

*Vulpes rueppelli*. By Serge Larivière and Philip J. Seddon

Published 26 December 2001 by the American Society of Mammalogists

*Vulpes rueppelli* (Schinz, 1825)

Rueppell's Sand Fox

*Canis ruppelii* Schinz, 1825:508. Type locality "Vatherland Dongola, Sudan."

*Canis famelicus* Cretzschmar, 1826:15. Type locality "Nubian Desert and Kordofan."

*Vulpes cyrenaica* Festa, 1921:3. Type locality "Dintorni di Bengasi," Cyrenaica, Libya.

**CONTEXT AND CONTENT.** Order Carnivora, family Canidae, genus *Vulpes*. Ellerman and Morrison-Scott (1966) listed 5 subspecies for Rueppell's sand fox. However, Hufnagl (1972) stressed the variability in size and color even within the same locality and thus considered the species monotypic (Qumsiyeh, 1996). We consider *V. rueppelli* monotypic, but the subspecies of Ellerman and Morrison-Scott (1966) are as follows:

*V. r. caesia* Thomas and Hinton, 1921:5. Type locality "South side Mt. Baguezan, Asben. 3,000 ft."

*V. r. cyrenaica* Festa, 1921:3, see above (*cufrana* De Beaux is a synonym).

*V. r. ruppelli* (Schinz, 1825:508), see above (*famelicus* Cretzschmar and *somalitiae* Thomas are synonyms).

*V. r. sabaea* Pocock, 1934:636. Type locality "Rub al Khali, Arabia."

*V. r. zarudnyi* Birula, 1912:270. Type locality "Kala-i-bid, Province of Makran (Sargad), Persian Baluchistan."

**DIAGNOSIS.** *Vulpes rueppelli* (Fig. 1) is smaller (<81 cm in total length) with a smaller hind foot (90–115 mm), shorter tail (<36 cm), and proportionally larger ears than the sympatric red fox (*Vulpes vulpes*). Pelage is also finer, softer, and of pale sandy color compared to reddish color of the red fox. In addition, back of ear is pale to cinnamon rufous for *V. rueppelli* compared to black in *V. vulpes*. Finally, *V. rueppelli* has white undersides compared to grayish undersides of *V. vulpes* (Gasperetti et al. 1985; Petter 1952).

Rueppell's sand fox is sympatric with the fennec (*Vulpes zerda*), but *V. rueppelli* is larger (body mass > 1.5 kg), with a longer tail (70% of head and body length versus 50% in the fennec), proportionally smaller ears, and white tip on tail compared to black tip of fennec. Nonetheless, confusion is common between juvenile *V. rueppelli* and adult *V. zerda* (Gasperetti et al. 1985). *V. rueppelli* can be differentiated from the pale fox (*V. pallida*) because a white-tipped tail is never present in *V. pallida* (Ellerman and Morrison-Scott 1966).

**GENERAL CHARACTERS.** Rueppell's sand fox is a small (ca. 2 kg) fox with rather short legs, long broad ears, and a light-colored, very dense coat. Middle of muzzle and forehead are rusty colored, and a conspicuous dark brown patch on side of muzzle extends toward eye. Vibrissae are well developed and reach up to 70 mm in length (Harrison 1968). Lips, sides of face, and chin are white. Ears are white inside and deep cinnamon rufous outside. A cinnamon rufous dorsal band broadens in middle of back then narrows backwards. Pelage is silvery in appearance because of numerous white hairs. Hairs of underfur reach 35 mm in length. Predominating color of flanks is very pale buffy orange, with a light grayish suffusion close to dorsal stripe (Harrison 1968). Underparts are white. Limbs are rufous with some black hairs. Lower parts and feet are whitish, and soles of feet are densely furred. Tail is long, bushy (hairs ca. 50–55 mm in length), buff colored, more or less mixed with black hairs, and has a white tip (Dorst and Dandelot 1970; Gasperetti et al. 1985; Harrison 1968).

Mean body measurements (in mm) and parenthetical *SD* of 8

males and 3 females from Saudi Arabia (Harrison 1968), respectively, are: total length, 742 (43), 661 (67); length of tail, 299 (32), 275 (26); length of hind foot, 107 (6), 98 (8); and length of ear, 98 (6), 94 (1). Sexual dimorphism in body mass is not reported; body mass of adults averages 1.7 kg (range: 1.3–2.2 kg,  $n = 176$ —Olfermann 1996).

Skull (Fig. 2) is small and delicate. Tympanic bullae are well developed. Distance between anterior orbital margin and gnathion is slightly shorter than distance between the same point and posterior part of zygoma. Nasal bones are short, upwardly deflected posteriorly, and slightly constricted medially. Brain case does not have a strong ridge: temporal ridges pass directly backwards from posterior root of postorbital process and remain widely divergent until just in front of lambda. Mean and parenthetical *SD* measurements (in mm) of skulls of 6 males and 4 females from Saudi Arabia (Harrison 1968), respectively, are: greatest length, 105 (4), 100 (7); condylobasal length, 102 (3), 95 (8); and zygomatic breadth, 56 (1), 53 (3).

Males are typically larger than females (Harrison 1968; Osborn and Helmy 1980), but sexual dimorphism varies locally. In Arabia, measurements (in mm, mean  $\pm$  *SD*) of canine diameters of males ( $4.44 \pm 0.15$ ,  $n = 5$ ) are only 1% larger than those of females ( $4.38 \pm 0.40$ ,  $n = 3$ ), but in Israel/Palestine they are 29% larger for males ( $4.79 \pm 0.21$ ,  $n = 4$ ) compared to those of females ( $3.72 \pm 0.49$ ,  $n = 2$ —Dayan et al. 1989, 1992). Similarly, condylobasal lengths of male skulls in Arabia ( $104.44 \pm 3.31$ ,  $n = 6$ ) are 2% larger than those of female skulls ( $99.28 \pm 3.44$ ,  $n = 4$ ), but in Israel/Palestine they are 15% larger for males ( $111.77 \pm 1.92$ ,  $n = 3$ ) compared to those of females ( $97.02 \pm 1.58$ ,  $n = 2$ —Dayan et al. 1989, 1992). Finally, lengths of male carnassials in Arabia ( $11.29 \pm 0.70$ ,  $n = 6$ ) are only 1% larger than those of females ( $11.18 \pm 0.85$ ,  $n = 4$ ), but in Israel/Palestine they are 17% larger for males ( $12.33 \pm 0.34$ ,  $n = 3$ ) compared to those of females ( $10.52 \pm 1.08$ ,  $n = 2$ —Dayan et al. 1989).

**DISTRIBUTION.** *Vulpes rueppelli* occurs in deserts of northern Africa south to Sudan and Somalia (Fig. 3). The species is also present in Algeria, central Niger, Libya, northern Chad, Egypt, south to Sudan, arid lowlands of Ethiopia, and northern Somalia. In Arabia, it is widespread, except on the littoral of the Red Sea and in the montane periphery (Gasperetti et al. 1985). Northern limit of its range extends to Iraq, Jordan, and Israel/Palestine, including the Negev (Harrison 1968). Eastward, *V. rueppelli* occurs in Persian Baluchistan, Afghanistan, and Pakistan (Amr et



FIG. 1. Adult *Vulpes rueppelli* in Saudi Arabia. Photograph by Kingdom of Saudi Arabia National Wildlife Research Center Photo Library.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Vulpes rueppelli* from Mahazat as-Sayd, western-central Saudi Arabia. Greatest length of cranium is 105 mm.

al. 1996; Cuzin 1996; Fox 1975; Harrison 1968; Qumsiyeh et al. 1993; Sheldon 1992).

**FOSSIL RECORD.** Canidae are known from Africa since the Miocene (Kowalski and Rzebik-Kowalska 1991). Remains of a *Vulpes*-like animal occur in late Pliocene deposits in Ahl al Oughlam (Morocco), but they may belong to either *V. rueppelli* or *V. zerda* (Geraads 1997). Otherwise, fossils of *Vulpes rueppelli* are unknown.

*Vulpes rueppelli* diverged from other *Vulpes* later than *V. zerda*, suggesting that it entered desert regions more recently (Geffen et al. 1992). Its closest relative is *V. bengalensis*, *V. vulpes*, or *Alopex lagopus* (Clutton-Brock et al. 1976; Geffen et al. 1992). Desert adaptations evolved independently at least twice in the Canidae, once in the precursor to *V. zerda* and *V. cana* (Blanford fox), and more recently in *V. velox* (swift fox) and *V. rueppelli* lineage (Geffen et al. 1992).

**FORM AND FUNCTION.** *Vulpes rueppelli* has good vision and hearing (Petter 1952). Soles of feet are covered in long and soft hairs that conceal the pads completely, an adaptation to extremes of temperatures in the desert (Sheldon 1992). During winter, captive animals held outside grew thick underfur (Petter 1952).

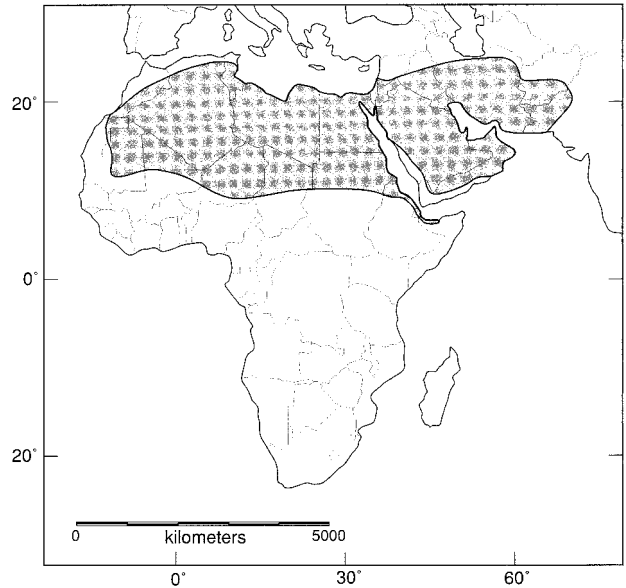


FIG. 3. Distribution of *Vulpes rueppelli*, modified from Cuzin (1996), Dorst and Dandelot (1970), Gasperetti et al. (1985), Harrison (1968), Kingdon (1990, 1997), Kowalski and Rzebik-Kowalska (1991), and Misonne (1986). We consider *V. rueppelli* monotypic.

Gastro-intestinal tract of *V. rueppelli* can partially digest bones and teeth (especially molars) of prey. The subsequent changes of both the structure and chemical composition of bone and tooth fragments alters fossilization (Denys et al. 1992).

Captive Rueppell's sand foxes will readily drink water where available, and they are found in the wild near wells and springs (Osborn and Helmy 1980), but they are also present in areas without standing water for much of the year (Olfermann 1996; Osborn and Helmy 1980; Seddon et al. 1997).

Dental formula is  $i\ 3/3, c\ 1/1, p\ 4/4, m\ 2/3$ , total 42 (Harrison 1968). Males have a relatively straight baculum ca. 40-mm long (Harrison 1968).

**ONTOGENY AND REPRODUCTION.** *Vulpes rueppelli* maintains monogamous pairs throughout the year (Olfermann 1996). In Saudi Arabia, female Rueppell's sand foxes prepare breeding dens beginning mid-October, and enlargement of male testes occurs from early October to early January.

Females are monoestrous. Mating occurs in mid to late November, and 1 timed copulation lasted 11 min (Olfermann 1996). Pups are born near the middle of January after a gestation period of 52–53 days: in the Béni-Abbès region, young *V. rueppelli* were found in May (Petter 1952). Mean litter size of 15 litters from central Saudi Arabia was 3.3 cubs, and females have been recorded above ground with 2–6 cubs (Olfermann 1996). A female collected in June in Egypt had 3 placental scars (Osborn and Helmy 1980). A captive female had a litter of 3 young, and a litter of 2 young was evidently born in March (Nowak 1991).

Cubs are born blind, become independent at 4 months, and reach sexual maturity in their first year (Kingdon 1997). Juveniles may have a light reddish coat, reminiscent of that of the Arabian red fox, *Vulpes vulpes*. In Arabia, color of the pelage of Rueppell's sand foxes changes markedly with age, season, and locality. Pelage becomes paler with age, and some older individuals (>5 years) may be almost white (E. Olfermann, pers. comm.).

Sex ratio of juvenile Rueppell's sand foxes favors males, being 1.7:1 and 1.6:1 in 2 consecutive years (Olfermann 1996). Of 67 museum specimens in Egypt, 39 were males and 28 were females (a ratio of 1.4:1—Osborn and Helmy 1980). Dispersal of young Rueppell's sand foxes starts in July and August when cubs are 6–7-months old, and dispersing juveniles may be found between July and September (Olfermann 1996). Mortality of dispersing juveniles during this very hot, dry period may be high.

**ECOLOGY.** Rueppell's sand foxes are widely distributed across habitats within their desert and semidesert range. *V. rueppelli*

*PELLI* prefers dry sand and stone deserts (Kingdon 1997). In North Africa, it is present in stony deserts, steppe, bramble savannah, and woodlands, and is the most ubiquitous fox species in Egypt (Fox 1975; Osborn and Helmy 1980). In Pakistan, it is typically associated with rolling sand dunes (Roberts 1977). In the Arabian Peninsula, it is present throughout the arid steppe and in sandy, stony, and rocky deserts (Green 1986; Olfermann 1996; Seddon et al. 1997).

Throughout its range, *V. rueppelli* is sympatric with other canids, including *Canis aureus*, *C. lupus*, *Vulpes vulpes*, and *V. cana* (Dayan et al. 1989; Johnson et al. 1996; Kock and Nader 1996; Qumsiyeh et al. 1993; Seddon et al. 1997). Rueppell's sand foxes predominate in the more waterless regions (Linn 1988; Olfermann 1996). When in competition with *V. vulpes*, *V. rueppelli* is forced out of the ecologically richest areas (Ginsberg and Macdonald 1990; Kock and Nader 1996). Increasing agricultural activity in the Arabia Valley and the northern Negev in Israel/Palestine has favored the more adaptable *V. vulpes* (Ilani 1988).

Rueppell's sand foxes are omnivorous and opportunistic feeders (Alderton 1994; Kowalski 1988). Diet varies according to local availability (Lindsay and Macdonald 1986). In Morocco and parts of North Africa, Rueppell's sand foxes are largely insectivorous (Aulagnier and Thevenot 1986; Dorst and Dandelot 1970), though in the Sahara their diet includes rodents, birds, lizards, insects, and fruit, notably dates (Le Berre 1990). In Egypt, they consume rodents; small birds; lizards, notably *Uromastix aegyptius* and *Mesalina*; and insects such as grasshoppers, mole crickets, and scarab beetles. They climb date palms and will gnaw fibrous fruits of dom palms (Osborn and Helmy 1980). In Iran, Rueppell's sand foxes take diverse plant and animal material, including small mammals (e.g., *Jaculus blanfordi*—Roberts 1977), reptiles, insects, and leaves of succulent plants (Harrington 1977). In Pakistan, they occur in areas containing extensive colonies of rodents, such as *Meriones libycus* and *Gerbillus nanus* (Roberts 1977). In the Arabian Peninsula, *V. rueppelli* feed on small mammals, birds, lizards, insects, grass, and desert succulents (Gasperetti et al. 1985; Harrison and Bates 1991; Lindsay and Macdonald 1986). Of 100 scats in Oman, small mammals were the most common prey and lizards the second most abundant; insects were common but accounted for only 7.3% by volume, whereas a third of the scats contained grass (Lindsay and Macdonald 1986). In Saudi Arabia, small mammals and invertebrates were most frequent and abundant prey remains, representing 80–95% of total intake ( $n = 2,985$  scats). Small mammals predominated between September and February, whereas invertebrates were most common from April to August. Bird, reptile, and fruit remains occurred infrequently, but other plant material was often present in small quantities. All scats contained sand and small stones; those with a high volume of insect remain tended to contain more sand than others. Sheep and goat hair were sometimes present (Olfermann 1966). In the Egyptian Sahara, the diet of *V. rueppelli* consisted mainly of insects (77% occurrence in 634 scats), birds, and dates (63% occurrence; *Phoenix dactylifera*—Kowalski 1988). Snakes (Colubridae) and rodents (*Gerbillus gerbillus*) were consumed opportunistically (Kowalski 1988). Fruits of cultivated plants may be taken from human garbage (Kowalski 1988). Insects were mostly Coleoptera and Orthoptera. Garbage occurred in 2% of scats ( $n = 634$ ). Items consumed from garbage included paper, cord, wrapping foil, watermelon, orange, and grape seeds (Kowalski 1988). Birds were the most hunted vertebrates and were present in 58–100% of scats depending on the region (Kowalski 1988). Although, Rueppell's sand foxes scavenge at camps and dumps (Alderton 1994; Harrison and Bates 1991; Seddon et al. 1997), they avoid human settlements (Saudi Arabia Ministry of Agriculture and Water 1992).

Virtually no systematic estimates of population density have been made for *V. rueppelli*. Rueppell's sand fox densities were measured using mark-recapture methods within a large trapping grid inside a fenced protected area in central Saudi Arabia and yielded estimates that ranged between 0.18 and 0.44 foxes/km<sup>2</sup> (Olfermann 1996). Elsewhere Rueppell's sand foxes are described as being rare (Jubail, eastern coastal Saudi Arabia—Kock and Nader 1996), present but less numerous than *V. vulpes* (northern Saudi Arabia—Seddon et al. 1997), and relatively common (Rub Al Khali, southern Saudi Arabia—Harrison and Bates 1991).

Rueppell's sand foxes are highly mobile, covering distances of >9 km during nocturnal foraging (Olfermann 1996). Adult resident foxes maintain territories that are clearly separated from same-sex

neighbors. However, individuals from monogamous pairs have home ranges that are largely congruent with extensive overlap (Olfermann 1996), but with complete separation from adjacent pairs (Lindsay and Macdonald 1986). Average home range size in central Saudi Arabia was 16.3 km<sup>2</sup>, with males having larger (20.9 km<sup>2</sup>) home ranges than females (13.2 km<sup>2</sup>—Olfermann 1996). Much larger territories were recorded in Oman, where the mean home range size was 69.1 km<sup>2</sup>, and again male home range was larger (84.4 km<sup>2</sup>) than that of females (53.8 km<sup>2</sup>—Lindsay and Macdonald 1986). Juveniles dispersing from natal areas cover distances from 14 to 48 km (mean 32 km—Olfermann 1996). Occasional adult emigration occurs, when individuals are driven off their territories, moving between 5 and 48 km (mean = 14 km,  $n = 4$ —Olfermann 1996).

In remote or reserve areas, the main causes of mortality for Rueppell's sand foxes are starvation and predation, particularly by aerial predators such as steppe eagles (*Aquila nipalensis*) and eagle owls (*Bubo bubo*—Olfermann 1996). *V. rueppelli* caught in cage traps may fall prey to honey badgers (*Mellivora capensis*—Lenain and Ostrowski 1998). Rueppell's sand foxes are subject to persecution through shooting or trapping, or by the indiscriminate use of poisoned baits (Gasperetti et al. 1985). The ability of the Rueppell's sand fox to thrive in the more arid areas may maintain viable populations. Rueppell's sand foxes have a longevity in captivity from 6.5 years (Flower 1931; Ginsberg and Macdonald 1990) to 12 years (Le Berre 1990). The maximum confirmed age in the wild is 7 years, but tooth cementum analysis indicates ages >9 years are possible (Olfermann 1996).

Rueppell's sand foxes have been caught in cage (Olfermann 1996) and foot-hold traps (Seddon et al. 1999). *V. rueppelli* is readily caught in cage traps with a variety of baits, and a high percentage of trapped animals can be repeatedly caught in cages. They can be immobilized using ketamine/xylazine (Olfermann 1996). Age is determined by counting annular cementum rings in premolars and canines, and less accurately for older animals, by the degree of tooth wear (Olfermann 1996).

Rueppell's sand foxes harbor fleas (*Caenopsylla laptevi*, *Coptopsylla joannae*, *Synosternus pallidus*, and *Xenopsylla conformis*) and ticks (*Haemaphysalis* and *Rhipicephalus*—Hoogstraal et al. 1980; Lewis and Lewis 1990). In central Saudi Arabia, 93.6% ( $n = 78$ ) of Rueppell's sand foxes examined carried ectoparasites; either fleas (31.5%), ticks (30.1%), or both (38.4%—Olfermann 1996).

Rabies is the most widespread viral infection of *V. rueppelli*. In Saudi Arabia 35% of positive-testing animal samples stem from foxes, but the statistics do not distinguish among species (Stöhr 1995).

**BEHAVIOR.** The basic social unit is the monogamous pair (Lindsay and Macdonald 1986), and pairs maintain territories throughout the year (Olfermann 1996). The female prepares the breeding dens alone, whereas the male contributes to pup rearing by carrying prey (mainly small mammals) to the cubs, and also by playing with and attending them (Olfermann 1996). Observations of parties of 3 to 5 individuals (Nowak 1991) may represent family groups.

Rueppell's sand foxes are strictly crepuscular and nocturnal and shelter underground during the day (Lindsay and Macdonald 1986; Olfermann 1996; Petter 1952; but see Le Berre 1990). Rueppell's sand foxes use 2 distinct dens: breeding dens and resting dens. Breeding dens are used during mating and pup rearing in winter and spring and are shared by a pair. In central Saudi Arabia, female Rueppell's sand foxes visit dens of the spiny tailed lizard (*Uromastix aegyptius*) in October and November, selecting 3–6 dens within their territory for cleaning, enlargement, and addition of entrances (Olfermann 1996). Most breeding dens in Oman have only 1 entrance, but some have up to 5 (Lindsay and Macdonald 1986). In contrast, resting dens are smaller and generally have space for only 1 animal. They are used for resting underground during daylight hours outside the breeding season. Animals change dens on average once every 4.8 days (Lindsay and Macdonald 1986) and cubs will be transferred to a new den if the site is disturbed (Olfermann 1996).

Rueppell's sand foxes communicate by facial expression, vocalization, and scent marking. Vocalizations, recorded during mating behavior, consist of a series of single short barks, with 20–40 s between each series (Olfermann 1996; Petter 1952). In captivity, the vocal repertoire is varied and includes hissing during aggres-

sion, trilling noise during tension, and high-pitched whistles when calling for attention (Kingdon 1997). Animals may wag their tails in a manner similar to that of domestic dogs. Rueppell's sand foxes exude an anal gland secretion when frightened (Kingdon 1997; Le Berre 1990) and will mark with urine, but not with feces which do not have the characteristically strong odor of red fox feces (Olfermann 1996).

Interactions between red fox and Rueppell's sand fox usually result in the latter fleeing (Kingdon 1997). *V. rueppelli* are very agile and can easily climb fences, trees, and cliffs in search of fruits or in pursuit of birds (Kingdon 1997). They can also jump 1.5 m horizontally while running (Petter 1952). Caching behavior is well developed in captivity, and captive animals dig constantly and are very playful (Petter 1952).

**GENETICS.** Rueppell's sand fox has  $2n = 40$  chromosomes. The X chromosome is metacentric, and the Y chromosome is very small. Autosomes are metacentric and submetacentric except for 2 pairs of acrocentrics (Matthey 1954).

**CONSERVATION STATUS.** *Vulpes rueppelli* is listed as insufficiently known by the International Union for the Conservation of Nature (Wozencraft 1993).

**REMARKS.** The presence of Rueppell's sand foxes in even the most waterless areas has given rise to the Arab fable that *V. rueppelli* drinks from the wind by sleeping with its head into the breeze (Hurst 1910). The slight build of *V. rueppelli* is indicated by the French common name renard famélique, which means famished fox (Sheldon 1992). Other vernacular names include fennec de la Hamada (French), renard du désert (French), and sandfuchs (German). The generic name is Latin for fox and the specific epithet honors the 19th Century German naturalist Wilhelm Peter Eduard Simon Rüppell.

D. Dyck and M. Mierau helped with the map. Thanks to D. Lenain and I. Nader for providing the fox skull, to P. Paillat for skull preparation, and to M. Gunther for taking the skull photos. L. Allen kindly arranged for production of all photographic material. Z. S. Amr and M. Qumsiyeh kindly reviewed an earlier draft of this manuscript.

#### LITERATURE CITED

- ALDERTON, D. 1994. Foxes, wolves and wild dogs of the world. Blandford, London, United Kingdom.
- AMR, Z. S., G. KALISHAW, M. YOSEF, B. J. CHILCOT, AND A. AL-BUDARI. 1996. Carnivores of Dana Nature Reserve (Carnivora: Canidae, Hyanidae and Felidae), Jordan. *Zoology in the Middle East* 13:5–16.
- AULAGNIER, S., AND M. THEVENOT. 1986. Catalogue des mammifères sauvages du Maroc. Série Zoologie. Institut Scientifique, Rabat 41:1–163.
- BIRULA, A. A. 1912. Contributions à la classification et à la distribution géographique des mammifères. III. Carnivores, recueillis dans la Perse par M. N. A. Zaroudny en 1896, 1898, 1900–1901 et 1903–1904. Annales du Musée de Zoologie et des Sciences de St. Pétersbourg 17:219–280.
- CLUTTON-BROCK, J., G. B. CORBET, AND M. HILLS. 1976. A review of the family Canidae, with a classification by numerical methods. *British Museum of Natural History* 29:117–199.
- CRETZSCHMAR, P. J. 1826. Rüppell's Atlas zu der reise im nördlichen Afrika. Frankfurt am Main: Gedruckt und in Commission bei H. L. Bronner, 1826–1828. Säugeth (not seen, cited in Ellerman and Morrison-Scott 1966).
- CUZIN, F. 1996. Répartition actuelle et statut des grands mammifères sauvages du Maroc (Primates, Carnivores, Artiodactyles). *Mammalia* 60:101–124.
- DAYAN, T., E. TCHERNOV, Y. YOM-TOV, AND D. SIMBERLOFF. 1989. Ecological character displacement in Saharo-Arabian Vulpes: outfoxing Bergmann's rule. *Oikos* 55:263–272.
- DAYAN, T., D. SIMBERLOFF, E. TCHERNOV, AND Y. YOM-TOV. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society* 45:315–331.
- DENYS, C., K. KOWALSKI, AND Y. DAUPHIN. 1992. Mechanical and chemical alterations of skeletal tissues in a recent Saharian accumulation of faeces from *Vulpes rueppelli* (Carnivora, Mammalia). *Acta Zoologica Cracoviensia* 35:265–283.
- DORST, J., AND P. DANDELLOT. 1970. A field guide to the larger mammals of Africa. Houghton Mifflin Company, Boston, Massachusetts.
- ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. Checklist of Palearctic and Indian mammals 1758–1946. Second edition. British Museum of Natural History, London, United Kingdom.
- FESTA, E. 1921. Missione zoologica del Dott. E. Festa in Cirenaica. III. Mammiferi. Bollettino Musei di Zoologia ed Anatomia Comparata della Università di Torino 36(740):1–7.
- FLOWER, S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals. *Proceedings of the Zoological Society of London* 1931:145–234.
- FOX, M. W. 1975. The wild canids: their systematics, behavioral ecology and evolution. Robert E. Krieger Publishing Company, Malabar, Florida.
- GASPERETTI, J., D. L. HARRISON, AND W. BUTTIKER. 1985. The Carnivora of Arabia. *Fauna of Saudi Arabia* 7:397–413.
- GEFFEN, E., A. MERCURE, D. J. GIRMAN, D. W. MACDONALD, AND R. K. WAYNE. 1992. Phylogenetic relationships of the fox-like canids: mitochondrial DNA restriction fragment, site and cytochrome *b* sequence analysis. *Journal of Zoology, London* 228:27–39.
- GERAADS, D. 1997. Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Geobios* 30:127–164.
- GINSBERG, J. R., AND MACDONALD, D. W. 1990. Foxes, wolves, jackals and dogs. An action plan for the conservation of canids. International Union for the Conservation of Nature, Gland, Switzerland.
- GREEN, A. A. 1986. Status of large mammals of northern Saudi Arabia. *Mammalia* 50:483–493.
- HARRINGTON, F. A., JR. (ED.). 1977. A guide to the mammals of Iran. Department of Environment, Tehran, Iran.
- HARRISON, D. L. 1968. The mammals of Arabia: Carnivora, Artiodactyla, Hyracoidea. Ernest Benn Limited, London, United Kingdom 2:1–381.
- HARRISON, D. L., AND P. J. J. BATES. 1991. The mammals of Arabia. Second edition. Harrison Zoological Museum, Kent, United Kingdom.
- HOOGSTRAAL, H., H. Y. WASSEF, AND W. BUTTIKER. 1981. Ticks (Acarina) of Saudi Arabia. Fam. Aragasidae, Ixodidae. *Fauna of Saudi Arabia* 3:25–110.
- HUFNAGL, E. 1972. Lybian mammals. The Olander Press, New York.
- HURST, H. E. 1910. A journey from Wadi Hilfa to Aswan. *Cairo Science Journal* 4:8–10.
- ILANI, G. 1988. Red fox replacing sand fox. *Israel Land and Nature* 14:244.
- JOHNSON, W. E., T. K. FULLER, AND W. L. FRANKLIN. 1996. Sympatry in canids: a review and assessment. Pp. 189–218 in *Carnivore behavior, ecology and evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York 2:1–644.
- KINGDON, J. 1990. Arabian mammals: a natural history. Academic Press, London, United Kingdom.
- KINGDON, J. 1997. The Kingdon field guide to African mammals. Academic Press, San Diego, California.
- KOCK, D., AND NADER, I. A. 1996. Terrestrial mammals of Jubail Marine Wildlife Sanctuary. Pp. 421–437 in *A marine wildlife sanctuary for the Arabian Gulf: environmental research and conservation following the 1991 Gulf War oil spill* (F. Krupp, A. H. Abuzinada, and I. A. Nader, eds.). National Commission for Wildlife Conservation and Development, Riyadh and Senckenberg Research Institute, Frankfurt, Germany.
- KOWALSKI, K. 1988. The food of the sand fox *Vulpes rueppelli* Schinz, 1825 in the Egyptian Sahara. *Folia Biologica* 36:89–94.
- KOWALSKI, K., AND B. RZEBIK-KOWALSKA. 1991. Mammals of Algeria. Polish Academy of Sciences, Institute of Systematics and Evolution of Mammals, Krakow, Poland.
- LE BERRE, M. 1990. Faune du Sahara. Mammifères. R. Chabaud, Paris, France 2:1–360.
- LENAIN, D., AND S. OSTROWSKI. 1998. Opportunistic predation of trapped mammals by the ratel (*Mellivora capensis*). *Zoology in the Middle East* 16:13–18.
- LEWIS, R. E., AND J. H. LEWIS. 1990. An annotated checklist of the fleas (Siphonaptera) of the Middle East. *Fauna of Saudi Arabia* 11:251–276.
- LINDSAY, I. M., AND D. W. MACDONALD. 1986. Behaviour and ecology of the Rüppell's fox *Vulpes rueppelli*, in Oman. *Mammalia* 50:461–474.

- LINN, I. 1988. The distribution and ecology of carnivorous mammals in the Wahiba Sands. Pp. 277–304 in *The scientific results of the Royal Geographical Society's Oman Wahiba Sands Project 1985–1987* (R. W. Dutton and D. A. Bray, eds.). *Journal of Oman Studies, Special Report* 3:1–576.
- MATTHEY, R. 1954. Chromosomes et systématique des canidés. *Mammalia* 18:225–230.
- MISONNE, X. 1986. Sur la répartition de quelques mammifères désertiques. *Revue de Zoologie Africaine* 100:13–28.
- NOWAK, R. M. 1991. *Walker's mammals of the world*. Fifth edition. The John Hopkins University Press, Baltimore, Maryland 2: 643–1629.
- OLFERMANN, E. W. 1996. Population ecology of the Rüppell's fox (*Vulpes rueppelli*, Shinz 1825) and the red fox (*Vulpes vulpes*, Linnaeus 1758) in a semi-desert environment of Saudi Arabia. Ph.D. dissertation. University of Bielefeld, Germany, 291 pp.
- OSBORN, D. J., AND I. HELMY. 1980. The contemporary land mammals of Egypt (including Sinai). *Field Museum of Natural History*, Chicago, Illinois.
- PETTER, F. 1952. Le renard famélique. *La Terre et Vie* 1952:190–193.
- POCOCK, R. I. 1934. Preliminary diagnoses of some new races of south Arabian mammals. *Annals and Magazine of Natural History, Series 10*, 13:635–636.
- QUMSIYEH, M. B. 1996. *Mammals of the Holy Land*. Texas Tech University Press, Lubbock.
- QUMSIYEH, M. B., Z. S. AMR, AND D. M. SHAFEL. 1993. Status and conservation of carnivores in Jordan. *Mammalia* 57:55–62.
- ROBERTS, T. J. 1977. *The mammals of Pakistan*. Ernst Benn Limited, London, United Kingdom.
- SAUDI ARABIA MINISTRY OF AGRICULTURE AND WATER. 1992. *Natural history of Saudi Arabia. An introduction*. Obekan Company for Printing and Publishing, Riyadh, Saudi Arabia.
- SCHINZ, H. R. 1825. *G. Cuvier's Thierreich Das Thierreich eingetheilt nachdem bau der thiere als grundlage ihrer naturgeschichte und der vergleichenden anatomie*. Volume 4 (not seen, cited in Ellerman and Morrison-Scott 1966).
- SEDDON, P. J., Y. VAN HEEZIK, AND R. F. MALONEY. 1999. Evaluation of leghold trap injuries to two species of fox in Saudi Arabia. Pp 67–77 in *Mammal trapping* (G. Proulx, ed.). Alpha Wildlife Limited, Edmonton, Alberta, Canada.
- SEDDON, P. J., Y. VAN HEEZIK, AND I. A. NADER. 1997. Mammals of the Harrat al-Harrah Protected Area, Saudi Arabia. *Zoology in the Middle East* 14:37–46.
- SHELDON, J. W. 1992. *Wild dogs: the natural history of the non-domestic Canidae*. Academic Press, New York.
- STÖHR, K. 1995. Rabies control in Saudi Arabia. Mission report 19–21 April 1995. World Health Organization, Veterinary Public Health Unit, Geneva, Switzerland, 12 Pp.
- THOMAS, O., AND M. A. C. HINTON. 1921. Captain Angus Buchanan's air expedition. II. On the mammals (other than ruminants) obtained during the expedition to Air (Asben). *Novitates Zoologicae* 28:1–13.
- WOZENCRAFT, W. C. 1993. Order Carnivora: Canidae. Pp. 285–287 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

Associate editors of this account were ELAINE ANDERSON and VIRGINIA HAYSSSEN. Editor was VIRGINIA HAYSSSEN.

S. LARIVIÈRE, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, 112 SCIENCE PLACE, SASKATOON, SASKATCHEWAN S7N 5E2, CANADA, AND DELTA WATERFOWL FOUNDATION, R.R. #1, BOX 1, PORTAGE LA PRAIRIE, MANITOBA R1N 3A1, CANADA. P. J. SEDDON, NATIONAL WILDLIFE RESEARCH CENTER, NATIONAL COMMISSION FOR WILDLIFE CONSERVATION AND DEVELOPMENT, P.O. BOX 1086, TAIF, KINGDOM OF SAUDI ARABIA.