3%; Reptilia, 2%; Amphibia, 2%; and Aves, 1%. Infrequent consumption of vertebrates is confirmed in several studies: 6% ($n = 18$—Zumpt, 1968); 18% ($n = 17$—Smithers, 1971); 0% ($n = 2$—Viljoen and Davis, 1973); 0% ($n = 1$—Herzig-Straschil, 1977). Vertebrate species taken include: birds—*Myrmecocichla formicivora;* reptiles—*Agama hispida, Ermias namaquaensis, Typhlosaurus lineatus, Nucras intertexta;* amphibians—*Pyxicephalus delalandi, Cacosternum boetgeri* (Lynch, 1980; Smithers, 1971). Fitzsimons (1919) reported that suricates prey on mice but there is no evidence of this in recent studies. Captive animals, however, will kill small mammals with a single bite at the back of the skull. Prey is not shaken and no practice or learning is involved in determining the speed and accuracy of the bite-killing orientation (Ewer, 1973). The relative abundance of invertebrates in the diet was: Coleoptera, 58%; Lepidoptera, 43%; Isoptera, 40%; Orthoptera, 34%; and Diptera, 23% (Lynch, 1980). Lepidoptera were eaten most often, i.e., 38% of the stomachs were full of these invertebrates, and 21% contained only Coleoptera. Food preferences vary seasonally. In winter Coleoptera and Lepidoptera predominate in the suricate diet, both qualitatively and quantitatively. During summer, the food spectrum shifts such that suricates most frequently eat Coleoptera and Isoptera, but Lepidoptera, Orthoptera, and Diptera compose the bulk of the diet (Lynch, 1980). *S. suricatta* becomes omnivorous in captivity taking a wide variety of fruit and vegetables (Ewer, 1963b).

Human management and interest in suricates relate primarily to the ecological effects of burrow construction (Snyman, 1940) and the role of suricates in the ecology of rabies and plague (Zumpt,

1968). In the Orange Free State, *S. suricatta* is considered second in importance only to the yellow mongoose as a vector of rabies (Barnard, 1979; Snyman, 1940; Zumpt, 1976). Only 10 cases of rabid suricates attacking humans or domestic animals were documented in the last decade, but it has been suggested that *S. suricatta* promotes the spread of rabies by expelling *Cynictis* from its burrow (Barnard, 1979). Plague has not been found in suricates, but they are a vector of tick-borne diseases, hosting three tick species of economic importance (Theiler, 1964). Suricates arguably may be of economic significance in retarding the increase of cyclic lepidopteran populations which damage agricultural crops and pasture. *S. suricatta* is usually protected by farmers who do not consider it to be a vector of rabies, but some are killed during rabies control programs aimed at *Cynictis* (Lynch, 1980). Of several trapping methods (including boxtraps, pitfall traps, flooding, and fumigating), only shooting and mechanical excavation of burrows with a trench digger were successful (Lynch, 1980).

Suricates have a sociable disposition and are easily tamed (Barnard, 1979; Ewer, 1966; Pallas, 1777); hence their potential use as a model for investigating binocular vision (Moran et al., 1983). They are kept in homes in rural areas of South Africa to kill mice and rats (Nowak, 1991). Because they epitomize small African mammals, suricates are widely maintained and bred in zoos (Degre and Robert, 1989; Jones, 1982; Partridge, 1990; Sheperdson et al., 1990; Stowe, 1989).

BEHAVIOR. Behavioral studies have mostly involved captive animals (Dücker, 1962; Moran and Sorenson, 1986; Sorenson, 1981; Wemmer and Fleming, 1974; but see Macdonald, 1984 for observations of naturally occurring populations). Suricates are highly social, living in packs comprising two or three family units, with each family containing a pair of adults and their young. Pack members are amicable, but ferociously hostile to other packs, suggesting the possibility of territoriality (Ewer, 1973). Suricate females are larger than males and dominant to them with regard to food access (Ewer, 1973). However, in the wild, there is little evidence of a linear rank hierarchy within or between the sexes. There is a division of labor, in which males act as sentinels and females as baby-sitters on a rotating basis (Skinner and Smithers, 1990).

The daily activity cycle of suricates is controlled largely by soil temperature and they are almost entirely diurnal (Ewer, 1973). Animals emerge from warrens only when the morning sun is warm, and retire to them well before sundown, not emerging at all on cold, overcast days or during inclement weather. Upon emergence in the morning, *S. suricatta* stand clustered around the burrow entrance grooming and basking in the sun until the entire pack has gathered. Daily activity is initiated when one individual drops to all fours, begins moving about, and is followed by the rest of the pack (Smithers, 1971). Activity decreases between 1200 h and 1400 h in summer, when animals may retire to their burrows to escape the heat (Lynch, 1980).

Foraging behavior is typical of social mongooses, in which animals spread out and forage individually while maintaining visual and vocal contact (Ewer, 1963b). A pack forages systematically and thoroughly within its home range, taking a different route each day and usually allowing at least a week for an area to renew its food supply between visits (Roberts, 1981). Concealed prey are located by smell and dug out with the forefeet. Adults readily share food with juveniles in the pack (Ewer, 1973). In captive animals, three innate responses to active prey have been noted: a tendency to chase any small fleeing object; to bite at the most actively moving part; and to eat mammalian prey starting at the head. The throwing response of other mongooses, whereby hard-shelled prey and eggs are broken, appears in a very incomplete form in domesticated suricates and is probably of no real significance in the wild. Pet suricates exhibit food envy to a marked degree, perhaps as an artifact of the type of food and unnatural proximity of individuals while feeding (Ewer, 1973).

Vocal communication consists of three threat sounds (growl, explosive spit, harsh repetitive scolding) and seven other vocalizations within specific contexts: an almost continuous contact call (possibly equivalent to purring—Zannier, 1965); satisfaction—when eating; settling down—when going to sleep; pure fear call—warning of aerial predator; mixed fear-aggression call—warning of danger on ground; alarm barking—contagious call which alerts to some general but not clearly localized disturbance; dissatisfaction call—made in captivity by males only, not directed at conspecifics (Ewer, 1973).

The absence of a pain cry is notable. Moran (1984) provided sonograms of two sounds, possibly equivalent to the fear calls catalogued above. The hoot (=pure fear call) demonstrates little modulation, is of variable duration, and has a fundamental frequency of 600–900 Hz with formants ranging as high as 3 kHz. The bark vocalization (=mixed fear-aggression call) is stereotyped and occurs in bursts with 0.5–1 s between calls. The major energy distribution is in the 0–3 kHz and 7–11 kHz range, with much noise between these regions.

Anal-drag, leg-lift, body-rub, and sniffing behaviors may mediate olfactory communication in suricates, using anal-gland secretions, urine, and communal latrines (Ewer, 1963b; Moran and Sorenson, 1986). Secretions may be applied on horizontal surfaces by anal-drag, which apparently has a social communicatory as well as a grooming function. Secretions are deposited at nose height by cocking one leg like a dog micturating (leg-lift), simultaneously everting the pouch and smearing down (Ewer, 1963b). Using captive animals, Moran and Sorenson (1986) demonstrated that all animals leg-lift, although the frequency varied among individuals and over time. These differences were unrelated to age or sex. Particular locations in the environment were regularly monitored and consistently marked to maintain a certain level of odor on those objects. Proximate causes of scent marking were a lowered odor intensity on established scent posts, agonistic motivation, and changes in social relationships or status. Body-rubs pick up odor from an object, and together with leg-lift and sniffing behaviors, may provide a group odor and orient individuals in the group. The function of raised-leg urination is unknown. Use of communal latrines may originate when littermates, beginning in the 3rd month of life, use places where other suricates have excreted (Estes, 1991).

Agonistic behavior in suricates is limited, and there is no submissive signal or posture. Withdrawal if threatened, or a snap and growl in situations involving food, are sufficient to avoid conflict (Ewer, 1973). Fighting between group members is ritualized and harmless (Ewer, 1963b), but is often fierce during encounters between different packs (Skinner and Smithers, 1990). Suricate antipredator behavior encompasses a variety of strategies. They maintain a constant vigilance against raptors, sounding the alarm if one is sighted and fleeing for cover if an attack seems imminent (Ewer, 1963b). Alarm calls are brief, abrupt and repeated several times in series. Because the source of such calls is easy to locate, orientation by other suricates is swift and accurate (Ewer, 1973). Alarm calls by either parent cause the young to run to the mother, remaining close as long as she calls and mirroring her movements (Ewer, 1973). In keeping with their preference for open habitat and poorly developed athletic ability, suricates have evolved elaborate threat displays. Antipredator displays transform a slender, low animal into a larger, almost spherical object (Ewer, 1963b). The hair bristles, legs are extended, tail is stiffly erected, back is arched, and head is slightly lowered. Rocking back and forth in approximately the same place, it appears to approach the enemy in stiff-legged high bounds. Growling, head-darting, and spitting intensify as the enemy approaches. If the attack proceeds, the suricate lies on its back with all weapons presented and the nape of its neck protected (Estes, 1991).

Sexual behavior is undescribed in the wild, but sexual activity of captive suricates was observed by Ewer (1963b). There was no extensive precopulatory display. Sexual activity usually began with a bout of semi-serious fighting, when one gripped its partner firmly by the muzzle. If the female resisted mounting, the male would grip her by the nape, inducing passivity. During copulation the male maintains his position by clasping the female's middle without the neck grip. In the wild, a pack may have several breeding males and females (Rood, 1986). Nonbreeding helpers of both sexes guard and provision the suricate young, and fathers may take an active part in guarding the young. The mother does neither until after weaning but keeps foraging to sustain an adequate milk supply (Macdonald, 1984). Interactions with her offspring are not competitive or strenuous (Ewer, 1963a; Smithers, 1971). The technique used in carrying young varies with age of the mother; young mothers pick up kittens randomly, whereas older mothers always use the neck grip (Ewer, 1973).

Neonates produce a continuous twittering bird-like noise, which changes to a distinctive high-pitched contact call after a few days. There is evidence of a form of teat recognition that does not imply exclusive ownership. Each neonate selects a teat at the start of the feeding session, later shifting several times so that all teats are used by the litter. During the weaning process, mothers exploit the food-envy trait of the young to teach them to forage for themselves. With food in her mouth, the mother runs back and forth before her cubs encouraging them to snatch and eat the item (Ewer, 1963b, 1973). A strong following tendency and high-pitched, repetitive contact call keep the young closely grouped until they become nutritionally self-sufficient (Estes, 1991). For a brief period that begins at 24 days of age, young suricates cover the toilet pit after use. This juvenile behavioral trait is never seen in mature animals and is probably vestigial (Dücker, 1962).

All pack members participate in play behavior and frequently engage in acrobatic sparring during rest periods (Skinner and Smithers, 1990). Elements of antipredator threat displays, feeding, and fighting techniques are also seen in play (Ewer, 1963b; Wemmer and Fleming, 1974). Playfulness declines significantly with age (Ewer, 1973).

GENETICS. The diploid chromosome number is 36 (FN = 66). There are 34 metacentric, submetacentric, and subtelocentric autosomes, a submetacentric X and telocentric Y (Todd, 1966; Wurster and Benirschke, 1968). *S. suricatta* does not share the common Herpestinae pattern in which the male Y chromosome is translocated onto one of the autosomes, and the karyotype does not resemble that of *Cynictis penicillata* (Fredga, 1972).

REMARKS. There are numerous colloquial names for *S. suricatta*. Meerkat is common in English but also applies to other mongoose species. In earlier literature *S. suricatta* is referred to as mierkat (Shortridge, 1934). Mier is Afrikaans colloquial for termite and kat means mongoose. Lynch (1980) speculates they may be named for their frequent association with termite mounds or the termites they consume. In Afrikaans *graatjiemeerkat* is used (Kritzinger et al., 1986) but *stokstertmeerkat* is well entrenched and descriptive (Skinner and Smithers, 1990). Suricate, a South African native name, apparently of French derivation borrowed from the Dutch (Gotch, 1979), is the most appropriate name (Skinner and Smithers, 1990).

Whereas Herpestidae is generally recognized as a distinct and monophyletic family, relationships within the herpestine-mungotine lineage are poorly understood and require further systematic work (Wozencraft, 1989a, 1989b).

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