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Madoqua kirkii.

By Steven C. Kingswood and Arlene T. Kumamoto

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Madoqua kirkii (Günther, 1880)

Kirk's Dik-Dik

Neotragus kirkii Günther, 1880:17. Type locality "near Brava, in the South Somali country," Somalia.

Neotragus damarensis Günther, 1880:20. Type locality "Damara Land," Namibia.

Madoqua cavendishi Thomas, 1898:278. Type locality "Lake Rudolf region," but probably the region south of Baringo, Kenya (Roosevelt and Heller, 1914:632).

Rhynchotragus thomasi Neumann, 1905:89. Type locality "Tisso (Kwa Meda) in Nord-Ugogo," Tanzania.

Madoqua langi Allen, 1909:153. Type locality "Elmenteita," Kenya.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Superfamily Bovoidea, Family Bovidae, Subfamily Antilopinae, Tribe Neotragini, Genus *Madoqua*, Subgenus *Rhynchotragus*. Seven subspecies are recognized by Ansell (1971) as follows:

M. k. cavendishi Thomas, 1898:278, see above (*langi* Allen is a synonym).

M. k. damarensis Günther, 1880:20, see above (*variani* Drake-Brockman is a synonym).

M. k. hindei Thomas, 1902:242. Type locality "Kitui, British East Africa" (=Kenya).

M. k. kirkii Günther, 1880:17, see above.

M. k. minor Lönnberg, 1912:66. Type locality "north of Guaso Nyiri, below Chanler Falls," Kenya.

M. k. nyikae Heller, 1913:3. Type locality "Ndi, near Voi, British East Africa" (=Kenya).

M. k. thomasi Neumann, 1905:89, see above.

Madoqua kirkii may consist of two sibling species, represented by the small-sized subspecies *M. k. kirkii* and *M. k. minor* in the northeast and the larger *M. k. cavendishi*, *M. k. damarensis*, and *M. k. thomasi* in the southwest (Grubb, 1994; Kumamoto et al., 1994). *M. k. hindei* and *M. k. nyikae* are intermediate in size and distribution (Grubb, 1994).

DIAGNOSIS. Dik-diks of the subgenus *Rhynchotragus* (*M. kirkii* and *M. guentheri*) are distinguished from the subgenus *Madoqua* by having a more strongly developed proboscis, S-shaped premaxillae, and a third lobe on lower m3. *M. kirkii* and *M. guentheri* are difficult to distinguish, but Kirk's dik-dik is generally recognized by its longer nasals and premaxillae and its shorter proboscis, giving the head a more wedge-shaped profile than Guenther's dik-dik (Ansell, 1971; Hofmann, 1973). In *M. kirkii*, length of the nasal chamber does not exceed interorbital width of the skull as it does in *M. guentheri* (Roosevelt and Heller, 1915). Body masses (in kg) of adult *M. kirkii* and *M. guentheri*, respectively, are 3.8–7.2 and 3.7–5.5 (Kingdon, 1982).

GENERAL CHARACTERS. Kirk's dik-diks are of small size and slender build (Fig. 1). The hindquarters are at the same level or slightly higher than the shoulder. Typical of *Madoqua*, Kirk's dik-diks have a tuft of long hair on the crown and a pointed, elongated nose which is entirely covered with hair, except for the lower part of the nasal septum; the rhinarium is nearly absent (Bryden, 1899; Sclater, 1900). Coloration is cryptic with inconspicuous markings (Estes, 1991). The back, rump, and hocks are grizzled with black, brown, or yellow, slightly fading to pale brown with tints of gray, red, or yellow on the head, neck, shoulders, flanks, and legs and buff to white on the lips, chin, throat, breast, belly, and inside legs. Kirk's dik-diks have a small head, long neck, and a short tail. Males have short, black horns that are straight or curved slightly backward from the profile of the face. The basal half of the horns has seven to nine annular ridges, which are often concealed by the crest. Eyes are large and placed anterolaterally; eyes, eyelids, and preorbital glands are black and are surrounded by a white eye ring. Ears are large and white interiorly. The legs are relatively long and slender. Hooves are black, slender, and pointed anteriorly; the lateral hooves are tiny (Günther, 1880; Lydekker and Blaine, 1914; Sclater, 1900).

Madoqua kirkii is sexually dimorphic; females are larger and lack horns. In males, the muzzle is more developed and the crest is longer and lighter in color than in females (Günther, 1880; Lönnberg, 1912). Means (and ranges) of external measurements (in mm) of adult males and females, respectively, are as follows: total length, 676 (570–780, $n = 31$) and 690 (640–750, $n = 35$); length of tail, 45 (30–77, $n = 22$) and 51 (32–70, $n = 20$); length of hind foot, 198 (159–218, $n = 41$) and 203 (191–216, $n = 34$); length of ear, 78 (57–86, $n = 39$) and 79 (57–85, $n = 35$); length of horn (males), 83 (47–114, $n = 263$); basal circumference of horn (males), 45 (29–70, $n = 227$); distance between horn tips (males), 44 (19–124, $n = 250$); height at shoulder, 383 (300–445, $n = 189$) and 397 (340–444, $n = 157$); height at sacrum, 455 (445–460, $n = 4$) and 463 (450–475, $n = 2$); chest girth, 367 (340–385, $n = 6$) and 369 (350–381, $n = 4$); body mass (kg), 4.59 (2.6–6.0, $n = 181$) and 5.13 (2.7–6.4, $n = 151$—Allen, 1909; Allen and Loveridge, 1933; Allen et al., 1936; Best and Raw, 1975; P. Brotherton, in litt.; Bryden, 1899; De Beaux, 1923; Drake-Brockman, 1913; Günther, 1880; Heller, 1913; Hill and Carter, 1941; Kellas, 1955; Loveridge, 1923; Roberts, 1954; Roosevelt and Heller, 1915; Sachs, 1967; Shortridge, 1934; Tinley, 1969).

Madoqua k. kirkii and *M. k. minor* are the smallest races of *M. kirkii*, and *M. k. cavendishi* and *M. k. damarensis* are the largest. Pelage coloration also varies geographically. Dorsal coloration of *M. k. minor*, a pale desert race, is buffy. *M. k. kirkii* and *M. k. nyikae* are slightly darker ochre-tawny on the back, but like

FIG. 1. Adult male *Madoqua kirkii damarensis* at Etosha National Park, Namibia. Photograph by Chris and Tilde Stuart/African-Arabian Wildlife Research Centre.

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Madoqua kirkii* (British Museum 38.6.22.1) from Banagi Hill, Tanzania. Greatest length of skull is 117.5 mm, and biorbital width is ca. 58 mm (damaged). Photographs by Peter Grubb.

M. k. minor, their pale buff flanks show little contrast to their white abdomen (Lydekker and Blaine, 1914; Roosevelt and Heller, 1915). Specimens of *M. k. nyikae* often have white spots on their legs (Loveridge, 1923). *M. k. hindei* and *M. k. cavendishi* are darker highland races that resemble *kirkii*, *minor*, and *nyikae* but differ by having rufous sides in sharp contrast to their white underparts; *M. k. cavendishi* is generally less rufous than *hindei*, and it approaches the grayness of *M. k. nyikae*. *M. k. thomasi* is similar to *M. k. hindei* but is generally more rufous. *M. k. damarensis* is similar to *M. k. cavendishi* by having a gray rump, but in *M. k. damarensis*, the anterior back is lighter and the crest is blacker (Günther, 1880; Lydekker and Blaine, 1914; Roosevelt and Heller, 1915). Certain hues (e.g., reddish and pinkish tints of ventral areas) are often a result of local soils; thus, they are of no taxonomic value (A. M. Simonetta, in litt.).

Skulls of *M. kirkii* (Fig. 2) have the following characteristics: in males, horn cores are keeled and strongly inclined; posterior cranial roof is strongly angled downward; anterior sides of the braincase widen anteriorly; temporal ridges are very wide; lachrymals are expanded; maxillary tuberosities are prominent; infraorbital foramina are high and more posterior; palatal ridges touch one another; median indentation at the back of the palate is very anterior to lateral indentations; and auditory bullae are large (Gentry, 1992). Compared to *M. k. kirkii* and *M. k. damarensis*, skulls of *M. k. cavendishi* have larger (i.e., wider and higher) nasal openings. Subspecies of *M. kirkii* have been compared on the basis of size and shape of the nasals (Lönnberg, 1912; Lydekker and Blaine, 1914), but these characters should not be relied upon as they can be affected by age (True, 1892). Means (and ranges) of greatest length of skull (in mm) of males and females, respectively, are as follows: *M. k. cavendishi*, 120.8 (116–124, $n = 8$) and 119.5 (116–127, $n = 6$); *M. k. damarensis*, 109.7 (105–113, $n = 3$) and 118 (116–120, $n = 3$); *M. k. hindei*, 113.7 (110–116, $n = 3$) and 109 ($n = 1$); *M. k. kirkii* (males), 103.5 (101–106, $n = 4$); *M. k. minor*, 106 (102–108, $n = 6$) and 110.5 (105–114, $n = 4$); *M. k. nyikae*, 111.7 (106–116, $n = 6$) and 113.5 (112–115, $n = 2$); and *M. k. thomasi*, 115 ($n = 126$) and 117 ($n = 85$). Means (and ranges) of length of maxillary toothrow (in mm) of males and females, respectively, are as follows: *M. k. cavendishi*, 39.2 (37.7–41.4, $n = 6$) and 37.6 (36.2–40.2, $n = 5$); *M. k. damarensis*, 37.1 (35.2–39, $n = 2$) and 39.4 (38–41, $n = 5$); *M. k. hindei*, 36.8 (36.2–37.3, $n = 2$) and 32.6 ($n = 1$); *M. k. kirkii* (males), 34.2 (32–37, $n = 5$); *M. k. minor*, 34.4 (32.7–35.5, $n = 5$) and 36.2 (35.5–37.2, $n = 3$); *M. k. nyikae*, 37.2 (34.4–39, $n = 8$) and 36.1 (35.9–36.2, $n = 2$); and *M. k. thomasi*, 37 ($n = 131$) and 38 ($n = 86$—Allen, 1909; Allen et al., 1936; De Beaux, 1923; Drake-Brockman, 1909, 1913; Heller, 1913; Hill and Carter, 1941; Hollister, 1924; Kellas, 1955; Roberts, 1954; Roosevelt and Heller, 1915; True, 1892). Organ masses (in g) of adults ($n = 1$–2) are, brain, 37; heart, 37; kidneys, 21; liver, 93; lungs, 44; and stomach, 140–150 (Altman and Ditmer, 1962; Tinley, 1969). Means (and ranges) of organ dimensions (in cm) of adult males ($n = 2$–4) and females ($n = 2$), respectively, are, girth of heart, 36 (34–39) and 38; length of small intestine, 345 (315–375) and 348 (346–349); and length of large intestine, 145 (114–175) and 182 (179–184—Sachs, 1967; Tinley, 1969). The spleen is about 4 by 6 cm (Hofmann, 1973).

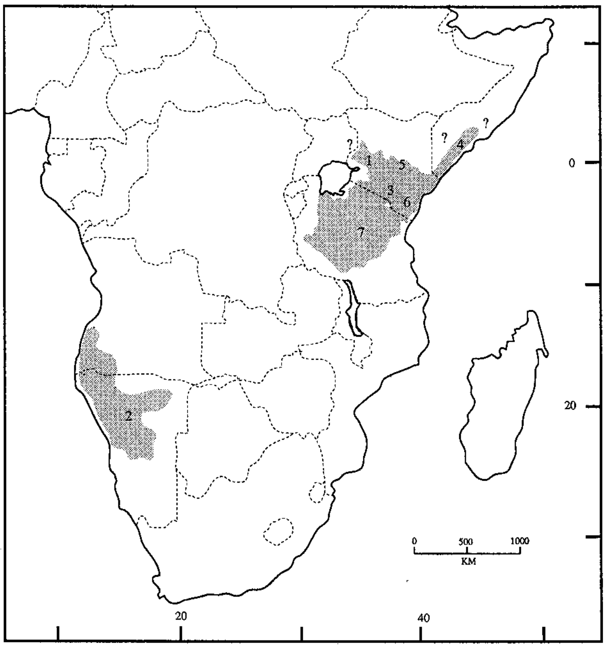

FIG. 3. Geographic distribution of *Madoqua kirkii* in eastern and southwestern Africa. Approximate type localities of the subspecies are: 1, *M. k. cavendishi*; 2, *M. k. damarensis*; 3, *M. k. hindei*; 4, *M. k. kirkii*; 5, *M. k. minor*; 6, *M. k. nyikae*; and 7, *M. k. thomasi*. Adapted from Ansell (1971), East (1988, 1989), Kingdon (1982), Roosevelt and Heller (1915), and Tinley (1969). Map prepared by J. Jason Douglas.

DISTRIBUTION. Kirk's dik-diks are endemic to savanna areas of eastern and southwestern Africa (Fig. 3), occurring primarily in the Somali and Southwest arid biotic zones but encroaching slightly into the Southern savanna biotic zone. Their geographic distribution is discontinuous and includes southern Somalia, central and southern Kenya, northern and central Tanzania, southwestern Angola, and northwestern to central Namibia. *M. kirkii* has been listed for Uganda, but apparently it does not range so far northwest; *M. guentheri* likely occurs there (Ansell, 1971). Within their geographic range, Kirk's dik-diks often occur in scattered patches because of their habitat requirements (Skinner and Smithers, 1990). In Namibia, for example, they apparently occur in isolated localities along the Fish River, and they do not have a continuous distribution south of Windhoek (Joubert and Mostert, 1975). Kirk's dik-diks are absent from the true desert of the Namib, but they penetrate desert in thickets along watercourses; here, dik-diks usually do not occur closer than about 30-50 km to the coast (Shortridge, 1934; Tinley, 1969). In Kenya, Kirk's dik-diks are found at the coast on Manda Island, but they are not found on the coast south of the Sabaki River (Sclater and Thomas, 1896–1897).

FOSSIL RECORD. Fossils of *M. kirkii* occur in Pleistocene deposits of East Africa (Hopwood, 1936). *M. kirkii* putatively evolved from an ancestor similar to the conservative *M. saltiana*, which is restricted to the Horn of East Africa. The ancestor of Kirk's dik-dik may have diverged from *M. saltiana* while inhabiting a hotter and drier belt to the south, where it developed a more efficient nasal cooler. The present distribution pattern suggests that *M. kirkii* is ecologically the most versatile of dik-diks but is excluded from much of the Horn by *M. guentheri* and *M. saltiana* (Kingdon, 1982). The discontinuous distribution of Kirk's dik-dik is believed to be the result of climatic changes that began during the Pleistocene. Increased rainfall in the region between eastern and southwestern Africa apparently caused dik-diks to disappear from this area as succession replaced savanna with more mesophytic forest vegetation (Skinner and Smithers, 1990).

FORM AND FUNCTION. When alarmed or excited, as during courtship or territorial defense, males of Kirk's dik-dik erect the hair on their forehead to form a distinct crest (Tinley, 1969). Hair length on the crest is ≤45 mm, compared to ca. 25 mm on the shoulders and 30 mm on the rump. The hair shaft is dumbbell-shaped in cross section; there are two or three cuticular scales across the width of the shaft, giving it an irregular, wavy pattern (Skinner and Smithers, 1990). Morphological differences of the guard hair of 14 species of East African ruminants, including *M. kirkii*, are summarized by Feder (1975).

Kirk's dik-diks have four inguinal mammae (Skinner and Smithers, 1990). Other skin glands include pedal and preorbital glands, which are used for scent marking. Pedal glands are absent in *M. k. damarensis*, and inguinal glands are absent in *M. kirkii* altogether (Estes, 1991; Tinley, 1969). Preorbital glands are enclosed by connective tissue, and they consist of a white layer of apocrine glands surrounding a black core of sebaceous glands. The apocrine glands produce a clear secretion, and the sebaceous glands secrete exudates containing lipoids or melanin, all of which combine in a central duct to form a black, tarry substance (Estes, 1991; Richter, 1971). Kirk's dik-diks have large preorbital glands, with a distinct opening in the shape of a semilunar slit; males have larger preorbital glands than females (Günther, 1880; Hofmann, 1973; Shortridge, 1934). In place of functional pedal glands, *M. k. damarensis* has a small fold of skin between the digits that contains a tuft of hairs about 15 mm in length; here the number and size of sweat and sebaceous glands is normal (Tinley, 1969). Compared to cattle (*Bos taurus*), dik-diks have a relatively low density of sweat glands (Maloiy et al., 1988).

Skulls of *M. kirkii* resemble those of other mammals having a trunk-like snout, such as saiga (*Saiga tatarica*) and tapirs (*Tapirus*); nasals are reduced in size, the nasal chamber is enlarged to accommodate the proboscis, and the roof of the nasal cavity is supported by cartilage for greater flexibility (Günther, 1880; Roosevelt and Heller, 1915). Lachrymal pits are large and shallow to accommodate preorbital glands. Short nasal bones, large lachrymal pits, and a large narial opening of the skull allies *Madoqua* closer to *Gazella* than to other Neotragini (Roosevelt and Heller, 1915). The proboscis is distensible, and it can be pointed in any direction to smell or extended down to whistle; the modified ethmoid turbinal may function as a whistle. However, the nose is not prehensile and cannot be used for pulling food to the mouth (Kingdon, 1982; Tinley, 1969). Typical of *Madoqua*, the rhinarium is nearly absent, and nasal openings cannot be closed as in other arid zone ungulates that have slit-like nostrils. The nostrils are lined internally with moist epithelium as far back as the nasal bones, which may be an adaptation for inhaling dry, hot air (Tinley, 1969). The dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Fig. 2). A pair of small, upper canines is often found in juvenile skulls and rarely in skulls having permanent molars (Kellas, 1955; Poggesi et al., 1982). Other dental characteristics of *M. kirkii* include i1 that is moderately-sized; cheek teeth that are high-crowned; back half of m3 that is enlarged; and lingual walls of the lower molars that are flattened (Gentry, 1992).

Hindlegs of *M. kirkii* are relatively long; lumbosacral height is greater than shoulder height. Lengths of foreleg and hindleg bones (in mm; $n = 2$) are as follows: humerus, 85–88; metacarpal, 94–96; radius, 95–96; metatarsal, 105–107; femur, 112–113; and tibia, 139–142. When standing, Kirk's dik-dik rounds its back, and this posture is often kept when it walks through dense vegetation (Hofmann, 1973; Hopwood, 1936). Among eight species of East African antelopes, including *M. kirkii*, hindleg bones are more uniform in structure than foreleg bones. This may be a result of the chief role that hindlimbs have in propulsion; conversely, forelimbs function to retain gained ground, and variable structure of their bones may reflect the variety of terrain encountered by these eight species. Thus, the relatively short forelegs of dik-diks are more efficient for climbing over broken terrain than the relatively long forelegs of antelopes that inhabit level ground (Hopwood, 1936). *M. k. damarensis* has rubbery digital pads behind the hooves which may be an adaptation for rocky ground (Estes, 1991; Tinley, 1969). Spoor measures about 20-23 mm long and 12-13 mm wide (Skinner and Smithers, 1990).

In *M. kirkii*, variation in diameter of muscle fiber is positively correlated with body mass. The longissimus dorsi is 26% red muscle fiber, 32% intermediate muscle fiber, and 42% white muscle fiber (Stickland, 1979). The plantaris is a simple tripennate muscle. Lengths, diameters, and cross-sectional areas of the principal bones, muscles, and tendons in the legs of seven species of antelopes, including *M. kirkii*, are approximately proportional to $(\text{mass})^{0.25}$, $(\text{mass})^{0.375}$, and $(\text{mass})^{0.75}$, respectively. When galloping at maximum speed, stresses in bones, muscles, and tendons are likely independent of body mass, but total work done by the muscles in each stride and the energy saved by elastic storage are roughly proportional to body mass (Alexander, 1977).

Kirk's dik-diks are concentrate selectors, feeding selectively on dicotyledonous plants that can be rapidly fermented and passed through the stomach, i.e., leaves and fruits high in nutrients and water but low in fiber and cellulose. Grasses are eaten only when sprouting (Hofmann, 1973; Hoppe et al., 1983). Kirk's dik-diks have a relatively small stomach capacity and mass, 8.5–10.8% of body mass when full and 2.2% when empty. Averages of capacity of the rumen and reticulum and of the omasum and abomasum are 945 and 100 ml, respectively; the sequence of sizes of the four chambers is rumen, reticulum, abomasum, and omasum. The rumen is a simple, folded tube with dense papillation that increases the absorptive mucosal surface by 6-18 times. Specialization for the diet also involves the rumen blindsacs and omasal papillae (Hofmann, 1973).

Each day, Kirk's dik-diks consume about 2 kg fresh browse or 160 g dry hay, ca. 3.8% body mass; stomach contents weigh ca. 400 g (Hendrichs, 1975; Hoppe, 1977*a*). Intake rates (in g/day) during the dry season and wet season, respectively, are as follows: dry matter, 225 and 269; protein, 15.0 and 43.8; and plant-borne water (in ml/day), 134 and 462 (Manser and Brotherton, 1995). Because of their high food requirements and small stomach capacity, they feed and ruminate throughout the day and night. Mean nutrient composition (in % dry matter) of rumen contents from Kirk's dik-diks are the following: ash, 16.2-17.2; ether extract, 9.9–10.7; crude protein, 13.1–25.9; fiber, 20.7–42.4; and nitrogen-free extracts, 25.5 (Hoppe, 1977*a*; Hoppe et al., 1983). Fecal pellets measure ca. 6–8 mm in length, about the size and shape of grains of rice (Amubode and Boshe, 1990; Shortridge, 1934). Dung production is at least 100 g/day for each animal (Hendrichs, 1975).

Kirk's dik-diks conserve water and avoid heat stress in a number of ways: licking dew from their nose, resorbing water from feces, concentrating and restricting urine output, employing respiratory evaporative cooling (panting), limiting cutaneous evaporation, allowing body temperature to rise during the heat of the day, lowering metabolic rate, resting in the shade during midday, and orienting the body surface to the convective force of the wind (Hoppe, 1977*b*; Kamau, 1988; Maloiy et al., 1988). They drink little or no water, usually obtaining their needs from selected food plants. Plant species avoided by dik-diks in the wet season are sought out in the dry season for their water content. Rapid passage of large amounts of food through the digestive tract increases the ingestion and retention of plant-borne water (Hoppe, 1977*a*, 1977*b*; Maloiy et al., 1988; Manser and Brotherton, 1995). Among ungulates so far studied, dik-diks have the lowest daily water expenditure, and they produce the driest feces and most concentrated urine. Dik-diks save additional water through the process of heat storage. Under heat stress, body temperatures can reach a maximum of 43°C from a morning temperature of 38.7°C; this excess heat is later lost to the environment without using water for evaporation (Maloiy et al., 1988). Between ambient temperatures of <25°C and 40°C, thermal conductance of Kirk's dik-diks increases by more than 20 times (Kamau and Maloiy, 1982). Long, thin legs allow them to gain and lose heat rapidly under changing environmental temperatures (Kamau, 1988).

In terms of evaporative cooling, panting is more selective than sweating because it preferentially cools the brain tissue, which is most vulnerable to elevated temperature (Hoppe, 1977*b*). At an ambient temperature of 44°C, 95% of the body heat produced by *M. kirkii* is lost via respiratory evaporation; despite an increase in rectal temperature, cutaneous evaporation does not increase. Under these conditions, respiratory rate can reach 630 breaths/min, and at lower temperatures it can drop to 27 breaths/min (Kamau, 1988). The most obvious adaptation of dik-diks for avoiding heat stress is modification of the nose to allow cooling the blood by panting (Hoppe, 1977*b*; Kingdon, 1982).

Heart rate (in beats/min) of Kirk's dik-diks ranges from 98 (at ambient 25°C) to 216 (at 5°C); at 45°C, heart rate averages 127 beats/min. At ambient temperatures <25°C, there is a positive correlation between heart rate and oxygen consumption (Kamau and Maloiy, 1982). Oxygen consumption shows a circadian rhythm, with a minimum at midnight and a maximum at midday (Kamau, 1988).

In mature males, testes measure ca. 2.4 by 1.8 cm, and the pair usually has a mass of 4.0-5.7 g; generally, testes >2.39 g reflect sexual activity, and those <2.39 g reflect sexual inactivity. Vasa deferentia enter the urethra separately but open together on the colliculus, and seminal vesicles are attached dorsoventrally to the top of the urethra. Length of the penis is 14.5–16.0 cm and average mass is 2.6 g (Kellas, 1955). In females, ovaries are round to oval, often flattened, and have a smooth surface. Only very large follicles protrude from the surface, and the corpus luteum cannot always be distinguished superficially. Diameter of the corpus luteum is ca. 5–7 mm and of follicles is ≤4.6 mm; only pregnant animals have follicles ≥4 mm. Until puberty, there is a progressive rise in ovary mass (to 0.3 g) with age; in adults, ovary mass does not increase. Masses (in g) of reproductive organs in nonpregnant and pregnant females, respectively, are uterus, ≤10 and 3.9–1,282; cervix, <2 and ≤7.6; and vagina, ≤3.8 and 8. In nonpregnant dik-diks, size of the vagina is ca. 7 by 12 cm. Masses of mammary glands are ≤7 g in immature females; 2–8 g in mature, nonpregnant, non-lactating females; 2–10 g in pregnant, non-lactating females; 4–31 g in pregnant, lactating females, and 9–58 g in nonpregnant, lactating females. Lactation is often observed during early pregnancy but not during late pregnancy (Kellas, 1955).

ONTOGENY AND REPRODUCTION. Kirk's dik-diks reach sexual maturity by 6–8 months of age (Kellas, 1955). In captivity, a few precocious females conceive at less than 4 months of age, and males can sire offspring before 6 months of age (Kumamoto, 1995). In Tanzania, females produce their first young at the age of 15–18 months (Hendrichs, 1975). Estrus occurs 5–30 days postpartum and lasts 11–48 h. Copulation may occur three to five times during a 9-h period. If females are not bred, they cycle every 3–4 weeks (Bowker, 1977; Dittrich and Böer, 1980; Estes, 1991). Sperm are found in the epididymides of mature males year-round, but the testes, epididymides, and seminal vesicles show a seasonal rise and fall in mass that corresponds with the breeding rhythm of females and with the rise and fall of solar radiation (Kellas, 1955). Breeding cycles may be synchronized with greatest availability of browse, that is, occurring at the beginning of the rains when there is a flush of woody plants and at the beginning of the dry season when fresh litter is abundant. In Namibia during late February, Tinley (1969) noted the following: a 1-month-old calf; a female carrying a fetus of about 1 month's development; a non-pregnant female with a ripe ovarian follicle and, in the other ovary, an old corpus luteum; and a pair in courtship. However, Shortridge (1934:486) remarked: "None of the females collected in the Kaokoveld [Namibia] between May and August contained a foetus." Breeding reaches peaks during June-July and December-January in Tanzania (Kellas, 1955). Kirk's dik-diks can remain reproductively mature past 10 years of age; a calf was sired by a male at about 13 years, 4 months, and a female gave birth at an estimated age of 12 years (Kumamoto, 1995). In wild populations, females are reproductive at least up to 6 years; of 202 females sampled, only one was postparturient (Hendrichs, 1975; Kellas, 1955).

In *M. kirkii*, ovulation usually involves a single egg. Implantation generally occurs in the right uterine horn (106 of 109 pregnancies), and since both ovaries are equally active, ca. 50% of the ova migrate from the left horn. In Tanzania, percentage of females that are pregnant during the year is probably >81% (Kellas, 1955). During mid-gestation, the uterine cornu occupied by a fetus is lined by amniochorion. There are ca. 80 cotyledons. Chorionic villi are covered by cytotrophoblasts containing intraepithelial capillaries. Mucosal crypts are partly denuded of uterine epithelium and partly lined by epithelial syncytium. No extravasates of maternal blood exist at mid-gestation, nor have the walls of the mucosal crypts undergone degeneration beyond partial loss of epithelium. At the base of each placentoma, the mucosa forms swollen mononuclear cells and multinuclear syncytial masses and undergoes some cellular necrosis (Wislocki, 1941). Movements of the fetus are observed 2 months before birth, and about 8 days before calving the udder is noticeably developed (Dittrich, 1967; Dittrich and Böer, 1980).

Gestation periods of 166–174 days have been reported (Dittrich, 1967; Dittrich and Böer, 1980). Kirk's dik-diks give birth to one calf. Calving peaks during April-June and November-December in East Africa when there is abundant food; in Namibia, calving normally occurs between December and April and peaks during February-March (Bowker, 1977; P. Brotherton, in litt.; Hendrichs and Hendrichs, 1971; Kellas, 1955). In captivity, parturition occurs year-round but peaks during April-May and October-November (Kumamoto, 1995). At the Zoologische Garten Hannover, first labor was noted 5 days before parturition. Among four births, parturition lasted 39–44 min and occurred during 2300–0415 h. The afterbirth appeared 2–3 h after parturition and was eaten by the mother. The male was present during these births, without incident (Dittrich, 1967; Dittrich and Böer, 1980). The interbirth interval averages 180 days and ranges from 170 to 206 (n = 6—Bowker, 1977); in captivity it averages 198 days (range, 163–268; n = 34—Luce, 1987).

Neonates are precocious, standing 5–15 min after birth and nursing within 1–2 h. Calves remain hidden in thickets during their first 10–20 days, after which time they begin to join their parents; at 5–7 weeks of age, calves stay with their parents day and night. Females nurse their calves for 1.5–5 months, although calves begin eating solids at 1–5 weeks of age (Bowker, 1977; Dittrich, 1967; Dittrich and Böer, 1980; Hendrichs and Hendrichs, 1971; Kranz, 1984). Among larger mammals, weaning is related to a critical body mass attained by offspring, which is ca. 1.78 kg in *M. kirkii* (Lee et al., 1991). A satisfactory diet for hand-raising Kirk's dik-diks is milk of either cows or goats, given at the rate of 160–300 g/day (Dittrich, 1967).

At birth, *M. kirkii* has a mass ca. 13% of maternal mass, but this proportion is ≤10% in larger, uniparous ungulates (Dittrich and Böer, 1980). The generally increasing effort for smaller ungulates, such as *M. kirkii*, may be due to the necessity of producing an adequately large, advanced neonate capable of dealing with thermoregulation and predation (Robbins and Robbins, 1979). Means (and ranges) of body mass (in g) at birth of males (n = 5) and females (n = 5), respectively, are 648 (585–795) and 607 (560–680); these masses approximately double by 3 weeks and triple by 5 weeks of age (Dittrich and Böer, 1980). Kirk's dik-dik calves are about one-half adult size at 4 months of age and nearly adult size at 6 months; at 8 months, calves are generally as tall but not as heavy as adults. A 1-year-old female weighed 4.96 kg (Dittrich, 1967; Dittrich and Böer, 1980). Growth curves begin to flatten within 165–221 days of birth; at 277 days, the curves are virtually flat. Males appear to stop growing sooner than females (Kellas, 1955).

Kirk's dik-diks and other hider species have two-thirds the muscle mass at birth that they have as adults, whereas follower species have as much muscle proportionally as they have as adults (Grand, 1991). Proportional mass of the head decreases with age as a function of brain growth, which occurs in advance of the musculature—following the law of cephalocaudal development (i.e., growth is more advanced anteriorly). Muscular growth increases mass of the shoulders, hips, and thighs, while distal segments become relatively lighter; consequently, the center of gravity moves closer to the hips. Proportion of body components and body segments to body mass (in %) in neonates and adults, respectively, are skin, 16 and 10; muscle, 27 and 45; head, >10 and 4; each thigh, ca. 5 and 8; and below elbow and knee, ca. 16 and 10. Proportion of regional muscle to total muscle mass (in %) in neonates and adults, respectively, are hindlimb, 41 and 45; forelimb, 27 and <22; and back extensors, 17 and >20 (Grand, 1991). As with flesh dimensions, skull dimensions increase linearly, except in the oldest groups where there is a relative decrease in the rate of skull growth (Kellas, 1955). Relative breadth of the skull remains approximately constant in males but decreases with age in females. Skull measurements, including horn growth, show a sharp rise in length up to ca. 1 year of age and only a slight increase thereafter. Growth rate and closure time of skull sutures do not appear to be influenced seasonally; thus, closure of certain skull sutures can be used as an index of age. Tooth eruption and replacement in the lower jaw provide a less satisfactory classification of sexual maturity, and tooth wear and closure of epiphyses of long bones are of little use as age indices. Permanent molars are usually in place before deciduous premolars are shed; premolars are replaced at about the same time but not always in the same sequence (Kellas, 1955).

Longevity in the wild is often not more than 5 years, but it may exceed 10 years (Hendrichs, 1975; Kellas, 1955). A captive-born male lived nearly 16 years, 6 months, and a wild-caught female, estimated to be 3 years of age at the time of capture, died after nearly 15 years, 5 months in captivity (Kumamoto, 1995). The life cycle of *M. kirkii* is as follows: age ca. 1 month, not moving with parents; 3 months, moving with parents, horns and preorbital gland ducts not visible; 6 months, moving with parents and alone, horn length = one-half crest length, preorbital gland ducts visible and used for marking; 9 months, expelled from parental territory, nearly full grown (≤ 4 kg), horn length = two-thirds crest length (one-half final length), preorbital gland ducts distinct; 1 year, territory and pair bond established, fully grown, horns = crest in length; 1.5 years, first calf raised by pair, horn length = 1.5 times crest length; 2 years, horn length = ear length, preorbital glands with distinct glandular pockets; 3 years, behavior still playful, horns shiny-black; 5 years, behavior still elastic, horns brownish-gray and dull, preorbital glands with large glandular pockets; 8 years, behavior loosing elasticity, horns grayish-white at base and splintering; and 9 years, holding territory but not breeding (Hendrichs, 1975).

ECOLOGY. Kirk's dik-diks live in habitats characterized by thicket vegetation such as arid and semiarid thornbush (e.g., nyika), savanna grassland-woodland, and riverine grassland-woodland (East, 1988, 1989). Typical habitat is a mosaic of thickets and open glades with a well-developed shrub layer and sparse, short grass cover; this provides dik-diks with a large amount and variety of browse, open understory at their eye level, cover from predation, and extensive shade (Tinley, 1969). In Lake Nakuru National Park, Kenya, 57% of the dik-diks are found in shrub habitats, 25% in forest, and 19% in open grassland (Wirtz and Lörscher, 1983), and canopy cover of stable and unstable territories in Arusha National Park, Tanzania are 13.8% and 25.3%, respectively (Amubode and Boshe, 1990). Kirk's dik-diks occur on level plains and broken ground of rolling areas and foothills, but they avoid climbing hills, rock outcrops, and peaks; habitats range from areas having dry, sandy soil to calcrete rubble (Estes, 1991; Roosevelt and Heller, 1915; Sclater and Thomas, 1896–1897; Shortridge, 1934; Tinley, 1969). On the Serengeti Plain, dik-diks occur in kopjes, which are granitic outcrops consisting of large boulders spread over an area of a few km^2 and interspersed with tracts of dense woody vegetation and patches of shrubs and herbs (Hendrichs, 1975).

Distribution of *M. kirkii* is generally between the 75 and 500 mm isohyets for mean annual rainfall, areas often without surface water (Kingdon, 1982; Loveridge, 1923; Tinley, 1969). Specialized hooves, having rubbery digital pads, may confine Kirk's dik-diks in Namibia to the stony ground characteristic of these drier areas, but their absence from suitable thicket habitat there may also be due to the cold winter (P. P. Hoppe, in litt.; Tinley, 1969). During the rainy season, dik-diks exhibit local movements from areas with thick grass to areas where the undergrowth is more open (Tinley, 1969). Conditions favorable for dik-diks may result from overgrazing and trampling by wild and domestic herbivores or from clearing and cultivation, which cause savanna grassland and woodland to be replaced by bushes and shrubs (Estes, 1991). Dominant vegetation of Kirk's dik-dik habitats includes *Acacia*, *Adansonia*, *Balanites*, *Barleria*, *Boscia*, *Capparis*, *Cassia*, *Cissus*, *Colophospermum*, *Combretum*, *Commiphora*, *Croton*, *Cymbopogon*, *Cynodon*, *Delonix*, *Dichrostachys*, *Ehretia*, *Euclea*, *Euphorbia*, *Exotheca*, *Grewia*, *Hyphaene*, *Kalanchoe*, *Lippia*, *Maerua*, *Ocimum*, *Peltophorum*, *Premna*, *Psiadia*, *Salvadora*, *Securinega*, *Spirostachys*, *Sporobolus*, *Sterculia*, *Tamarindus*, *Tamarix*, *Terminalia*, and *Ziziphus* (Amubode and Boshe, 1990; Bowker, 1977; Hendrichs and Hendrichs, 1971; Kingdon, 1982; Lamprey, 1963, 1964; Tinley, 1969).

Kirk's dik-diks eat leaves, flowers, shoots, fruits, stems, twigs, and litter of forbs, grasses, shrubs, and trees (Hofmann, 1973). Diets in Tarangire Game Reserve, Tanzania consist of 56% shrubs, 23% trees, 17% grasses, 3% forbs, and 1% sedges (Lamprey, 1963). In Etosha National Park, Namibia, they are primarily browsers, but grasses and herbs form part of the diet in the wet season. Preferences for food species during the dry season are influenced by relative abundance and water content and during the wet season by dry matter content (Manser and Brotherton, 1995). Principal food plants include *Acacia*, *Asparagus*, *Blepharis*, *Boscia*, *Cassia*, *Cataphractes*, *Cenchrus*, *Commelina*, *Commiphora*, *Crotalaria*, *Croton*, *Dichrostachys*, *Dyschoriste*, *Ecbolium*, *Ficus*, *Grewia*, *Hermannia*, *Hibiscus*, *Indigofera*, *Maerua*, *Maytenus*, *Microglossa*, *Notonia*, *Opilia*, *Pluchea*, *Rhigozum*, *Rhus*, *Rhynchosia*, *Salvadora*, *Solanum*, *Spirostachys*, *Terminalia*, *Thephrosia*, and *Ziziphus* (Bowker, 1977; Hendrichs and Hendrichs, 1971; Lamprey, 1963; Manser and Brotherton, 1995; Tinley, 1969). Germination rate of *Acacia tortilis* seeds that have passed through the digestive tract of Kirk's dik-diks and other herbivores is 11%, compared to 3% for those that have not passed. In the same study, infestation rate by the beetle *Bruchidius spadiceus* is 45% in passed seeds and 95.6-99.6% in unpassed seeds (Lamprey et al., 1974). Kirk's dik-dik sometimes lick bones and rocks or eat sand (Bowker, 1977; Kingdon, 1982; Manser and Brotherton, 1995). In captivity, they are fed alfalfa, grains, fruits, vegetables, and fresh browse, and they are offered minerals (Dittrich, 1967; Hoppe, 1977*a*). Dik-diks are independent of surface water, but they obtain moisture from plant juices, dew, and rain (Hendrichs, 1975; Sclater and Thomas, 1896–1897; Tinley, 1969). During pregnancy and lactation, females increase food and water consumption (Dittrich and Böer, 1980; Hoppe, 1977*a*).

A population of Kirk's dik-diks on the Serengeti was 43–45.5% female, 43–45.5% male, and 9–14% young. Annual turnover rates were 7% for females and 16% for males; thus, the average age of adult males remained about 2.9–3.0 years, but the average age of adult females increased from 2.9 to 5.4 years, leaving the population with uneven sex ratios within age classes (Hendrichs, 1975). Population turnover in Kenya during a 10-month period was 32%—16% for adults and 46% for young <3 months of age (Bowker, 1977). During a 25-month period in Etosha National Park, Namibia, 69% of females and 85% of males disappeared, probably as a result of mortality rather than emigration (Tilson and Tilson, 1986). In a sample of 412 animals, 210 were males, and 202 were females (Kellas, 1955). Population densities (in animals/km^2) were 0.27–3.2 in Tarangire Game Reserve, Tanzania (Lamprey, 1964); 5–33 on the Serengeti (Estes, 1991; Hendrichs, 1975); 15–25 in the Kedong Valley, Rift Valley, and Tsavo West National Park, Kenya (Hofmann, 1973); 55 and 63 during morning and evening counts, respectively, in Arusha National Park, Tanzania (Amubode and Boshe, 1990); and 109 in Tsavo East National Park, Kenya (Komers, 1996). In Tarangire Game Reserve, fluctuations in the population density of Kirk's dik-diks closely followed those of wart hogs (*Phacochoerus aethiopicus*). During the rainy season, there was some dispersal of dik-diks away from the Tarangire River; during droughts, dispersal away from the river was lessened. They were more easily seen after grass fires, and this may account for their higher densities recorded at the end of the dry season (Lamprey, 1964). Although the reproductive potential of *M. kirkii* was 2 calves per female per year, the Serengeti population raised 1 calf per female per year. Standing biomass of this population was 138–162 kg/km^2, and annual production (in kg/km^2) of meat and dung was ca. 48 and 1,000, respectively; this population required ca. 20,000 kg of forage km^{-2} year^{-1} (Hendrichs, 1975).

Madoqua kirkii is sympatric with *M. guentheri* along a narrow belt across central Kenya and possibly southern Somalia, *M. kirkii* replaces *M. guentheri* in more mesic savannas of southern Kenya, and *M. guentheri* replaces *M. kirkii* in more arid scrub north of the Shebelle River in Somalia. Although distributions of *M. kirkii* and *M. saltiana* overlap slightly in Somalia between the Juba and Shebelle Rivers, they are ecologically separated as *M. saltiana* is found in more open habitats (Ansell, 1971; East, 1988; Kingdon, 1982; A. M. Simonetta, in litt.). Baboons (*Papio*), murid rodents, hyraxes (*Heterohyrax brucei* and *Procavia capensis*), black rhinoceroses (*Diceros bicornis*), giraffes (*Giraffa camelopardalis*), and small antelopes are potential food competitors (Hendrichs, 1975; Tinley, 1969). Black rhinoceroses and giraffes occupy the same ecological position as Kirk's dik-diks, but they are effectively separated by virtue of their size and feeding levels. Dik-diks benefit from feeding activities of other browsers (e.g., birds, primates, rodents, and giraffes) that litter the ground with buds, flowers, leaves, and pods (Lamprey, 1963), and they benefit from larger herbivores that keep food and shelter within reach by felling trees, breaking branches, or foraging (Tinley, 1969). Loud calls and sudden movements of birds alert dik-diks to potential danger (Bowker, 1977), and they may forage with domestic goats (*Capra hircus*)—which gives them protection (Roberts, 1954).

Predators of Kirk's dik-diks include olive baboons (*Papio anubis*), silver-backed jackals (*Canis mesomelas*), African hunting dogs (*Lycaon pictus*), caracals (*Caracal caracal*), lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), bateleur eagles (*Terathopius ecaudatus*), tawny eagles (*Aquila rapax*), African hawk-eagles (*Hieraaetus spilogaster*), martial eagles (*Polemaetus bellicosus*), and Verreaux's eagle-owls (*Bubo lacteus*—Bowker, 1977; Kellas, 1955; Spinage, 1986; Strum, 1975; Tinley, 1969). Kirk's dik-diks are the main prey of leopards and eagles in Tsavo National Park, Kenya (Bowker, 1977; Spinage, 1986), but leopards can benefit dik-diks by keeping smaller predators away (Estes, 1991). Over 110 km^2, eagles killed an estimated 1,000–1,500 dik-diks/year, or 36–56% of the population; bateleur, martial, and tawny eagles took adults and juveniles, but hawk-eagles selected for juveniles (Spinage, 1986). Pairs on certain territories consistently lost their calves to predation (Bowker, 1977).

Ectoparasites of *M. kirkii* include fleas (*Ctenocephalus felis*, *C. isidis*), lice (*Linognathus damarensis*, *L. geigyi*), muscid flies (*Stomoxys*), ticks, and possibly tabanid flies (*Philoliche*—Ledger, 1971; Loveridge, 1923; Sachs and Sachs, 1968; Tinley, 1969). Endoparasites include cestodes (*Monezia expansa*), nematodes (*Anoplocephala*, *Capillaria hepatica*, cosmocercids, *Dictyocaulus*, *Haemonchus contortus*, *Ostertagia kenyensis*, *Setaria*, *Strongyloides*, *Trichuris*), pentastomids, and protozoans (*Entodinium dubardi*, *E. nanellum*, *Opisthothrichum janus*, *Sarcocystis*—Dittrich, 1967; Hoppe et al., 1983; Gibbons and Khalil, 1980; Partington and Montali, 1986; Sachs and Sachs, 1968; Tinley, 1969). Protozoa are scarce or absent in dik-diks, probably as a result of the short retention time of food and water in the reticulorumen (Hoppe et al., 1983). In captivity, dik-diks are sensitive to cold, humid weather and are prone to lung infections. Causes of mortality include fibrinous, suppurating pneumonia ($n = 2$); a combination of pericarditis, pleuritis, and pneumonia ($n = 1$); bacterial infection by *Yersinia pseudotuberculosis* ($n = 1$); parasitic infection of the stomach and intestines ($n = 1$); and predation ($n = 2$—Baskin et al., 1977; Dittrich, 1967; Partington and Montali, 1986). Mortality of juveniles in captivity is 53–67% for inbred young and 27–41% for young that are not inbred (Ballou and Ralls, 1982). Wild populations of Kirk's dik-diks have a low susceptibility to rinderpest (Plowright, 1982).

Madoqua kirkii is widespread in southern Somalia and locally common but widespread in coastal to southwestern Kenya, northern to central Tanzania, southwestern Angola, and northwestern to central Namibia (East, 1988, 1989). Kirk's dik-diks are hunted widely in Tanzania; nevertheless, they can persist in areas close to human settlement (East, 1988). Drought has adversely effected populations in marginal habitats of central Namibia (East, 1989). Populations are estimated to number >100,000 in eastern Africa and >12,000 in Namibia. There may be at least 100,000 in Tanzania alone, with 32,000 and 5,000 in Serengeti and Tarangire National Parks, respectively, and dik-diks are the most abundant antelope in many of Kenya's parks and reserves (e.g., Meru and Samburu-Isiolo). In Namibia, >11,000 are estimated to occur on farmland, particularly in the Outjo and Grootfontein districts, and there are >800 in Etosha National Park (East, 1988, 1989); in Etosha alone, there may be as many as 15,000 (P. Brotherton, in litt.).

Bushmen and farmers are said to protect Kirk's dik-diks, and for this reason, they often occur near settlements (Roberts, 1954). Hunter-gatherers and pastoralists in southwestern Africa sometimes hunt dik-diks with bows and arrows or with snares made from tree bark (Tinley, 1969). In Kenya, they are often captured with wire snares (Bowker, 1977). However, because of their small size, cryptic coloration, and alertness, Kirk's dik-diks may not be hunted where larger and more easily obtained game exists; Shortridge (1934:485) writes: "Their pale grey bodies assimilate with colourless limestone surroundings; even when running the shadows cast are more conspicuous than the animals themselves, and they vanish like wisps of smoke." Sclater and Thomas (1896–1897) report that the meat is disagreeable to the taste, but according to Shortridge (1934), the meat is rather tasteless and resembles that of springhares (*Pedetes capensis*). The fur was once used in Germany for lining the inside of gloves (Shortridge, 1934).

Fentanyl/azaperone, haloperidol/perphenazine, ketamine/xylazine, and tiletamine-zolazepam are used to chemically immobilize Kirk's dik-diks. Small antelopes are best caught in nets, manually restrained, and then given a neuroleptic (McKenzie, 1993). Husbandry and management of Kirk's dik-diks in captivity are described by Wortman (1980) and Kumamoto (1995).

BEHAVIOR. Kirk's dik-diks usually occur in groups of two to four—typically an adult pair with one or two immature offspring (Bowker, 1977; Kellas, 1955; Tinley, 1969; Wirtz and Lörscher, 1983). In Namibia, they are observed as mated adult pairs with or without offspring, unmated resident females, and transient solitary individuals of both sexes; if males die, they are replaced by another male within 2–3 days, but it is often >30 days before females are replaced (P. Brotherton, in litt.; Tilson and Tilson, 1986). Occasionally, groups of 6–10 may be within sight of one another, but they are likely temporary groups of neighbors at territorial boundaries (Hendrichs and Hendrichs, 1971; Kingdon, 1982; Tinley, 1969). Adults do not always forage close to each other, but they often rest together under shrubs (e.g., 1230–1500 h—Tilson and Tilson, 1986). Although a fixed territory is generally occupied by a pair, more than one adult female may share the territory of a male in areas where dik-diks occur in high densities (Spinage, 1986). In captivity, it is possible to keep dik-diks in family groups of one male, two females, and their offspring; in the presence of females, males usually fight and must be separated (Dittrich, 1967). In a captive group of one male and two female Kirk's dik-diks kept together for several years, the putatively dominant female calved every 6 months while the other female gave birth about once a year (Kranz, 1984).

Kirk's dik-diks are facultatively monogamous, based on the following behavioral characteristics: pair bonds are quickly established; typically pair members interact infrequently; males are more active and assume most of the responsibility for territorial maintenance, such as scent marking; largely through efforts of the male, pair members maintain close proximity and exhibit a moderate degree of behavioral synchrony (Kranz, 1984, 1991). Other behaviors that serve to maintain pair and family bonds include a dunging ceremony, mutual grooming, mutual vigilance (possibly including alarm-call duetting), and play. Contact involves sniffing and licking the preorbital glands, neck, and rump (Estes, 1991; Hendrichs, 1975). Pair bond formation begins when single females find unpaired males holding a territory, although the pair bond is independent of the territorial bond; the pair bond often lasts for life, but the territorial bond does not. Paired males show no interest in neighboring females, including unpaired females, but they may tolerate these females in their territory, suggesting that Kirk's dik-diks are obligately monogamous (Bowker, 1977; Hendrichs, 1975; Komers, 1996).

Monogamous species have slight need of courtship rituals; there is little pre-mating and no post-copulatory behavior in *M. kirkii* (Kranz, 1991). Estrus females are restless, and they stand stiffly with arched back and tail lifted; during estrus, they urinate and defecate frequently (Bowker, 1977; Dittrich and Böer, 1980). Courtship behavior of the male includes chasing; lowstretch approach and close following of the female; anogenital sniffing and licking; urine-testing (flehmen); and foreleg-lifting (Estes, 1991; Kranz, 1991; Tinley, 1969). Due to the elongated proboscis, the flehmen grimace is not as pronounced as in other bovids (Leuthold, 1977). Just prior to making contact with the female, the male erects his head and performs a mechanical gait. Receptive females respond to genital licking by raising their tail and squatting slightly. Males then mount bipedally with forelegs folded, without touching the female's back with their forelegs; copulation is brief, ca. 1–15 s (Dittrich and Böer, 1980; Estes, 1991; Kranz, 1991).

Kirk's dik-diks are hiders during their first weeks of life, hiding voluntarily and seeking cover when alarmed. Usually, mothers do not approach and make contact with their calf; rather, they call from 10 m away and await its emergence (Bowker, 1977; Hendrichs and Hendrichs, 1971; Kranz, 1984). Dams stay near their calves for the first week; thereafter, they accompany their mates and juvenile offspring but visit the hidden calf a few times during a 24-h period. Calves are nursed 4–30 times/day, and each bout lasts 1–3 min. In captivity, calves may nurse from other females (Bowker, 1977; Dittrich, 1967; Dittrich and Böer, 1980; Hendrichs and Hendrichs, 1971). During nursing, dams lick their infants anogenitally and consume their wastes (Estes, 1991). The following behaviors have been observed in calves (with the approximate age of development): jumping and erecting the crest (2 days), running (10 days), scent marking with the preorbital gland (2–4 weeks), dunging ceremony of the male (18–37 days), feeding bipedally (4 weeks), and head butting with their mother (1 month—Bowker, 1977; Dittrich, 1967; Dittrich and Böer, 1980). Male and female calves attempt to mount their mother, but she terminates their attempts by walking forward or kicking up her hindlegs. For 6–8 weeks after birth, calves are with their mothers, from 2–6 months of age, young are increasingly with their fathers or alone, and by 6 months of age juveniles spend more time alone (Bowker, 1977). Kirk's dik-diks essentially lack paternal care—males do not defend resources for their offspring (or mates), and they apparently do not reduce the risk of predation for their young (Brotherton and Rhodes, 1996; Komers, 1996). Calves are submissive and avoid close contact when males approach. At the onset of puberty, sires become aggressive to their young and drive them from their natal territory; female young may be forced from the territory by their dams. In Etosha National Park, Namibia, young males disperse at 7–19.5 months of age ($\bar{X} = 11$, $n = 8$) and females disperse at 5.5-9.5 months ($\bar{X} = 7$, $n = 7$). After their expulsion, youngsters attempt to establish a pair bond and territory (Bowker, 1977; P. Brotherton, in litt.; Dittrich, 1967; Dittrich and Böer, 1980; Hendrichs, 1975).

Kirk's dik-diks are predominantly crepuscular and nocturnal, being most active at dawn, late afternoon, dusk, and night. In Namibia, there is a low level of activity throughout the day during the cold-dry season but not during the hot-dry and hot-wet seasons. They emerge from cover during these periods and move slowly while feeding along thicket edges or across open areas. When feeding, they keep to shaded areas and are difficult to see. During the course of an hour, dik-diks alternately feed and rest, often continuing this over the 24-h cycle (Bowker, 1977; Manser and Brotherton, 1995; Tinley, 1969). On the Serengeti, they are active during the day and night in areas with extensive cover, but they are nocturnal in areas with scarce cover (Hendrichs, 1975). During an average day, Kirk's dik-diks spend 12.5 h on their feet and 11.5 h resting, including about 7.5 h feeding and 6 h ruminating. Main rest periods are from midnight to pre-dawn and 0900–1200 h, during which time they either bed down or stand motionless and ruminate (Estes, 1991). Dittrich and Böer (1980) interpreted crest erections and noises, made during periods of sleep, as possible signs of dreaming. Adult females are the most alert, and they determine patterns of activity and movement (Bowker, 1977). Daily activity of a captive group was similar to the activity-rhythm of dik-diks in the wild. Activity of the pair decreases a few days before and after parturition (Dittrich and Böer, 1980).

Kirk's dik-diks rarely feed intensively on one plant; instead, they wander about selecting a variety of vegetation (Hofmann, 1973). They extend their long proboscis to search for preferred foods, and to maximize their food supply they move daily throughout the territory, invade neighboring territories, and feed bipedally (Bowker, 1977; Kingdon, 1982; Tinley, 1969). While feeding, Kirk's dik-diks gnaw and chew on the juicy tips of shrubs. Their water requirements are partially met by eating succulents and bulbs, which they dig out by scratching with their forelegs (Hofmann, 1973). They may drink from rain puddles; in the laboratory they lap water like a cat (Hoppe, 1977*b*; Tinley, 1969).

Most vocalizations of *M. kirkii* are variations of a whistle, which is produced by expelling air through the modified turbinal in the nose and extending the proboscis forward and downward to amplify the call (Bowker, 1977; Estes, 1991; Tinley, 1969). Family members use a soft whistle as a contact call and a loud, breathy alarm whistle that sounds like "zik-zik" (hence the native name "dik-dik"). Kirk's dik-diks also emit squealing distress calls and sometimes a horselike snort while feeding (Bowker, 1977; Estes, 1991; Hendrichs and Hendrichs, 1971). When an alarm whistle is given, others answer immediately (Tinley, 1969). Roberts (1954: 334) remarked: "They utter a peculiar squeaking grunt, which sounds almost like talking to one another, and perhaps that is why the Bushmen are superstitious about [not killing] them." Nursing is often initiated by soft, twittering whistles of the mother and/or offspring (Dittrich and Böer, 1980; Walther, 1984).

The development of scent glands and scent-marking behavior suggest that olfactory communication is important to *M. kirkii* (Estes, 1991; Leuthold, 1977). In the dunging ceremony, Kirk's dik-diks urinate and defecate on localized and repeatedly-used dung piles that are up to 2 m across and 10 cm high. Dung piles straddle territorial boundaries, and they may be used communally by each family, but they are occasionally located in the center of the territory (Bowker, 1977; Tinley, 1969). Old, established boundaries have about 3 dung areas/100 m, but contested boundaries have up to 10/100 m. In a typical dunging ceremony, the female urinates and then defecates without sniffing or pawing. The male stands behind her and often tests the urine. When she moves away, he sniffs her droppings, paws vigorously, urinates, and then defecates. Both sexes then mark nearby twigs with their preorbital glands (Estes, 1991; Hendrichs, 1975). They may smell dung piles and move off without marking, presumably gaining information about the animals which previously marked (Bowker, 1977). Kirk's dik-diks defecate over the dung of elephants (*Loxodonta africana*), black rhinoceroses, and antelopes (Shortridge, 1934; Tinley, 1969). Preorbital gland deposits are also used for scent marking the territory, but in contrast to dung piles, the deposits are located throughout the territory; deposits are up to 8 mm in diameter (Tilson and Tilson, 1986; Tinley, 1969). Scent marks are made by placing the preorbital gland against a twig or stem and slightly moving the head. Males mark more often than females, and adults mark more than juveniles, but young smell and lick deposits more often than adults; marking of partners has been observed in captive animals (Bowker, 1977; Dittrich and Böer, 1980). Scent-marking can occur 18–21 times in 28–45 min along 275–400 mm; in captivity, males mark ca. 6 times/h (Hendrichs and Hendrichs, 1971; Kranz, 1984; Tilson and Tilson, 1986). Preorbital gland deposits provide a visual and olfactory association of the resident with his territory (Kranz, 1984).

Territories are advertised by ceaseless scent marking, in which both partners participate, but males play the lead role (Hendrichs and Hendrichs, 1971). Territories of *M. kirkii* generally contain a mixture of open areas for feeding and brush for hiding, but stands of dense thickets are usually avoided. Boundaries tend to occur along landscape features such as paths (Boshe, 1984; Bowker, 1977). Territory sizes (in ha) are ca. 0.05–30 in Tanzania (Amubode and Boshe, 1990; Boshe, 1984; Hendrichs, 1975; Hendrichs and Hendrichs, 1971), 0.1–2.4 in Kenya (Bowker, 1977; Hofmann, 1973; Komers, 1996), and 0.3–12 in Namibia (Tilson and Tilson, 1986; Tinley, 1969). During the dry season, territorial boundaries may be extended; likewise, a reduction of shrub density and cover may result in territorial abandonment or boundary extension to compensate for reduced resources (Amubode and Boshe, 1990; Boshe, 1984). Although territorial boundaries are relatively stable in shape, they undergo minor shifts with changes in relative dominance between males. On a daily basis, Kirk's dik-diks may cover at least 80% of their territory; territorial use (and invasion pressure) are highest during months of least rain and food (Bowker, 1977). Site fidelity can last the lifetime of the pair, and it may even extend to successive generations (Tilson and Tilson, 1986).

Males defend territories against other conspecifics of both sexes and against other species, and territorial behavior peaks when females are in estrus. Juvenile males may begin to participate in territorial defense at 6 months of age (Bowker, 1977; Dittrich and Böer, 1980; Hendrichs and Hendrichs, 1971). Aggression between territorial males may involve dominance or threat displays (erect crest and posture, hunched-back posture, stotting, medial-horn presentation and head-ducking, object-horning, and scent marking) and fighting (air-cushion fights, chasing, and stabbing—Bowker, 1977; Estes, 1991; Walther, 1984). Chasing may involve entire fam-

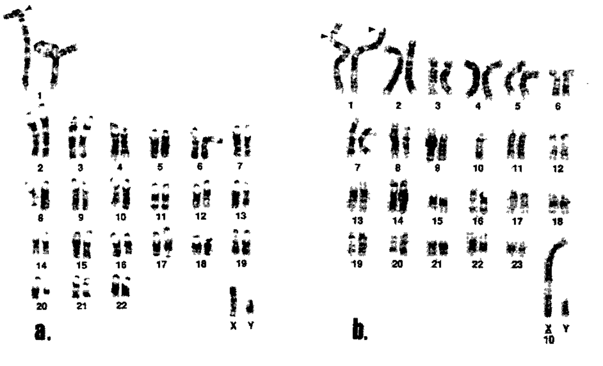

FIG. 4. G-banded karyotypes of two male *Madoqua kirkii*: a, cytotype A (2n = 46; studbook number 438); and b, cytotype B (2n = 47; studbook number 256; see Kumamoto, 1995). In cytotype B, a pericentric inversion polymorphism occurs in pair 1, and a translocation of autosome 10 to the X chromosome is designated X/10. Arrowheads indicate centromere positions.

ilies. Trespassing animals are usually submissive, and they leave the area to avoid aggression from the territory owner. Submissive behavior includes flattening the crest, crouched posture, head-low/chin-out posture, udder-seeking, and lying-out (Bowker, 1977; Estes, 1991). Serious fighting is unusual; during air-cushion fights, males face-off by threatening and lunging at each other, but usually they approach no closer than 0.5 m (Bowker, 1977; Hendrichs and Hendrichs, 1971). When in a neighbor's territory, intruders take flight if they encounter another dik-dik. When in an unoccupied area, however, the pair or the male when alone will freeze and try to identify the other dik-dik; a female when alone will take flight. If the other dik-dik is a close neighbor, they avoid it; if it is a stranger or a neighbor from farther away, they chase it off (Hendrichs, 1975). In captivity, females may become aggressive with one another, especially postpartum and during estrus (Dittrich and Böer, 1980).

Kirk's dik-diks run with lowered head and abrupt changes of direction, and they can reach speeds of 42 km/h. Generally they seek cover at the least alarm, and frightened dik-diks race to the nearest vegetation and dive with their head down and wedge-shaped body forward (Estes, 1991; Hofmann, 1973; Kingdon, 1982). They are shy, but curious, and sometimes they can be observed at distances of 5–60 m if the observers are still (Bowker, 1977; Tinley, 1969). Flight distances of dik-diks for a slowly approaching motor vehicle are 10–30 m in areas with extensive cover and 50–150 m in areas with scarce cover (Hendrichs, 1975). If suddenly frightened, they bound away 4–5 times in a stotting-like gait and make a short, explosive whistle at each contact with the ground (Bowker, 1977; Tinley, 1969). When resting, Kirk's dik-diks often face different directions. The head is usually up with ears alert and pointed in opposite directions, but they may rest with their head down and eyes closed for several min (Bowker, 1977; Dittrich and Böer, 1980; Hendrichs and Hendrichs, 1971). In Namibia, they shelter on hillsides during the day, and at night they stand where they can detect the approach of predators (Roberts, 1954).

Birds are objects of curiosity and play for juveniles. New calves occasionally play and butt heads with their older siblings, but the older juveniles do not initiate play with their younger siblings (Bowker, 1977). Kirk's dik-diks frequently groom themselves with their lower incisors. Reciprocal grooming has only been observed between mothers and their calves (Bowker, 1977; Estes, 1991). When bothered by insects, dik-diks stamp their feet, shake and scratch the body, kick up the legs, leap and whirl wildly, and run (Bowker, 1977; Tinley, 1969).

GENETICS. *Madoqua kirkii* has 2n = 46–48 chromosomes, represented by four cytotypes: type A (2n = 46, FN = 48); type B (2n = 46–47, FN = 56–59); type C (2n = 48, FN = 52); and type D (2n = 48, FN = 50—Kumamoto and Kingswood, 1995; Kumamoto et al., 1994; Ryder et al., 1989; Fig. 4). In cytotype B, variation in diploid number occurs because of a translocation between an autosome and the X chromosome, resulting in males having an unpaired autosome; type B also has a pericentric inversion polymorphism. The four cytotypes are distinguished by six chromosomal rearrangements: two heterochromatic addition/deletions, two pericentric inversions, one tandem fusion, and an autosome-to-X translocation. Cytotypes A, B, and C are found in captive animals descendant from specimens captured in Kenya and Tanzania, and cytotype D is represented by *M. k. damarensis* in Namibia (Kumamoto and Kingswood, 1995; Kumamoto et al., 1994). Karyotypes of *M. kirkii* and *M. guentheri* (2n = 48–50) are distinguishable by at least two fixed chromosomal rearrangements, a pericentric inversion and a tandem fusion (Kingswood and Kumamoto, 1996).

Nei's genetic distances between *M. kirkii* and 26 other species of bovids range from 0.22 (from *Oreotragus oreotragus*) to 1.39 (from *Aepycerus melampus*); proportion of shared alleles with these taxa are 80% and 25%, respectively (Georgiadis et al., 1990). Based on all mutations, percentage divergence for pairwise comparisons of mitochondrial DNA sequences between *M. kirkii* and 10 other species of bovids ranges from 9.1% (from *Cephalophus maxwelli*) to 11.7% (from *Tragelaphus imberbis*—Allard et al., 1992). The mitochondrial genomes of cytotypes A and D have evolved ca. 2.3 times faster than that of cytotype B (Zhang and Ryder, 1995). An apparent case of partial albinism was reported by Roosevelt and Heller (1915) in which a family of Kirk's dik-diks, a pair and their juvenile offspring, were marked by large, white blotches on the neck, shoulders, flanks, and rump.

In captivity, *M. kirkii* has hybridized with *M. guentheri*, and within *M. kirkii*, cytotype A has hybridized with cytotype B; all F1 males were sterile (Kumamoto, 1995; Ryder et al., 1989). Despite extensive meiotic activity in the A × B hybrids, gametic maturation is completely arrested. These data suggest that cytotypes A and B may represent sibling species of *M. kirkii*. Testicular volume and circulating testosterone levels are not significantly different between hybrids and either type A or B individuals (Howard et al., 1989; Ryder et al., 1989). F1 females from the A × B crossings are fertile, and backcrossing these females to either type A or type B males produces viable F2 progeny (Kumamoto, 1995). Hybridization between natural populations of *M. kirkii* and *M. guentheri* is believed to occur at low frequencies but over a large area (Kingdon, 1982).

REMARKS. "Dik-dik" is an Arabic name derived from the "zik-zik" sound it makes when startled (Sclater and Thomas, 1896–1897). Other names for dik-diks include *kabii* (Kikamba), *dikidiki*, *paa* (Kiswahili), and *empanas* (Masai—Hofmann, 1973; Loveridge, 1923; Sclater and Thomas, 1896–1897). *M. kirkii* is named for John Kirk (1832-1922) of Scotland, who collected the type specimen near Brava, Somalia; he was a naturalist, physician, and British Consul General in eastern Africa (Gotch, 1979; Günther, 1880). Common names for the various subspecies of *M. kirkii* are *M. k. cavendishi*—Naivasha Kirk dikdik; *M. k. damarensis*—Damara or Angolan dikdik, *neusbokkie* or *bloubokkie* (Afrikaans), *couwib* (Heikum Bushmen of the Nama Hottentot), *othíni* or *okathíni* (Herero), *túngu* (Ovambo); *M. k. hindei*—Ukamba Kirk dikdik; *M. k. kirkii*—*tibi* (Kipokomo); *M. k. minor*—northern Kirk dikdik; and *M. k. nyikae*—*chizimba* (Chigogo), *kivi* (Duruma), *nguyhuya* (Kinyaturu and Kisandawi), *kizimba* (Kisagara), *sala* (Kisukuma), *sha* (Taita—Allen and Loveridge, 1933; Allen et al., 1936; Loveridge, 1923; Roosevelt and Heller, 1915; Shortridge, 1934; Tinley, 1969).

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S. C. Kingswood and A. T. Kumamoto, Center for Reproduction of Endangered Species, Zoological Society of San Diego, Post Office Box 551, San Diego, California, 92112-0551.