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Otocyon megalotis.

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Otocyon Müller, 1836

Canis: Desmarest 1822:538. Part; type species *Canis megalotis*.
Otocyon Müller, 1836:1. Type species *Otocyon caffer* Müller, 1836 (= *Canis megalotis* Desmarest, 1822), by monotypy (Melville and Smith 1987).
Agrodius H. Smith, 1840:258. Type species *Agriodus auritus* H. Smith, 1840 (= *Canis megalotis* Desmarest, 1822), by monotypy; described as a subgenus of *Canis*.

CONTEXT AND CONTENT. Order Carnivora, suborder Caniformia, superfamily Canoidea, family Canidae, subfamily Otocyoninae, tribe Vulpini. *Otocyon* is monotypic.

Otocyon megalotis (Desmarest, 1822)

Bat-eared Fox

Canis megalotis Desmarest, 1822:538. Type locality "le Cap de Bonne-Espérance," = Cape of Good Hope, Cape Province, South Africa.
Canis lalandii Desmoulins, 1823:18. Type locality "Cafrérie," = South Africa.
Otocyon caffer Müller, 1836:1. Type locality not given.
Agriodus auritus H. Smith, 1840:260. Renaming of *Canis megalotis*.
Otocyon virgatus Miller, 1909:485. Type locality "Naivasha Station, British East Africa."
Otocyon megalotis: Miller, 1909:485. First use of current name combination.
Otocyon canescens Cabrera, 1910:463. Type locality "Somaliland [= Somalia], 10 miles south of Burao."
Otocyon steinhardti Zukowsky, 1924:52. Type locality "ca. 45 Kilometer westlich Outjo, mittleres Ugabgebiet, Sutura basilaris geschlossen" = 45 km west of Outjo, Namibia.

CONTEXT AND CONTENT. Content as above. *Otocyon megalotis* has 2 subspecies (Coetzee 1977):

O. m. megalotis (Desmarest, 1822:538), see above; *auritus* (H. Smith), *caffer* Müller, *lalandii* (Desmoulins), and *steinhardti* Zukowsky are synonyms.
O. m. virgatus Miller, 1909:485, see above; *canescens* Cabrera is a synonym.

DIAGNOSIS. *Otocyon megalotis* (Fig. 1) and the raccoon dog (*Nyctereutes procyonoides*) have black facial masks, but mask of *N. procyonoides* surrounds eyes and goes back to ears, whereas facial mask of *O. megalotis* is less extreme. *O. megalotis* lacks the dispersed white band beneath each eye that stretches back to ears in *N. procyonoides* (Ward and Wurster-Hill 1990). *O. megalotis* can be distinguished from Rüppell's fox (*Vulpes rueppelli*) in that *V. rueppelli* has reddish-gray agouti pelage with dark guard hairs on tail and a dark patch between nose and eyes (Larivière and Seddon 2001). *O. megalotis* has large ears, but the fennec fox (*Vulpes zerda*) has larger ears relative to body size; pelage of *O. megalotis* lacks the off-white underparts of *V. zerda* (Larivière 2002). *O. megalotis* has much larger ears than those of the pale fox (*Vulpes pallida*) and lacks the dark, black-tipped tail and pinkish beige underparts of *V. pallida*. *O. megalotis* lacks the gray ears, dark-tipped tail, and blotchy black, brownish-gray, and white pelage of Blanford's fox (*Vulpes cana*); mask of *O. megalotis* is larger than that of *V. cana* (Geffen 1994).

GENERAL CHARACTERS. Head, dorsum, and upper parts of legs of *O. megalotis* are gray. Muzzle is black on top and white on sides (Mills and Hes 1997). Chest and underside of body vary from pale to honey yellow (Maas 1993). Back portion of ears, lower parts of legs, tail tip, upper side of tail, and facial mask are black (Maas 1993). Ears of *O. megalotis* are 113–135 mm in length and white inside (sexes combined—Maas 1993; Mills and Hes 1997). Shoulder height is 300–400 mm (sexes combined—Kingdon 1977; Smithers 1983). Length of head and body is 460–660 mm, length of tail is 230–340 mm, and mass is 3.0–5.3 kg (sexes combined—Nowak 1999).

Selected cranial measurements (in mm) for 7 individuals (sexes combined) are: condylobasal length, 104–115; basilar length, 99–107; zygomatic breadth, 55–66; breadth of braincase, 41–43; postorbital constriction, 26–30; interorbital constriction, 21–25; breadth of rostrum over canines, 17–19; length of mandible from condyle, 80–87; length of maxillary toothrow exclusive of incisors, 40–46; length of mandibular toothrow exclusive of incisors, 47–52 (Cabrera 1910; Miller 1909). Mastoid breadth for 1 individual was 48 mm (Miller 1909). Bat-eared foxes have at least 3 upper and 4 lower molars (Fig. 2; Guilday 1962; Huxley 1880; Macdonald 2001; Nowak 1999). Expansion of molar growth field has duplicated m1 and m2 at expense of carnassial teeth, which are shorter (Clutton-Brock et al. 1976).

DISTRIBUTION. Two allopatric populations occur in Africa (Fig. 3). *O. m. virgatus* occurs from Ethiopia and southern Sudan to Tanzania, whereas *O. m. megalotis* occurs from southern Zambia and Angola to South Africa (Pauw 2000). The southern subspecies extends as far east as Mozambique, Botswana, and Zimbabwe (Ginsberg and Macdonald 1990; Pienaar 1970) and is spreading into the Cape Peninsula and toward Cape Agulhas (Mills and Hes 1997).

FOSSIL RECORD. The earliest record is from the Later Pliocene Cave of Hearths locality, South Africa (Savage 1978; Savage and Russell 1983). Fossils of an extinct bat-eared fox, *Otocyon recki*, occur in the Late Pliocene–early Pleistocene sediments of Olduvai I, Tanzania (Savage 1978; Savage and Russell 1983).

FORM AND FUNCTION. Lower jaw has a steplike protrusion, called the subangular process, to anchor a large muscle for rapid chewing (Macdonald 2001). A modification of the digastric muscle allows opening and closing of jaw up to 5 times/s (Maas 1993; Malcolm 1986). Ears jet backward as the bat-eared fox chews and regain their normal position once the rapid chewing episode ends. Specialized soft diet of the bat-eared fox is not reflected in an increase of shearing facets of molars (Kieser 1995). Robust dentinal development, blunted pulp-horns, and multicuspal molars

FIG. 1. Photograph of an adult *Otocyon megalotis* from Tanzania. Used with permission of the photographer W. Stanley.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult *Otocyon megalotis virgatus* of unknown sex (museum of deposit, Field Museum of Natural History, Chicago, Illinois, catalog no. FMNH 106024). Used with permission of the photographer R. Banasiak.

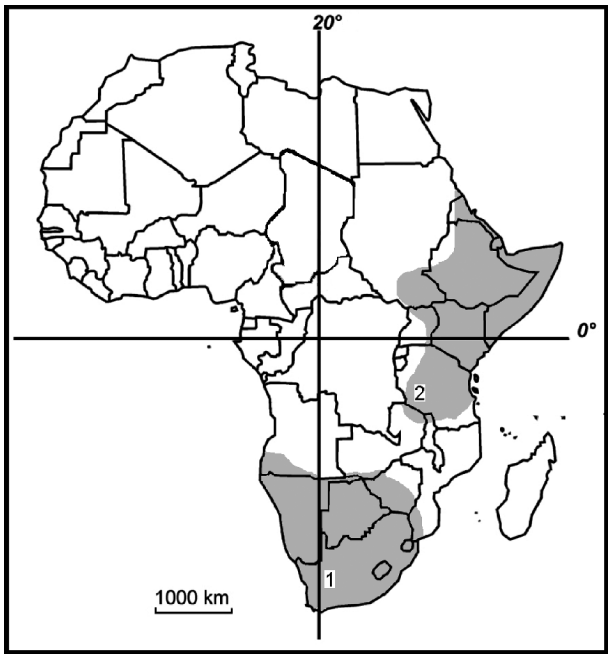

FIG. 3. Geographic distribution of subspecies of *Otocyon megalotis*. 1, *O. m. megalotis*; 2, *O. m. virgatus*. Map redrawn from Ginsberg and Macdonald (1990), Mills and Hes (1997), and Macdonald and Sillero-Zubiri (2004).

characterize bat-eared fox dentition (Kieser 1995). Dental formula is i 3/3, c 1/1, p 4/4, m 3–4/4–5, total 46–50 (Macdonald 2001).

Otocyon megalotis has the least overlapped cerebellum of all foxes. Frontal lobes are low and wide. Length of cruciate sulcus and length and bilateral constriction of proreal gyrus are variable and affected by size of brain (Lyras and Van Der Geer 2003).

Large ears of *O. megalotis* serve a thermoregulatory function (Maas 1993). Bat-eared foxes have not been observed drinking from free sources of water (Lamprecht 1979). Female bat-eared foxes have 4–6 mammae (Pauw 2000).

ONTOGENY AND REPRODUCTION. Breeding season occurs from June to September in the Serengeti, in January in Uganda, and reproduction may occur year-round in some parts of east Africa (Ginsberg and Macdonald 1990; Malcolm 1986). In the Kalahari, pair bonding, as evidenced by marking behavior, occurs in July and August (Nel 1984). Breeding is seasonal and locally timed such that births coincide with rains and peak insect densities. In east Africa, pups are born from late August to late October (Malcolm 1986) and in the Kalahari from September to November (Nel 1984). Births in Botswana occur from October to December (Nel et al. 1984). Gestation period is ca. 60–70 days (Bekoff 1983). Litter size ranges from 1 to 6 young. Newborn mass is ca. 100–140 g (Nowak 1999). Lactation lasts from 14 to 15 weeks (Lamprecht 1979). Most young disperse when ca. 5–6 months old and sexual maturity occurs at 8 or 9 months. Some young females stay with their family group to breed. Bat-eared foxes are primarily insectivorous, but usually do not bring insect prey back to the den. Adults carry some vertebrate prey to the young (Pauw 2000). Young bat-eared foxes depend heavily on milk (Malcolm 1986; Pauw 2000).

ECOLOGY. Bat-eared foxes are most common in short grass habitat (height of grass, 100–250 mm) and savanna in arid and semiarid regions, but will hide in tall grass or thick shrubs when threatened (Lourens and Nel 1990; Mackie and Nel 1989; Mills and Hes 1997; Waser 1980). During high winds and low temperatures, bat-eared foxes rest in vegetation or in self-dug dens (Lourens and Nel 1990). Bat-eared foxes modify existing holes and make use of small holes to seek shade in the middle of the day. *O. megalotis* prefers bare ground or grass kept short by ungulate grazing or burning (Malcolm 1986; Nowak 1999) and often rests under *Acacia* trees in South Africa (Dean et al. 1999).

Bat-eared foxes use their large ears to locate prey items. The harvester termite (*Hodotermes mossambicus*) comprises up to 80–90% of diet (Bothma 1966; Bothma et al. 1984; Kok and Nel 1992). Superimposed distribution maps of bat-eared foxes and harvester termites overlap by 95% (Mackie and Nel 1989). In areas without *Hodotermes*, bat-eared foxes consume other termite species; *Odontotermes* constitutes more than 90% of the diet in parts of Kenya (Malcolm 1986). Other invertebrates consumed by *O. megalotis* include ants (Hymenoptera), beetles (Coleoptera), crickets and grasshoppers (Orthoptera), millipedes (Myriapoda), moths and their larval forms (Lepidoptera), scorpions (Scorpionida), and sunspiders (Solifugae—Kuntzsch and Nel 1992; Nel 1978). Other food items include birds, small mammals, and reptiles (Andrews and Nesbit Evans 1983; Berry 1981). Bat-eared foxes inadvertently eat vege-

table matter, such as grass, while foraging and eating insects (Koop and Velimirov 1982). Berries, seeds, and wild fruit also are consumed. Bat-eared foxes move in a straight line from their den to berry trees and eat berries as the berries drop (Kuntzsch and Nel 1992). Taking of birds and carrion represents an advantageous opportunity rather than preference (Berry 1981). Seeds (fleshy-fruited shrubs, forbs, and mesembs) in scats of *O. megalotis* will germinate (Milton and Dean 2001). Bat-eared foxes refused to eat snouted harvester termites (*Trinervitermes trinervoides*) experimentally mixed with oil and added to their diets, presumably because bat-eared foxes do not tolerate chemical defense secretions of the termite soldiers (Richardson and Levitan 1994).

Otocyon megalotis can be diurnal or nocturnal, depending on season and circumstances (Koop and Velimirov 1982). Diurnal activity is closely associated with activity of insects, especially harvester termites (Koop and Velimirov 1982). *O. megalotis* located in the dry bed of the Nossob River, Kalahari Gemsbok National Park, South Africa, spent 70–90% of their time foraging and feeding, and their activity varied throughout the year. In winter, bat-eared fox groups in the riverbed were active during the day, and all individuals observed at night were lying down and presumably sleeping (Nel 1978). During the South African midsummer months of December and January, the activity cycle is reversed. Individuals were active well into the night and morning (Nel 1978).

Reported home range sizes vary from 0.3 to 3.5 km^2. Home ranges of groups show substantial or little overlap. Bat-eared foxes prefer clumped prey (termite colonies); this leads to higher densities and smaller home ranges of bat-eared foxes when feeding on termites (15–19 foxes within 0.5–5.3 km^2) than when consuming other prey. Home ranges are smaller during the South African winter when termites comprise a larger percentage of the diet than during summer (Mackie and Nel 1989).

Group size varies with time of year and ranges from 2 to 15 foxes (Mackie and Nel 1989; Malcolm 1986; Nel et al. 1984; Nowak 1999; Waser 1980). The father guards the den and pups while the mother forages to maintain milk production (Malcolm 1986; Nel 1984). Family groups forage together from December to July, after which the groups break up. A group size of 2 occurs most frequently (Malcolm 1986). Larger groups of adults consist of parents with their full-grown offspring (Lamprecht 1979). Known pairs and groups of bat-eared foxes were not found the following breeding season in a given area, signifying that bat-eared foxes do not use the same area year after year (Lamprecht 1979). Outside the breeding season, bat-eared foxes leave their home ranges when the grass becomes too high.

Otocyon megalotis usually ignores ungulates. Bat-eared foxes also ignore white-tailed mongooses (*Ichneumia albicauda*) and bands of dwarf mongooses (*Helogale parvula*) and banded mongooses (*Mungos mungo*—Malcolm 1986). Bat-eared foxes are wary of larger mammalian carnivores such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) chase foxes (Malcolm 1986), and a pack of African wild dogs specialized in hunting bat-eared foxes (Rasmussen 1996). Brown hyenas (*Parahyaena brunnea*), cheetahs, leopards (*Panthera pardus*), and lions have captured adult bat-eared foxes; black-backed jackals (*Canis mesomelas*) are the biggest threat to bat-eared fox pups (Pauw 2000). Bat-eared fox pups take refuge in dens with small entrances to discourage entrance by larger mammalian carnivores (Arjo et al. 2003). *O. megalotis* mobs species that come close to breeding areas, including black-backed jackals, slender mongooses (*Galerella sanguinea*), spotted hyenas, and white-tailed mongooses. Large raptors, such as martial eagles (*Polemaetus bellicosus*), can catch adult bat-eared foxes in open areas (Macdonald and Sillero-Zubiri 2004; Malcolm 1986). When pursued by mammalian carnivores and avian predators, bat-eared foxes change directions quickly, and thus increase their chances of escape. African rock pythons (*Python sebae*) have killed and eaten bat-eared foxes (Macdonald and Sillero-Zubiri 2004).

Otocyon megalotis contracts and spreads rabies (Bengis et al. 2002; Courtin et al. 2000; East et al. 2001), canine distemper virus (Carpenter et al. 1998; Van de Bildt et al. 2002), and canine parvovirus (Steinel et al. 2000). *Trichinella nelsoni* was identified in 1 bat-eared fox from the Serengeti ecosystem, Tanzania (Pozio et al. 1997). Outbreaks of rabies from 1986 to 1989 accounted for 90% of adult deaths in 1 population of bat-eared foxes (Maas 1993). In the Serengeti, rabies epidemics are the most common cause of mortality during times of adequate termite numbers and density (Ginsberg and Macdonald 1990). A captive bat-eared fox lived 13 years and 9 months (Jones 1982).

Otocyon megalotis has some commercial use; native people in Botswana hunt bat-eared foxes from April to July for pelts, which they trade (Ginsberg and Macdonald 1990; Kingdon 1977). Bat-eared foxes are an efficient and important predator on harvester termites, which are considered a serious pest of rangeland (Nel 1967).

BEHAVIOR. Bat-eared foxes are gregarious (Nel and Bester 1983). They forage as a group, rarely move >200 m from another individual, and are usually <30 m apart in open terrain. They rest together and frequently allogroom (Nel and Bester 1983). Communal foraging by family groups is an antipredator strategy and a method of exploiting time-dependent insect patches (Lamprecht 1979). Bat-eared foxes are usually monogamous; however, polygyny and allonursing occur (Pauw 2000).

Visual displays are important in communication. Muzzle, eye region (mask), and especially ears and tail are important sources of visual signals. When a bat-eared fox is looking intently at an object, such as a conspecific or jackal, head is held high with eyes open, ears erect and directed forward, and mouth closed (Nel and Bester 1983). When showing fear or submission, such as when approached by a predator or another bat-eared fox, ears are pulled back against head and head is held low. This display can grade into a grin with head still low, mouth slightly open, and lips pulled back (Nel and Bester 1983).

Black tip and dorsal stripe of tail are effective signaling devices. Position of tail varies from hanging down to erect and arched in an inverted U-shape. Arched tail position is evident during encounters involving dominance, threat, or aggression. It is also used during sexual arousal, play, and defecation. Straight horizontal tail positions are used while running, such as when chasing other species or fleeing danger (Nel and Bester 1983). In extreme cases of threat, piloerection of hair on neck, shoulder, rump, and tail can occur, increasing visual size of the fox. Piloerection is commonly directed at approaching predators and occurs in conjunction with an arched back and tail.

Greeting involves visual and olfactory signals. Bat-eared foxes recognize individuals up to 30 m away. When recognition occurs, bat-eared foxes ignore the individual, stare intently, and sometimes approach slowly or attack without any displays. The approach display usually functions as a form of symbolic submission, which includes a lowered head, extended neck, pulled back ears, and muzzle pointing toward the corner of the mouth of the recipient. The approach display is acknowledged by the recipient with a high head–tail down posture (Nel and Bester 1983).

Bat-eared foxes use few loud vocalizations. Vocalizations are either contact calls or warning calls and occur more frequently during winter. Contact calls are soft and do not function over long distances. Warning and mobbing calls are high-pitched and travel farther than contact calls, but are less frequent. Adults use contact calls to call pups to or from a den, and to call each other over to a productive feeding area. Warning and mobbing calls are used to warn other bat-eared foxes of an approaching predator (Nel and Bester 1983).

Bat-eared foxes use 3 postures when urinating: lean forward, raised leg, and squat. For physical urination (function is simple elimination; not directed at a particular object or previous urination), males commonly use the lean forward posture and females use the squat posture. When marking with urine (directing urine onto a particular object, previous urination, or feces), males use the raised leg posture and females squat. Marking with urine occurs more frequently in winter than in summer. Double marking sometimes occurs, in which the female marks 1st, and then the male places a mark over her mark. Females begin to mark with urine when coming into estrus; frequency of male marking does not change in response to a female becoming receptive (Nel and Bester 1983).

Use of glandular secretions for communication is unknown in bat-eared foxes. Scratching, other than digging for food, is absent. Digging is considered an important aspect of food finding for *O. megalotis* and is energetically expensive (Koop and Velimirov 1982). Smells are important during bodily contact. Physical contact occurs mainly when resting together and during approach situations (Nel and Bester 1983).

Huddling by pups and adults is common, and allogrooming between young and adults and between adults occurs throughout the year (Lamprecht 1979). During huddling, the chin of 1 bat-eared fox usually rests on the rump of another. During allogrooming, most attention is given to the face, and mask is used as a grooming invitation (Kleiman 1967). Allogrooming is the predominant social interaction between adults. When adults return to the den, pups often lick and nibble at the muzzle, but no regurgitation occurs. This behavior continues into adulthood (Nel and Bester 1983). Adults and young engage in play, usually after a rest or when foraging. Play can be brief or last several minutes. Play usually consists of chasing and more rarely wrestling.

Bat-eared foxes have not been observed caching food or fighting over food items (Lamprecht 1979) and in zoos usually abandon surplus meat. At 1 zoo, bat-eared foxes were fed horsemeat, live mice, fruits, vitamins, and minerals (Rosenberg 1971).

GENETICS. Diploid number for *O. megalotis* is 72 (Geffen et al. 1992; Wayne 1993). Autosomal complement consists of 35 pairs, almost all of which are acrocentric. Number of metacentric and submetacentric chromosomes is undefined (Chiarelli 1983).

REMARKS. Vernacular names include big-eared fox, black-eared fox, cape fox, Delalande's fox, Delande's fox, Delandi's fox, eared dog, and motlosi. *Otocyon* comes from the Greek words *otus* meaning "ear" and *cyon* meaning "dog" in reference to the large ears and doglike appearance of the fox. Specific name *megalotis* comes from the Greek words *mega* and *otus*, meaning "large eared." Placement of the bat-eared fox into its own subfamily is not generally accepted (Darbre and Lehmann 1976).

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