

Felis margarita (Carnivora: Felidae)

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Abstract: *Felis margarita* Loche, 1858 is a felid commonly called the sand cat. It is 1 of 6 species in the genus *Felis*. One of the smallest of the wild cats, *Felis margarita*, is adapted behaviorally and morphologically to live in desert environments. Prey includes rodents, birds, reptiles, and arthropods. This species has a wide, but disjunct distribution through northern Africa, the Arabian Peninsula, and southwest and central Asia. *F. margarita* occurs at low densities throughout its range and is listed as “Near Threatened” by the International Union for Conservation of Nature and Natural Resources due to habitat degradation and its low and potentially declining population. *F. margarita* is bred in zoos in North America and Europe.

Key words: Africa, Arabia, Asia, desert carnivore, felid, sand cat

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Felis margarita Loche, 1858

Sand Cat

Felis margarita Loche, 1858:50. Type locality “les environs de Négonça (Sahara) [Algeria].” Type location was a misprint of Négousa (Rosevear 1974).

Felis marginata Gray, 1867:275. Incorrect subsequent spelling of *Felis margarita* Loche, 1858.

Felis caligata margaritae: Trouessart, 1897:363. Name combination and incorrect subsequent spelling of *Felis margarita* Loche, 1858 (see “Nomenclatural Notes”).

Felis libyca margueritei: Trouessart, 1904:273. Name combination and incorrect subsequent spelling of *Felis margarita* Loche, 1858.

Felis ocreata margueritei: Trouessart, 1905:386. Name combination and incorrect subsequent spelling of *Felis margarita* Loche, 1858.

Eremaelurus thinobius Ognev, 1927:356. Type locality “Repetek, Transcaspian region.”

Felis ocreata margaritae: Antonius, 1929:375. Name combination and incorrect subsequent spelling of *Felis margarita* Loche, 1858.

Felis lybica margaritae: Koller, 1930:1. Name combination and incorrect subsequent spelling of *Felis margarita* Loche, 1858.

Otocolobus margarita: Heptner and Dementiev, 1937:240. Name combination.

Felis thinobius: Pocock, 1938a:45. Name combination.

Felis margarita margarita: Pocock, 1951:139. Name combination.



Fig. 1.—Adult *Felis margarita*. Photograph courtesy of Nancy Vandermeij used with permission.

Felis margaritei Dekeyser, 1955:279. Incorrect subsequent spelling of *Felis margarita* Loche, 1858.

CONTEXT AND CONTENT. Order Carnivora, suborder Feliformia, family Felidae, subfamily Felinae. Wozencraft (2005) recognized 6 subspecies: the 4 subspecies listed below, *F. m. airensis* Pocock, 1938b, and *F. m. meinertzhageni* Pocock, 1938a. This account follows Wilson and Mittermeier (2009) who considered *F. m. airensis* and *F. m. meinertzhageni* to be synonyms of *F. m. margarita* and recognized only 4 subspecies:

- F. m. harrisoni* Hemmer, Grubb and Groves, 1976:301. Type locality “northern edge of Umm as Samim, Oman, 21° 55' N, 55° 50' E.”
- F. m. margarita* Loche, 1858:50. See above.
- F. m. scheffeli* Hemmer, 1974a:32. Type locality “Nushki-Wüste, Westpakistan.”
- F. m. thinobia* (Ognev, 1927:356). See above.

NOMENCLATURE NOTES. Captain Victor Loche, a naturalist, described *Felis margarita* from a specimen collected in the northern Sahara (Loche 1858). This species was named in honor of General Jean Auguste Margueritte who was commandant of the French army unit stationed in Algeria in the 1850s (Loche 1858; Qumsiyeh 1996). The holotype of *F. margarita* was originally in Loche’s personal collection but has disappeared and is likely lost (Haltcnorth 1953; Schauenberg 1974; Kowalski and RzebiK-Kowalska 1991). Other names for the sand cat include sand dune cat, General Margueritte’s cat (English), chat des sables (French), sandkatze (German), gato de las arenas, gato del Sahara (Spanish), qit el ramel, qit ramli, biss ramli (Arabic), gorbesh sheni (Farsi, Iran), hattul holot (Israel), sevin (Kazakh), peshaya koshka, barchannaya koshka (Russian), qareshtar, aghsheter (Tamahaq, central Sahara), and mushuk (Uzbek—Nowell and Jackson 1996).

Rosevear (1974) speculated that Loche in naming *F. margarita* had intended to use the correct spelling of General Margueritte’s name, but a printing error occurred, causing the second “t” from Margueritte’s name to be dropped. Rosevear (1974) believes that it is unthinkable that Loche would have insulted a high-ranking officer and friend by deliberately attaching a feminine forename to an animal, which he hoped would commemorate this officer’s support. Trouessart (1897, 1904) eventually recorded what he thought was Loche’s original intention. However, the original spelling of the specific name *margarita* has been retained to avoid confusion because of its long and wide usage.

Ognev (1927) described a desert cat 1st collected in the Karakum Desert of Turkmenistan, 4,800 km away from Loche’s discovery, as *Eremaelurus thinobius*. The Transcaspian sand cat was named *Felis thinobius* by Pocock (1938a) and recognized as a separate species by Haltcnorth (1953) and Weigel (1961). Heptner and Dementiev (1937) argued that these sand cats belonged to *F. margarita*. No other evidence of the extent of the *F. margarita* distribution existed beyond these 2 widely separated areas until a specimen was collected in Arabia in the 1950s (Harrison 1968). The discovery of the sand cat in southwestern Balochistan, Pakistan, filled an important gap in the known distribution of this species (Lay et al. 1970). Loche’s *margarita* and Ognev’s *thinobius* were restudied and reclassified as subspecies of *F. margarita* (Heptner 1970; Hemmer 1974b; Schauenberg 1974; Wozencraft 2005; Wilson and Mittermeier 2009).

Heptner and Sludskii (1992) proposed that the forms *Felis airensis* and *F. meinertzhageni* from North Africa represented by only 1 specimen each were no more than individual variations of the nominate form, *F. margarita*. Hemmer et al. (1976) and Wilson and Mittermeier (2009) included *F. m. airensis* and *F. m. meinertzhageni* as synonyms under *F. margarita*.

DIAGNOSIS

Felis margarita is one of the most specialized felines (Heptner and Sludskii 1992). The specialization for desert life is seen in the general structure of the skull, its facial and cranial proportions, the position of the orbits, and especially in the maximal development of the auditory apparatus. This species has an extremely broad, flat face with large, triangular ear pinnae set low on the head and lacking an apical tuft (Sunquist and Sunquist 2002; Fig. 1).

Felis margarita has a stocky build with a tail that is about one-half the head and body length (Osborn and Helmy 1980; Sunquist and Sunquist 2002). In addition to ears set low on the head, *F. margarita* has relatively short legs giving this cat a low profile, a possible advantage in its sparsely vegetated desert environment (Osborn and Helmy 1980; Heptner and Sludskii 1992). The claws on the forelimbs are short, sharply curved, and highly compressed laterally. The claws on the hind limbs are less compressed, weakly curved, more elongate, and relatively blunt (Heptner and Sludskii 1992). The retractile apparatus of the claws is poorly developed.

The crown of the head is pale sandy with poorly defined striations. The upper and lower lips and chin are white, and throat has a faint buffy wash (Wilson and Mittermeier 2009). A faint reddish line runs from the outside corner of each eye down across the cheek (Roberts 1997; Sunquist and Sunquist 2002). The greenish yellow eyes are large and surrounded by a white ring. The rhinarium is black; the vibrissae are white and up to 8 cm long (Wilson and Mittermeier 2009). The backs of the ears are tawny brown at the base and black at the tip and the ears are directed outward from the crown (Roberts 1997). The inner ears are protected from blowing sand by a dense growth of long white hairs that spans the ear opening and continues along the ear margins to the apex (Rosevear 1974).

The pelage is typically pale sandy to straw gray in color, with the dorsum slightly darker than the venter (Sausman 1997b). The dorsum is usually without spots or stripes, but some individuals have a finely speckled pelage with black over the shoulders and silvery gray on the upper flanks (Sunquist and Sunquist 2002; Wilson and Mittermeier 2009). The venter is white. Two to 3 prominent black bands ring the forelegs. The last one-third of the tail has a varying number of black rings and the tail ends with a black tip. The thighs are marked with black barring and the flanks with 7–8 indistinct reddish-brown vertical stripes, broken into spots with black in places (Wilson and Mittermeier 2009). The palms and soles of the feet are covered with dense, long (15–30 mm), black fur that protects them from the hot desert substrate and assists in movement through loose sand (Heptner and Sludskii 1992). This characteristic makes the tracks of *F. margarita* indistinct and difficult to detect (Abadi 1993; Sunquist and Sunquist 2002).

In addition to being restricted to sandy and rocky desert habitat, *F. margarita* is distinguished from other potentially co-occurring small felids (*F. chaus*—jungle cat and *F. silvestris*—wildcat) by its pale pelage; prominent facial and foreleg

markings; large, broad, and low set ears that lack tufts; rounded cranium and shortened rostrum; and relatively broad paws that are covered with hair (Osborn and Helmy 1980; Harrison and Bates 1991; Serra et al. 2007).

The different races become gradually larger from west to east across the species range. Although there is considerable overlap in osteological measurements, *F. m. margarita* from North Africa has a relatively narrow skull, relatively small bullae, and small carnassials in comparison to *F. m. harrisoni* from the Arabian Peninsula (Hemmer et al. 1976; Goodman and Helmy 1986; Harrison and Bates 1991). *F. m. margarita* possesses brighter pelage with more distinct markings, buffy-white paws, and 2–6 tail rings compared to *F. m. harrisoni* with paler dorsal pelage, very white paws, and 5–7 rings on the tail (Hemmer et al. 1976).

GENERAL CHARACTERS

The *Felis margarita* adult has soft, dense fur, which protects it from the cold nighttime desert temperatures (Roberts 1997). There is no sexual dimorphism in pelage coloration, but there are marked age-related color differences. The pelage color of newborn *F. margarita* is pale yellow or chestnut-gray speckled with small brown, indistinct spots on the back and especially the flanks (Heptner and Sludskii 1992). A dark but indistinct band runs along the spine. The head has several dark longitudinal stripes, which widen at the neck. The tail has a black tip with 2 rings anterior to it and 3 or 4 dark spots along the dorsal surface. After the 1st molt, young grow pelage that is similar to adults, but darker on the dorsum along the spine and with small dark spots behind the shoulders. Banding on the legs and markings on the tail are more distinct than for newborns (Heptner and Sludskii 1992).

The *F. margarita* skull most closely resembles that of Pallas's cat (*Otocolobus manul*—Sunquist and Sunquist 2002; Fig. 2). The cranium is broad, the rostrum short, and the zygomatic arches wide. The anterior ends of zygomatic processes gradually taper in. The eye sockets are large, more spherical, and more forward directed than in *F. silvestris*. The tympanic bullae are more inflated than in other Old World cats. The skulls of both sexes are similarly proportioned, but the female skull is about 85% of the size of the male skull.

Hemmer et al. (1976) recognized *F. m. margarita* from North Africa as the smallest of the races. Mean (with range) skull measurements (mm) for 3 specimens of *F. m. margarita* were: occipital height 12.3 (12.0–13.0); bulla length 24.6 (24.0–25.0); bulla breadth 15.5 (14.5–16.0); carnassial length 10.2 (10.0–10.5); zygomatic breadth 66.7 (64.0–70.0); postorbital breadth 33 (32–34); infraorbital breadth 23.8 (23.0–25.5); interorbital breadth 17.3 (16.0–19.0); and skull length 89 (87–91—Goodman and Helmy 1986). *F. m. margarita* body measurements (mm) for 2 specimens mean (range) were: length of head and body 446 (420–471); tail length 266 (261–270); hind foot length 115 (110–120); and ear length 67 (64–70—Goodman and Helmy 1986).

Mean (with range) cranial measurements (mm) for 4 specimens of *Felis m. harrisoni* from the Egyptian Eastern Desert were: occipital height 13.6 (10.8–14.0); bulla length 25.3 (24.7–25.5); bulla breadth 15.8 (15.1–16.0); carnassial length 10.5

(10.5–11.5); zygomatic breadth 70.5 (66.0–74.0); postorbital breadth 33 (31–35); infraorbital breadth 25 (24–26); interorbital breadth 18.8 (17.9–19.5); and greatest length of skull 88.7 (86.0–90.5—Goodman and Helmy 1986). Mean (with range)



Fig. 2.—Dorsal, ventral, and lateral views of skull and a lateral view of mandible of *Felis margarita thinobia*. The specimen photographed was an adult male that was collected on 25 July 1966 by J. A. Anderson at Nushki, Pakistan, at an elevation of 1,068 m USMN (United States National Museum) 396080.

body measurements (mm) for 3 *F. m. harrisoni* specimens were: length of head and body 454 (440–452); tail length 270 (250–300); hind foot length 110 (110–110); and ear length 63.3 (57–68)—[Harrison and Bates 1991](#)).

Cranial measurements (mm) for males and females (mean, range, *n*; female data given in parentheses) for *Felis m. thinobia* collected from the Karakum Desert in central Asia were: greatest length of skull 95.4, 90.4–103.3, *n* = 7 (89.6, 82.0–98.7, *n* = 5); condylobasal length 89.0, 84.2–96.6, *n* = 7 (83.9, 76.4–92.0, *n* = 5); zygomatic width 73.0, 65.0–78.5, *n* = 7 (68.0, 60.9–76.1, *n* = 5); interorbital width 19.7, 17.6–23.6, *n* = 8 (18.4, 16.8–20.6, *n* = 4); postorbital width 34.1, 32.6–35.7, *n* = 6 (34.2, 33.3–35.2, *n* = 5); length of upper tooththrow 29.8, 28.3–31.3, *n* = 8 (28.5, 27.0–30.1, *n* = 5); and length of upper carnassial tooth 11.4, 10.6–12.0, *n* = 8 (11.1, 11.0–11.3, *n* = 5)—[Heptner and Sludskii 1992](#)). Minimum and maximum external measurements (mm; female data given in parenthesis) for *F. m. thinobia* from the same location were: head and body length 430–524, *n* = 12 (400–520, *n* = 6); tail length 278–290, *n* = 12 (232–310, *n* = 6); hind foot length 116–127, *n* = 12 (105–130, *n* = 5); and ear length 56–66, *n* = 12 (60–75, *n* = 5)—[Heptner and Sludskii 1992](#)).

Cranial measurements (mm; mean, range) of 2 Pakistan specimens of *Felis m. scheffeli* reveal these cats are smaller than those from Arabia and Turkmenistan in some respects, and very similar in most dimensions to 3 Saharan specimens: greatest length 85.8 (84.8–86.8); condylobasal length 80.2 (78.7–81.7); zygomatic breadth 64.4 (63.3–65.5); braincase breadth 42.0 (41.7–42.2); interorbital breadth 16.7 (16.6–16.8); tympanic bulla length 24.81 (24.0–25.5); tympanic bulla width 16.2 (15.9–16.5); diameter external auditory meatus 9.9 (9.7–10.1); upper tooththrow length (C–M1) 27.5 (26.6–28.3); mandibular tooththrow length (c–m1) 29.8 (28.9–30.6); P4 length 10.6 (10.2–10.9); and mandibular length 55.7 (54.5–56.9)—[Lay et al. 1970](#)). An adult male specimen of *F. m. scheffeli* from Nushki, Pakistan, had the following body measurements (mm): head and body length 570; tail length 280; hind foot length 118; and ear length 74 ([Roberts 1997](#)).

DISTRIBUTION

Felis margarita is found in sand and stony desert environments in a wide but disjunct distribution through the deserts of northern Africa, the Arabian Peninsula, and southwest and central Asia ([Nowell and Jackson 1996](#); [Sunquist and Sunquist 2002](#); [Wozencraft 2005](#); [Wilson and Mittermeier 2009](#); [Mallon et al. 2011](#); [Fig. 3](#)). The lack of *F. margarita* records in apparently suitable areas may reflect inadequate study rather than species absence ([Hemmer et al. 1976](#); [Nowell and Jackson 1996](#)). Consequently, distribution maps must be interpreted with caution.

In North Africa, *F. margarita* occurs in western Morocco and Western Sahara ([Hemmer et al. 1976](#); [Sliwa 2013](#)) east to Algeria ([Kowalski and Rzebik-Kowalska 1991](#); [Nowell and Jackson 1996](#); [Belbachir 2009](#)). Unconfirmed reports suggest its range may extend from the Adrar Souttoug Mountains of

Western Sahara into the Majabat al Koubra desert in Mauritania ([Hemmer et al. 1976](#); [Sliwa 2013](#)). Site records exist from Mali ([Mallon et al. 2011](#)), Niger ([Rosevear 1974](#); [Schauenberg 1974](#); [Dragesco-Joffé 1993](#)), and Tunisia ([Mallon et al. 2011](#)). Spoor has been found in Senegal, Chad, and Sudan ([Mallon et al. 2011](#)). Although sightings have been reported, no specimens have been collected in Libya ([Hufnagl 1972](#)) or in Egypt, west of the Nile River ([Goodman and Helmy 1986](#); [Mallon et al. 2011](#)). *F. margarita* may occur throughout the Sahara in appropriate habitat, but survey work is needed for confirmation ([Hemmer et al. 1976](#); [Kowalski and Rzebik-Kowalska 1991](#)).

Felis margarita occurs in Egypt, east of the Nile River into the Sinai ([Osborn and Helmy 1980](#); [Goodman and Helmy 1986](#)). *F. margarita* is found in Saudi Arabia ([Gasperetti et al. 1986](#); [Harrison and Bates 1991](#); [Strauss et al. 2007](#); [Mallon and Budd 2011](#)) extending south into Yemen and Oman ([Al-Jumaily 1998](#); [Mallon and Budd 2011](#)), eastward into Kuwait ([Khalaf-Sakerfalke von Jaffa 2007a](#)), Qatar ([Harrison and Bates 1991](#); [Hammer and Hammer 2005](#)), and United Arab Emirates ([Cunningham 2002](#)). This cat also occurs to the north in Jordan ([Hemmer 1978](#); [Bunaian et al. 1998, 2001](#)), in the Arava Valley ([Mendelssohn 1989, 1993](#); [Abadi 1993](#)) and the Gaza Strip in Israel ([Khalaf-Sakerfalke von Jaffa 2007b](#)), and in the Al-Talila Reserve in the Syrian Arab Republic near Palmyra ([Serra et al. 2007](#)). In 2012, *F. margarita* was recorded for the 1st time in Iraq in the Al Najaf desert ([Mohammad et al. 2013](#)).

Felis margarita occurs in high rolling sand dunes separated by flat stony plains at 900 m near Nushki, Pakistan ([Roberts 1997](#)). No connection between the *F. margarita* population in Balochistan province in Pakistan and the central Asia population via Afghanistan ([Habibi 2004](#)) or to the Arabian population via Iran and Syria ([Hemmer et al. 1976](#); [Nowell and Jackson 1996](#); [Sunquist and Sunquist 2002](#); [Mallon et al. 2011](#)) has been documented.

Felis margarita occurs east of the Caspian Sea from the Ustyurt Plateau in Kazakhstan and Uzbekistan to the northwest, south through the Karakum Desert in Turkmenistan to the Kopet Dag Mountains and the northern border of Afghanistan, and eastward through the Kyzylkum Desert in Uzbekistan and Kazakhstan to the Syr Darya River ([Sapozhenkov 1961](#); [Sabilaev 1962](#); [Sunquist and Sunquist 2002](#)). [Lay et al. \(1970\)](#) reported *F. margarita* collected from the Iranian Plateau suggesting the possibility of a connection between the central Asian and Arabian populations.

Distribution of the 4 subspecies ([Wilson and Mittermeier 2009](#)) is as follows: *F. m. margarita* ([Loche, 1858](#)) occurs from Western Sahara, Morocco, and Algeria southwards to northern Mali, Niger, and Egypt, east of the Nile River ([Goodman and Helmy 1986](#)). *F. m. harrisoni* ([Hemmer, Grubb and Groves, 1976](#)) occurs in the Arabian Peninsula and north into Jordan, Israel, the Syrian Arab Republic, and eastward to the deserts of Iraq ([Gasperetti et al. 1986](#); [Harrison and Bates 1991](#); [Abadi 1993](#); [Al-Jumaily 1998](#); [Cunningham 2002](#); [Khalaf-Sakerfalke](#)

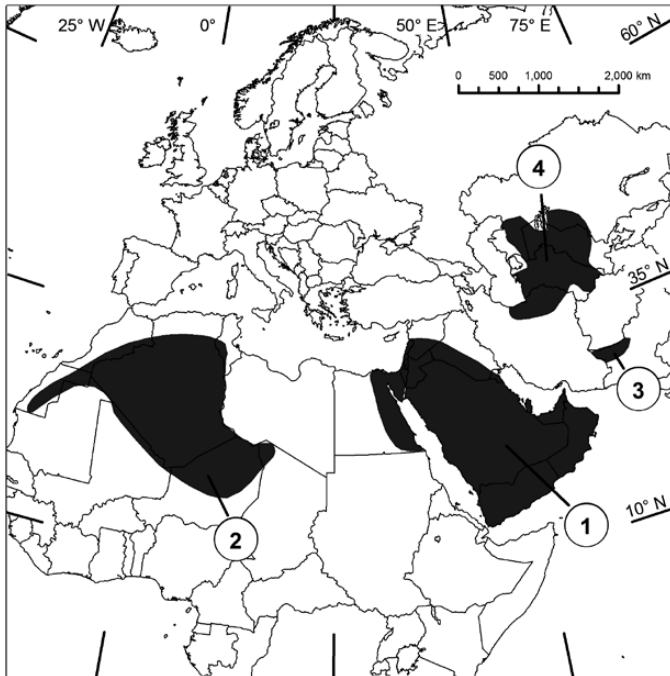


Fig. 3.—Geographic distribution of *Felis margarita*. Subspecies are: 1, *F. m. harrisoni* (Hemmer, Grubb and Groves, 1976); 2, *F. m. margarita* (Loche, 1858); 3, *F. m. scheffeli* (Hemmer, 1974a); and 4, *F. m. thinobia* (Ognev, 1927).

von Jaffa 2007a, 2007b; Strauss et al. 2007; Mallon and Budd 2011; Mohammad et al. 2013). *F. m. scheffeli* (Hemmer, 1974a) is restricted to the deserts of Pakistan. *F. m. thinobia* (Ognev, 1927) is found in the Karakum and Kyzylkum Deserts of Turkmenistan, Uzbekistan, and Kazakhstan south into northern Iran (Pocock 1951; Lay et al. 1970).

FOSSIL RECORD

Felis margarita jaw and skeletal elements were discovered in the Upper Pleistocene in El Harhourain I cave, Morocco (Aouraghe 2000). The cat mandible found at the Cueva de Don Gaspar archaeological site on Tenerife Island and dating from the 6th century AD is not from *F. margarita* as suggested by Sarrion Montañana (1985). This mandible was found to be from a juvenile *F. catus* (domestic cat—Hutterer 1990).

FORM AND FUNCTION

Felis margarita pelage is soft and dense with abundant soft wooly underfur (Heptner and Sludskii 1992). The winter pelage of *F. margarita* is long and dense. The mean length of guard hairs on the dorsum of *F. margarita* in the winter pelage was 55.3 mm and their mean thickness was 84.2 μ m. Heptner and Sludskii (1992) investigated the length and width of pelage hair by dividing the pelage into 4 layers. They reported hair length (mm) and width (μ m) decreased beginning at the pelage surface and ending at the underfur for each layer, respectively (49.0 and

100.5; 47.7 and 87.0; 43.9 and 74.0; and 38.4 and 32.0). The underfur was 30.0 mm long and 17.0 μ m wide. The mean density of the dorsum fur on 1 specimen was 4,532 hairs/cm² (Heptner and Sludskii 1992). The summer pelage lies closer to the skin and is shorter, sparser, and coarser in comparison to the winter pelage.

The skull of *F. margarita* is distinguished by several characteristics (Schauenberg 1974). The anterior end of the nasal bone is slightly raised, giving them a concave shape in side view. The nasal bones extend posteriorly beyond the frontomaxillary suture. The opening of the auditory meatus is extremely high and large (diameter is 10.5 by 6.8 mm). The lambdoidal ridge is well developed, the sagittal crest is prominent posteriorly, and the frontal ridges are continuous with the postorbital processes (Osborn and Helmy 1980). The tympanic bullae are greatly enlarged and separated by 4.0–7.5 mm.

Felis margarita has the dental formula of i 3/3, c 1/1, p 3/2, m 1/1, total 30. The canine teeth are relatively large and well developed. The inner cusp of the upper 3rd premolar is not well developed, but the protoconid is distinct (Osborn and Helmy 1980). The 2nd upper premolar is present in most specimens (Schauenberg 1974). The 1st lower premolar is without anterior or posterior secondary cusps; the 2nd lower premolar has well-developed secondary cusps, but the crown is scarcely widened behind (Rosevear 1974; Osborn and Helmy 1980; Harrison and Bates 1991).

The hearing of *F. margarita* appears to be more sensitive than other felid species, possibly an adaptation for hearing over long distances in their desert habitat. The enlarged tympanic bullae function as resonators for amplifying sounds and soil vibrations (Hemmer 1977). The ear pinnae are large, set low on the head, and inclined outward (Heptner and Sludskii 1992). Three bony features of the external and middle ear are distinguishing features. The bony ear canal is unusually prominent, the region between the bullae is unusually narrow because of the increased bullar width, and the anterior extreme of the bullae is further anterior than the glenoid fossa, a consequence of the long length of the bullae (Schauenberg 1974; Heptner and Sludskii 1992; Huang et al. 2002). Huang et al. (2002) reported dimensions (mean \pm SE) of the *F. margarita* external ear: pinna flange area 14.4 \pm 0.94 cm² (n = 8), cartilaginous ear canal cross-sectional area 59.2 \pm 3.3 mm² (n = 8), and ear canal length 28.3 \pm 0.85 mm (n = 8). In comparison to *F. catus*, the mean cross-sectional area of the ear canal at the midpoint is roughly 3 times larger and the ear canal length is 2 times larger in *F. margarita*.

The large external ear canals and auditory bullae of *F. margarita* suggest that this species may be adapted to absorb more acoustic power at frequencies below 2 kHz and especially at frequencies < 0.8 kHz than *F. catus* (Huang et al. 2002). The frequency spectrum for intense mew calls of *F. margarita* is mainly restricted to this range. Huang et al. (2002) predicted from measurements and model calculations that the hearing sensitivity of *F. margarita* is about 8 dB greater than in *F. catus* for frequencies below 2 kHz. Considering sound attenuation patterns in open desert environments, Huang et al. (2002) suggested that this

increased sensitivity extends the hearing range of *F. margarita* beyond that of *F. catus* by 0.4 km at 0.5 kHz.

The baculum of *F. margarita* is completely ossified, and its length does not exceed 3 mm (Schauenberg 1974). Slender and straight, the baculum is convex dorsally. Its base is greatly expanded and flattened dorsoventrally. The ventral surface is strongly concave and possesses 2 lateral rounded protuberances, parallel to the axis of the bone. The distal end terminates in a blunt tip (Schauenberg 1974).

Crissey et al. (2003) investigated serum concentrations of lipids, vitamins A and E, and carotenoids in healthy and captive *F. margarita*. The serum concentrations of these nutrients influence normal growth, reproduction, and general health of *F. margarita*. Serum lipid concentrations (mean \pm SE; $n = 4$) recorded were for total cholesterol (3.5 ± 0.3 mmol/l), total triacylglycerides (0.33 ± 0.06 mmol/l), high-density lipoprotein cholesterol (2.4 ± 0.4 mmol/l), and low-density lipoprotein cholesterol (0.9 ± 0.1 mmol/l). Serum concentrations (mean \pm SE; $n = 8$) of vitamin A (retinol, retinyl stearate, and retinyl palmitate), vitamin E (α - and γ -tocopherol), and carotenoids (β -carotene) were: retinol $1,154 \pm 115$ nmol/l; retinyl palmitate $2,786 \pm 290$ nmol/l; retinyl stearate $4,882 \pm 1,318$ nmol/l; α -tocopherol 27.9 ± 3.0 μ mol/l; γ -tocopherol 312 ± 34 nmol/l; and β -carotene 410 ± 65 nmol/l (Crissey et al. 2003).

ONTOGENY AND REPRODUCTION

Ontogeny.—*Felis margarita* young are born helpless, blind, and with their ear passages closed, but covered with fur (Heptner and Sludskii 1992). The body measurements (mm) of a newborn were: head and body length 143; tail length 58; hind foot length 32; and ear length 9 (Heptner and Sludskii 1992). Birth mass of 2 newborns was 39 g (Scheffel and Hemmer 1974) and 50 g (Dragesco-Joffé 1993). The mean mass of 4 stillborn *F. margarita* young was 72 g (range 70–75 g) and the mean mass of 4 living newborns was 71 g (range 56–84 g—Sliwa 2013). A male 2–3 days old weighed 108 g and a female of the same age weighed 105 g (Heptner and Sludskii 1992). Young grow rapidly gaining roughly 12 g/day during the first 3 weeks of postnatal life (Hemmer 1977); their eyes open at 11–14 days (range 12–16 days). *F. margarita* young begin walking at 21 days (range 20–22 days) and eat solid food at 5 weeks.

Felis margarita young could become independent as early as 4 months (Dragesco-Joffé 1993) but normally are relatively independent by about 6–8 months of age (Sausman 1991). *F. margarita* young reach three-quarters of adult size by 5 months (Heptner and Sludskii 1992; Dragesco-Joffé 1993). Two young *F. margarita* caught in the Kyzylkum Desert in late August had body lengths of 38 mm; young cats caught in mid-September had a body length of 48 mm (Heptner and Sludskii 1992). At about 9 months of age, a male from the Karakum Desert had a body length of 390 mm and a mass of 1,720 g (Heptner and Sludskii

1992). At 10–11 months of age in central Asia, male weight was 1,720–3,050 g ($n = 5$) and may equal or exceed that of an adult female (1,350–2,800 g—Heptner 1970; Sunquist and Sunquist 2002). Both sexes reach sexual maturity at 9–14 months (Mellen 1989; Dragesco-Joffé 1993).

In central Asia, adult males weighed 3,350–3,500 g (Heptner and Sludskii 1992). Weights of wild *F. margarita* adults from Turkmenistan varied from 2,100 to 3,400 g for males ($n = 12$) and 1,400 to 3,100 g for females ($n = 5$ —Heptner 1970). The mean weight of 4 males from Pakistan was 2,780 g (range 1,350–3,100 g—Sunquist and Sunquist 2002). Two adult males from the Sinai weighed 2,139 and 2,674 g (Goodman and Helmy 1986).

Reproduction.—In captivity, *Felis margarita* is not a seasonal breeder and may breed more than once per year (Mellen 1989; Sausman 1991). In wild *F. margarita*, the reproductive season depends upon location, but the potential for 2 litters per year exists (Sunquist and Sunquist 2002). Births are reported from January to April in the Sahara (Dragesco-Joffé 1993). Young *F. margarita* have been found in March and April and a 6-week-old litter was found in October in Balochistan, Pakistan (Roberts 1997). *F. margarita* litters from this area typically have either 2 or 3 young. In Turkmenistan, births occur during April and nursing-young have been taken from burrows in late April and May (Heptner and Sludskii 1992). In many areas where *F. margarita* occurs, the best vegetation growth is in March and April, and many rodents breed during this time providing an abundant food resource (Roberts 1997). Differences in climate or resource availability influence breeding season length.

Felis margarita young may be born at almost any time during the year in captivity. However, most births (> 50%) occur in March, April, June, and August. Breeding is highest in March and April (15% of litter births) and lowest during November and December (2% and 4%—Breton 2013). Breton (2013) reports a mean litter size in captivity of 2.7 young ($n = 234$), slightly lower than the 2.9 young per litter ($n = 25$) reported by Mellen (1989). A litter size exceeding 4 is very rare (< 5%), but a litter of 8 has been reported (Breton 2013). Based on 9 *F. margarita* litters from the deserts of Turkmenistan and Uzbekistan, 2–5 young are born per litter, most often 3, in April (Heptner and Sludskii 1992).

Of the 734 captive births recorded in the *F. margarita* studbook, 30% of the young died before day 30 and 13% of the subadults died within their 1st year (Breton 2013). Between years 1 and 10, subadult and adult mortality was below 10%. Mortality increased after 10 years and only a few individuals lived beyond 16 years of age. Over time, neonatal mortality has declined as husbandry practices have improved, especially since the late 1990s.

Based on studbook data, female *F. margarita* becomes sexually mature slightly before males (Breton 2013). The mean age at 1st reproduction for females is 3 years and 6 days; however, 50% of the breeding females gave birth to their 1st litter before

2 years and 4 months. The mean age of 1st reproduction for males was 3 years and 59 days, although 50% of the males sired their 1st litter before 2 years and 9 months. The oldest female to give birth was 13 years and 11 months and the oldest male to sire a litter was 11 years and 11 months (Breton 2013). The shortest interval between births was 71 days, suggesting that females may come into heat 4–8 days after birth of a litter. The age-specific fecundity rate for both sexes reaches a maximum at 2–3 years of age and then begins to decline; the female fecundity rate declines more rapidly than that of the males (Breton 2013).

Herrick et al. (2005) studied aspects of the reproductive biology of *F. margarita* in captive cats. Ejaculates contained (mean \pm SE; $n = 10$) $43.5 \pm 11.0 \times 10^6$ total spermatozoa, with $77.0 \pm 2.3\%$ motility, $43.8 \pm 3.9\%$ normal morphology, and $93.1 \pm 1.3\%$ intact acrosomes. In response to exogenous gonadotropins given at random times during the estrus cycle, females ($n = 4$) produced 24.3 ± 5.6 follicles with 19.3 ± 5.1 total oocytes. Herrick et al. (2005) noted that in vitro fertilization using fresh spermatozoa could be a valuable strategy for genetic management of captive populations of *F. margarita*.

In central Asia, *F. margarita* molts twice per year, in the spring and at the end of the summer (Heptner and Sludskii 1992). Adult males and females caught March 23–April 3 still had winter pelage with very worn hairs, but no indications of a molt. The molt appears to begin in mid-April. An adult *F. margarita* caught in mid-June had summer pelage, which was relatively short and sparse versus the longer more dense winter coat.

ECOLOGY

Population characteristics.—*Felis margarita* is not well studied because this species lives in a harsh environment that is often remote, and these cats are nocturnal, subterranean, and secretive animals (Nowell and Jackson 1996). *F. margarita* occurs at low densities in disjunct populations throughout its range. No ecological explanation for the gaps in *F. margarita* distribution has been proposed despite seemingly appropriate habitat (Nowell and Jackson 1996). This species is often characterized as rare (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Sliwa 2013). Additional fine-scale distribution studies, estimates of home range size, and determinations of population density across the range of this species are needed. *F. margarita* populations are likely declining due to degradation of their desert habitat and related declines in prey abundance, but accurate information is lacking (Sunquist and Sunquist 2002; Wilson and Mittermeier 2009; Mallon et al. 2011).

There are few density estimates of *F. margarita* populations. Sliwa (2013) speculates that *F. margarita* densities may be very low in parts of the Sahara especially where habitat quality is low (e.g., shifting sand dunes). Sliwa (2013) also reported catching 11 cats in 375 km² in the Arava Valley in southeastern Israel. *F. margarita* abundance was found to be low (< 2 per 100 trap-nights) in a study in the Mahazat As-Sayd and Saja/Umm Ar-Rimth Protected Areas in central Saudi Arabia (Strauss

et al. 2007). Although more information is needed to confirm the population trend across the region, populations of *F. margarita* in the Arabian Peninsula are probably declining because their sand dune habitat continues to be lost (Abahussain et al. 2002; Al-Sharhan et al. 2003; Mallon and Budd 2011).

Felis margarita was common in the mid-1900s in central Asia where its abundance varied over time. An 8-year study in this area yielded 3 years with a higher density (2–3 cats per 100 km of survey route) and 5 years with lower density (1 per 100 km of survey route—Belousova 1993). The distribution of *F. margarita* appears to be declining in areas where human activity has negatively impacted its habitat and prey base (Heptner and Sludskii 1992; Wilson and Mittermeier 2009). The introduction of feral and domestic dogs and cats is another serious problem because of increasing competition, predation, and the potential for disease transmission. Snow cover in central Asia hampers hunting by *F. margarita*. For example, the severe winter conditions of 1953–1954 in the southern one-half of the Kyzylkum Desert with snow cover lasting for 3 months led to high *F. margarita* mortality. Following that winter, the number of *F. margarita* caught by fur traders declined 2–10 times. The population of *F. margarita* in the Chagai Desert of Baluchistan, Pakistan, was devastated by commercial collectors within a decade after their presence was discovered in the mid-1960s (Hemmer 1977; Roberts 1997). Although Nowell and Jackson (1996) indicated *F. margarita* still occurred widely in this area, this species is now considered endangered in Pakistan (Mallon et al. 2011).

Heptner and Sludskii (1992) speculated that in the mid-1900s, *F. margarita* populations in central Asia were stable despite harvests of 100–200 pelts per year. *F. margarita* was thought to be common in the Karakum Desert in the mid-1960s (Sunquist and Sunquist 2002). Belousova (1993) reported *F. margarita* being commonly sighted in the Ustyurt and Mangyshlak desert regions in western Uzbekistan and Kazakhstan and frequently found in the northern Kyzylkum Desert; however, some populations were declining because of development impacts.

Felis margarita is a solitary predator that hunts by walking, listening, and occasionally stopping to look around the area, rarely by siting and waiting (Sunquist and Sunquist 2002). This cat often travels long distances while hunting. Its paths are not regular and are probably influenced by den locations; the distances traveled apparently change with the seasons (Abbadi 1991, 1993). A radio-collared *F. margarita* male moved 8 km in 1 day during a study in Israel (Mendelssohn 1989). Males walked an average 5.5 km per night and females walked 3.2 km per night (Abbadi 1989). Two females each traveled 8 km per night, likely in search of a mate. Two *F. margarita* tracked in the Karakum Desert traveled 7 km during a summer night and 10 km during a winter night, respectively (Heptner and Sludskii 1992). On a winter day in the same area, 1 *F. margarita* covered 2 km while hunting.

Home range size may vary depending upon resource availability and competition for prey from sympatric carnivores (e.g., red fox [*Vulpes vulpes*], *F. silvestris*—Sunquist and Sunquist 2002). Home ranges of 3 radio-collared *F. margarita* males

overlapped in the Arava Valley in southeastern Israel (Abbadi 1991, 1993). One male traveled over a home range of 16 km². Home ranges of males and females appear to differ: a 2nd male traveled 17.1 km², an adult female traveled 9.4 km², and an adult female with young traveled 3 km² (Abbadi 1989). *F. margarita* in Jordan roamed over distances of up to 8–10 km² in its daily activities (Bunaian et al. 2001).

Space use.—*Felis margarita* is the only cat to occur exclusively in deserts, inhabiting vegetated sand desert, sand dune plains, sand and gravel desert, and rocky desert habitats (Schauenberg 1974; Hemmer et al. 1976; Gasperetti et al. 1986; Goodman and Helmy 1986; Harrison and Bates 1991; Abbadi 1993; Dragesco-Joffé 1993). This species is more common in sandy desert and less common where the substrate is compacted or composed of clay. The distribution and abundance of rodent prey influences where *F. margarita* occurs (Nowell and Jackson 1996). Its small-mammal prey often live clustered around vegetation and generally do not extend onto bare sand, especially during drought years.

In the Sahara, *F. margarita* occupies flat and open substrate covered with unstable sand with little grass or few shrubs (Dragesco-Joffé 1993). In the Arava Valley in southeastern Israel, *F. margarita* prefers open, sandy areas with shrubs (Abbadi 1993). In the United Arab Emirates, *F. margarita* inhabits areas where inter-dune gravel flats are bordered by sparsely vegetated sand dunes. *Haloxylon salicornicum* shrubs and *Pennisetum divinum* grass dominate the gravel flats (Cunningham 2002). In central Asia, *F. margarita* is typically found in desert areas among the sparsely vegetated ridges and sandy hills where various species of *Meriones* (jirds) are common (Sunquist and Sunquist 2002). *F. margarita* rarely occurs in areas of shifting sand where vegetation is lacking (Sunquist and Sunquist 2002). However, *F. margarita* appears abundant deep inside extensive sandy masifs where sand desert conditions are well developed and where compacted soils are absent or cover only a small area (Heptner and Sludskii 1992). This cat is rare in the sand and clayey plains of Ustyurt and in the Mangyshlak regions of Kazakhstan but is common in the southern Kyzylkum Desert.

Felis margarita inhabits an environment that experiences dramatic temperature variation. Daytime surface temperatures may approach 124°C and the air temperature can range up to 58°C in the shade, but night air temperatures are much lower, ranging down to –0.5°C (Yunker and Guirgis 1969; Goodman and Helmy 1986; Cunningham 2002). Air temperature during the day in the Karakum Desert can exceed 40°C in the summer; temperature on the desert surface can exceed 80°C (Sunquist and Sunquist 2002). It snows in the winter when temperatures may drop as low as –25°C (Heptner and Sludskii 1992).

Diet.—*Felis margarita* is an opportunistic feeder and takes prey when encountered. *F. margarita* eats mainly small desert rodents, although reptiles, small birds, and insects are also taken (Harrison and Bates 1991; Abbadi 1993; Qumsiyeh 1996; Roberts 1997; Bunaian et al. 1998, 2001; Sliwa 2013). These cats are capable of rapid digging to capture burrow-dwelling

rodents (Schauenberg 1974). *F. margarita* has also been observed leaving its den to feed on swarming locusts (Khan 1998). *F. margarita* is not known to scavenge but will cover large kills with sand and return later to feed (Dragesco-Joffé 1993). Most of the water in its diet is derived from its food. However, *F. margarita* will drink, if water is readily available. Unfortunately, the food habits of *F. margarita* are difficult to study because it covers its scats with sand obscuring the location (Hemmer 1977; Abbadi 1993). Like other felids, *F. margarita* is capable of eating large amounts of food when the food is available, but under normal circumstances probably consumes about 10% of its own body weight per day (Sunquist and Sunquist 2002).

The diet of *F. margarita* in the Sahara is dominated by small desert rodents, including spiny mice (*Acomys*), jirds, gerbils (*Gerbillus*), jerboas (*Jaculus*), and young cape hare (*Lepus capensis*)—Sliwa 2013). Other prey items include small birds, reptiles, and insects (Abbadi 1993; Dragesco-Joffé 1993; Khan 1998; Sliwa 2013). *F. margarita* is characterized by Saharan nomads as a proficient snake hunter, especially of horned and sand vipers (Dragesco-Joffé 1993). *F. margarita* hunts by stunning the snake using rapid blows to the head from its paws before killing it with a neck bite.

The distribution of *F. margarita* in Arabia coincides with the range of sand skinks (*Scincus*) and Arabian toad-head lizards (*Phrynocephalus arabicus*), which are important food sources where these species co-occur (Gasperetti et al. 1986; Sunquist and Sunquist 2002). These reptile species are diurnal foragers and likely taken by *F. margarita* during the day. Remains of spiny-tailed lizards (*Uromastix aegyptius*) found near *F. margarita* burrows in the United Arab Emirates also suggest that this cat may forage diurnally more than previously thought (Cunningham 2002). Abbadi (1991) observed *F. margarita* catch and eat a lesser Egyptian jerboa (*Jaculus jaculus*) and a gecko (*Stenodactylus*) at dawn.

Roberts (1997) suggests that *F. margarita* in the Nushki Desert, Pakistan, adapts its hunting to times when its prey are active. Rodents and reptiles are crepuscular foragers during the winter and are nocturnal foragers in the summer in this area.

Felis margarita stomach contents from cats collected in the Karakum Desert near Repetek in Turkmenistan ($n = 182$) indicated rodents dominated the diet; 65% of the stomachs contained rodent prey. Great gerbil (*Rhombomys opimus*—33.5%) and midday jird (*Meriones meridianus*—18.7%) dominated the *F. margarita* diet, but northern 3-toed jerboa (*Dipus sagittal*), comb-toed jerboa (*Paradipus ctenodactylus*), Tolai hare (*Lepus tolai*), long-clawed ground squirrel (*Spermophilopsis leptodactylus*) were also taken (Sapozhenkov 1961; Heptner and Sludskii 1992). The remaining 35% of the *F. margarita* diet in this area consisted primarily of reptiles and birds but also included insects and other arthropods.

During the summer in the Karakum Desert, *F. margarita* hunts predominantly in sand dune habitats and in the winter when most of the sand dune inhabitants hibernate, *F. margarita*

hunts among the white saxaul (*Haloxylon persicum*) and black saxaul (*Haloxylon aphyllum*) vegetation for Tolai hares and great gerbils (Heptner and Sludskii 1992). This cat also destroys bird nests, including those constructed in trees.

In the Kyzylkum Desert of Uzbekistan, the *F. margarita* diet as determined from stomach analysis ($n = 52$) is also dominated by sand-dwelling rodents, the great gerbil, comprises 88% of the diet (Mambetzhumaev and Palvaniyazov 1968; Lay et al. 1970). Jerboas are also important rodent prey species (Mambetzhumaev and Palvaniyazov 1968; Hemmer 1977) in this area.

Diseases and parasites.—Yunker and Guirgis (1969) recorded 19 species of parasitic Acarina from *Gerbillus* burrows in the Egyptian desert with *Androlaelaps marshalli*, *Haemolaelaps centropus*, *H. insculptus*, *Hirstionyssus craticulatus*, and *Hyalomma* being frequently collected ectoparasites. Because of the prominence of *Gerbillus* in the *Felis margarita* diet, these ectoparasite species likely infest *F. margarita* as well. Sapozhenkov (1961) reported fleas infesting *Gerbillus* co-occurring on *F. margarita* in Turkmenistan. Five *F. margarita* collected near Repetek, Turkmenistan, were infested with fleas (*Synosternus pallidus*, *Xenopsylla hirtipes*, and *X. gerbillii*). A tick (*Hyalomma asiaticum*) was also found on 1 *F. margarita* from this area. *F. margarita* from the northern Kyzylkum Desert is parasitized by fleas (*S. longispinus* and *S. pallidus*), which are typically found in association with the long-eared hedgehog (*Hemiechinus auritus*), another prey species (Heptner and Sludskii 1992).

Felis margarita collected from Bahrain had the following endoparasites: Cestoda: *Diplopylidium noelleri* and *Taenia krepkogorski*; Nematoda: *Ancylostoma braziliense* and *Rictularia affinis*; and Acanthocephala: *Echinopardalis atrata* (Bray 1972). *T. krepkogorski* was also reported for *F. margarita* in Turkmenistan (Heptner and Sludskii 1992). Sapozhenkov (1961) found *T. krepkogorski* as well as *Taenia taeniaeformis* and other helminthes infecting *F. margarita* in this region, probably acquired from gerbil and jerboa prey that were infested. All *F. margarita* examined by Sapozhenkov (1961) were infected by helminthes. Eight species of helminthes (*Hydatigera krepkogorskii*, *Dipylidium caninum*, *Diplopilidium* [*Diplopylidium*] *nölleri*, *Physaloptera praeputilialis*, *Vigisospirura skrjabini*, *Rictularia cahirensis*, *Toxocara mystax*, and *Unicinaria*) were collected from *F. margarita* in Uzbekistan (Heptner and Sludskii 1992). Helminthes, including *H. krepkogorskii*, *H. (Taenia) taeniaeformis*, *Diplopilidium (Diplopylidium) nölleri*, *Mesocestoides lineatus*, *R. affinis*, *Mesocestoides*, *Physaloptera*, and *Dipylidium*, were identified from *F. margarita* collected in Turkmenistan (Heptner and Sludskii 1992).

Morsy et al. (1999) investigated *F. margarita* in Saudi Arabia for infection with the *Leishmania* parasite to help identify the possible role of this cat in the epidemiology of leishmaniasis. They reported that 40% ($n = 10$) of the *F. margarita* examined were serologically and parasitologically positive for the *Leishmania* parasite, confirming that *F. margarita* may be

incidental or reservoir hosts of *Leishmania* species and that this species may play a role in the epidemiology of human leishmaniasis.

Felis catus is encroaching into habitat occupied by *F. margarita* in west central Saudi Arabia (Ostrowski et al. 2003). Populations of *F. margarita* were investigated at the Mahazat As-Sayd Protected Area in west central Saudi Arabia where this species occurs in sympatry with *F. silvestris*. Serological tests performed on *F. margarita* to determine its exposure to feline herpesvirus, feline calicivirus, feline coronavirus, feline panleukopenia virus, feline lentiviruses, and feline leukemia virus indicate that encroachment of *F. catus* represents a potential epidemiologic risk to *F. margarita* in this area (Ostrowski et al. 2003). A positive for feline leukemia virus was recorded for 7% of the *F. margarita* examined ($n = 14$). The rarity of wild cats in Israel may, in part, be due to their susceptibility to feline leukemia virus transmitted by feral cats (Ostrowski et al. 2003). The relative isolation of *F. margarita* may help prevent disease transmission from other mammal species.

Toxoplasmosis was confirmed as the cause of death of a young captive *F. margarita* in the United Arab Emirates (Pas and Dubey 2008; Dubey et al. 2010). Adult cats had high antibody titers to *Toxoplasma gondii* before pregnancy, suggesting that maternal immunity did not protect the young against infection with *T. gondii* and that maternal immunity might not have prevented transplacental transmission of the parasite.

Interspecific interactions.—The main predators of *Felis margarita* include larger birds of prey (e.g., Golden eagle—*Aquila chrysaetos*), snakes, and large mammalian predators (e.g., caracal—*Caracal caracal*, wolf—*Canis lupus*, golden jackal—*Canis aureus*, and likely feral and domestic dogs—Mendelsohn 1989; Abbadi 1991; Heptner and Sludskii 1992; Dragesco-Joffé 1993; Sliwa 2013). Juvenile *F. margarita* is also likely vulnerable to predation by the Eurasian eagle-owl (*Bubo bubo*) and red fox.

Interspecific competition for prey may also limit *F. margarita* populations. *F. margarita* is found in the Eastern Desert of Egypt living in association with the golden jackal, Rüppell's fox (*Vulpes rueppelli*), striped hyena (*Hyaena hyaena*), and *F. chaus* (Goodman and Helmy 1986). Rüppell's fox also co-occurs with *F. margarita* in the Mahazat As-Sayd Protected Area in Saudi Arabia (Strauss et al. 2007). In this area, the density of Rüppell's fox is 5 times greater than *F. margarita*, and both species rely heavily on small rodents for food. The larger Rüppell's fox density may result in interspecific competition for rodent prey that limits the abundance of *F. margarita* populations. *F. margarita* may be found living sympatrically with other carnivores, including *F. silvestris* and red fox in Israel (Abbadi 1993), red fox, Corsac fox (*V. corsac*), and less commonly *F. silvestris* in Turkmenistan (Heptner and Sludskii 1992). *F. margarita* also appears sensitive to human disturbance and habitat encroachment.

HUSBANDRY

Felis margarita was rarely found in zoos prior to 1967 (Sausman 1997a). Following the discovery and export of *F. m. scheffeli* from Pakistan in the late 1960s, the interest in its captive breeding increased significantly. The 1st individuals bred in captivity were primarily *F. m. scheffeli* (Witzenberger and Hochkirch 2013). Beginning in the late 1980s, the captive *F. margarita* population has grown rapidly; the international *F. margarita* studbook as of 31 January 2013 lists 174 cats in captivity at 44 facilities (Breton 2013). The European captive population is comprised only of *F. m. harrisoni*. The North American captive population consists of *F. m. harrisoni* and *F. m. harrisoni* × *F. m. scheffeli* hybrids (Breton 2013). *F. margarita* is 1 of 5 small cat species given priority for conservation in North American zoos (Herrick et al. 2005). However, it is likely that periodic introductions of genetic variability, longer generation intervals, and increases in population size will be required to maximize the long-term survival prospects for this species (Mallon et al. 2011).

Maintaining *F. margarita* in captivity, especially in northern hemisphere zoological parks, requires availability of warm and dry accommodations, especially in the winter and during rainy periods (Breton 2013). Historically, *F. margarita* has shown a susceptibility to respiratory infections often leading to death. The most common disease was infectious rhinotracheitis (Breton 2013). Captive *F. margarita* also died from enteritis, chronic bronchitis, liver degeneration, and myocarditis (Sausman 1997b). In recent years, the widespread use of domestic cat vaccines has proven to be an effective treatment for respiratory infections. However, captive sand cats are highly sensitive to toxoplasmosis, which can cause death (Breton 2013).

Captive *F. margarita* has been fed commercially available feline diets as well as freshly killed animals (e.g., chicks, pigeons, small mammals—Sausman 1997b). Crissey et al. (1997) compared the utilization of a dry kibble diet and a raw meat-based diet by captive *F. margarita*. *F. margarita* fed the dry kibble diet had lower digestibilities for dry matter, crude protein, and energy than cats fed a raw meat-based diet, suggesting that the dietary requirements of *F. margarita* may be different than those of *F. catus* (Crissey et al. 1997).

BEHAVIOR

Reproductive behavior.—*Felis margarita* is polyestrous (Hemmer 1977). In captivity, both sexes show pronounced behavioral changes during the days before and after copulation (Mellen 1989, 1993). One week before copulation, females show an increase in scent marking and cheek rubbing. Scent marking increased from 5 per hour during the week before copulation to a peak of more than 30 per hour at the time of copulation, and then declined back to 5 per hour in the week following mating (Mellen 1989, 1993). In contrast, the rate of

scent marking by males decreased during times of copulation. Males perform neck biting when mating and the mount lasts about 9 min.

Based on the behavior of captive *F. margarita*, Mellen (1989) estimated that estrus lasts 5–6 days. Copulation occurs frequently during estrus. Mellen (1989) reported that gestation lasts 66 days, longer than the 59–63 reported by Hemmer (1976), and is accompanied by increased calling and scent marking (Mellen 1989; Sunquist and Sunquist 2002). Captive *F. margarita* may give birth throughout the year, but limited records from the wild suggest that births are seasonal (Sunquist and Sunquist 2002).

Mellen (1993) reported selected reproductive data for captive *F. margarita*: the duration of mounts with intromission 8.83 ± 2.13 min ($n = 13$), length of estrus 5.25 ± 0.75 days ($n = 2$), gestation length 66.5 ± 0.5 days ($n = 2$), litter size 2.92 ± 0.21 , and male age at maturity (birth to 1st litter sired) 67.7 weeks. The typical copulatory sequence begins with the male approaching the female (Mellen 1993). The male grasps the female by the nape and mounts using the forelegs followed by hind legs. The female responds to the nape biting by adopting a lordosis posture and moving her tail to one side. The male follows with intromission and pelvic thrusting. Mounts resulting in intromission are followed by a copulatory cry (barely audible growl) by the female. The female then throws the male off and begins rolling on her back (typically lasting 5–30 s). Mellen (1993) found that a change in relative rates of some behaviors was the most reliable indicator of estrus and reproductive activity.

Communication.—*Felis margarita* vocalizations are similar to those of *F. catus*. Like *F. catus*, *F. margarita* may mew, growl, spit, hiss, scream, and purr, but some of their other vocalizations are quite different (Sunquist and Sunquist 2002). Their vocal repertoire includes the gurgle, a friendly, close contact call (Peters 1984). Both sexes use intense mew calls for multiple purposes including long-distance communication, attracting mating partners, predator avoidance, and calling young (Huang et al. 2002; Sunquist and Sunquist 2002). The intense mew calls of *F. margarita* are short (< 0.5 s), sharp calls, and typically several are uttered in rapid succession at medium–high pitch (Peters et al. 2009), reminding some workers of a small dog barking (Hemmer 1974b, 1977; Schauenberg 1974).

Peters et al. (2009) studied acoustic parameters of 119 intense mew calls by 2 *F. margarita* males including duration (mean, range; 275 ms, 160–490 ms), fundamental frequency (0.36 kHz, 0.15–0.53 kHz), and dominant frequency (0.63 kHz, 0.41–0.78 kHz). The frequency spectrum for *F. margarita* intense mew calls is mainly restricted to below 2 kHz, the range to which their ear is adapted (Huang et al. 2002). Peters et al. (2009) speculate that the spectral characteristics of *F. margarita* intense mew calls evolved to reduce call attenuation when propagating through desert habitats where vegetation is scarce or absent. Chan (2005) reported that *F. margarita* has lower mean acoustic thresholds (by 6–9 dB) between 0.25 and 5 kHz than other felid species that have been studied, supporting the hypothesis that *F. margarita* hearing is unusually sensitive.

Felis margarita also communicates using scent and claw marks on objects in their environment and by urine spraying (Wemmer and Scow 1977; Sunquist and Sunquist 2002). Scent marking is likely to be an important mode of communication in the barren landscapes where these cats live, although this behavior has not been studied. Both sexes rub their cheeks and heads on objects, leave claw marks on logs and branches, and spray urine. Scent marking behaviors observed by Mellen (1993) for 4 male and 5 female captive *F. margarita* included cheek and head rubbing against inanimate objects, sharpening claws (front paws used to scratch a surface), flehmen (open-mouth grimace), and urine spraying.

Miscellaneous behavior.—Social behavior represents only 1–2% of the time budget of captive small cats (Mellen 1989). Consequently, the rates of occurrence of various social behaviors are very low. The grooming behavior of *Felis margarita* is generally similar to that of *F. catus* (Hemmer 1977). Social behaviors recorded for *F. margarita* include spitting, hissing, growl, strike, strike using paw, anogenital sniff, social sniff, follow, displace, approach, and face off for both sexes (Mellen 1993). Males also exhibited mounting and nape biting. Females also exhibited lordosis and chase.

Wemmer and Scow (1977) studied contact patterns in *F. margarita*. Four patterns were common: rubbing, sniffing, biting, and patting with the forepaw. Body rubbing between siblings and between siblings and adults was infrequent. Sniffing was rare but was concentrated on the head–neck area when it occurred. Biting was concentrated on the head and neck, although other parts of the body were also bitten. Patting with the forepaw was directed primarily to the head and neck (ear, cheek, neck), less frequently to the tail, and infrequently to the hind legs and anogenital region (Wemmer and Scow 1977).

Bennett and Mellen (1983) observed a pair of *F. margarita* in captivity. These cats devoted the greatest amount of their time to pacing and resting. Social interactions occurred infrequently. The male marked and urinated/defecated more than the female. Only one of these cats was active at a time. The female paced and moved more during estrous periods.

Felis margarita is a solitary hunter with males and females coming together only for breeding. Adults travel extensively hunting in the desert, except when young are small (Sapozhenkov 1961). Because its legs are short and placed wide apart, *F. margarita* tends to graze the ground as it walks, often at a fast pace with occasional leaps (Sunquist and Sunquist 2002). However, *F. margarita* can sprint at speeds of 30–40 km/h for short distances (Dragesco-Joffé 1993). These cats are poor climbers and jumpers.

Felis margarita does not startle easily and often remains motionless with its chin resting on the ground until humans approach within a few meters (Sliwa 2013). When light is shown on this cat, *F. margarita* crouches low and closes its eyes so that there is no visible reflection. This behavior and the cryptic coloration of the pelage make *F. margarita* difficult to spot in the wild (Abbadi 1993). One interesting feature of *F. margarita*

behavior is its apparent tameness and lack of fear of humans (Lay et al. 1970; Goodman and Helmy 1986; Dragesco-Joffé 1993). Individual cats have been captured by hand when workers approached the cat from behind. Other individuals have been easily dug from their burrows.

Felis margarita is a prolific digger, an adaptation for hunting burrowing rodents and for constructing burrows. Their claws are not very sharp due to the lack of places to sharpen them (Dragesco-Joffé 1993). *F. margarita* does not rely on a specific den. Dens are shared by different individuals, but not at the same time (Abbadi 1989, 1991, 1993). However, *F. margarita* pairs may share the same burrows during the breeding season (Schauenberg 1974). Once a burrow is selected, *F. margarita* typically does not change burrows during the day. *F. margarita* utilizes burrows that it digs itself, burrows abandoned by other animals (e.g., red fox, Corsac fox, Rüppell's fox, or porcupine—*Erethizon dorsatum*), or it may enlarge a gerbil or ground squirrel burrow (Sunquist and Sunquist 2002). *F. margarita* usually burrows into the compact soil at the base of a small mound, beneath a shrub, or away from vegetation on a flat sand surface (Sunquist and Sunquist 2002). *F. margarita* may prefer to burrow in areas with rodent burrows, but tracks indicate that it regularly hunts over shifting sand dunes (Roberts 1997). One den in the northern Kyzylkum Desert was constructed by enlarging a gerbil burrow and was home to a female *F. margarita*, her 3 young, and 5 great gerbils (Heptner and Sludskii 1992). *F. m. thinobia* lives in shallow burrows in sand constructed among the roots of saltbushes or *Calligonum* plants. *F. m. margarita* may use fennec (*Vulpes zerda*) burrows, an ecologically similar species.

Two *F. margarita* burrows excavated in the Karakum Desert, each had a single entrance and was about 3 m long (Heptner and Sludskii 1992). Burrows in Turkmenistan are usually shallow and located on slopes of sandy knolls in dense growths of shrubs. Near Repetek, 2 burrows were dug among white saxauls, each with a single entry and 2.5–3.0 m long (Sapozhenkov 1961). A burrow in Niger was 15 cm in diameter and 1.5 m long (Sunquist and Sunquist 2002); it was dug in a straight line that sloped down to a point about 60 cm below the surface (Dragesco-Joffé 1993). A burrow excavated in Nushki, Pakistan, was 14 cm wide and 4.6 m long (Roberts 1997). *F. margarita* in the United Arab Emirates may occasionally utilize shaded areas above ground rather than burrows (Cunningham 2002).

Although activity patterns may vary with the seasons, *F. margarita* is primarily active at night, as indicated by radiotelemetry studies in Israel (Abbadi 1991, 1993), tracks seen in the central Karakum Desert (Ognev 1935), and activity patterns of captive cats (Hemmer 1977). *F. margarita* assumes a lookout position at the burrow entrance for roughly 15 min before leaving to hunt for the night and upon its return. These cats often bask near their burrows, including on warm winter days (Roberts 1997; Sunquist and Sunquist 2002). During snowfalls and after the 1st snowfall, *F. margarita* remains in its burrow for a few days.

Felis margarita in the Karakum and Kyzylkum deserts of central Asia is nocturnal only during the hottest period of the year (Heptner and Sludskii 1992). In spring, autumn, and winter, it hunts during the day often catching diurnal rodents. In the undisturbed areas of the Sahara Desert and in Arabia, *F. margarita* may also hunt prey during the daylight hours (Dragesco-Joffé 1993). In Pakistan, *F. margarita* is nocturnal during the summer and crepuscular in the winter. During the day, *F. margarita* stays in shallow burrows dug in the soil at the base of shrubs or small mounds (Harrison 1968; Lay et al. 1970).

Felis margarita has occasionally been observed above ground in daylight near its burrow lying on its back in a posture which, in captivity, is regularly adopted at temperatures above 30°C and presumably helps it to shed heat (Lay et al. 1970). During 6 months of radiotracking in Israel, *F. margarita* was only observed resting outside its burrow in the daytime following several days of rain (Abbadi 1991, 1993).

GENETICS

Jotterand (1971) indicated that the diploid number (2n) for *Felis margarita* was 38 and the fundamental number (FN) was 72. The number of metacentric and submetacentric autosomes is 32 and the number of acrocentric autosomes is 4 (Wurster-Hill 1973). The sex chromosomes of all cats are similar in appearance. A feature of felid karyology is the uniformity of karyotypic patterns among the species (Wurster-Hill 1973). However, small differences in patterns permit each species to be categorized into 1 of 5 distinct karyotype groups. *F. margarita* is placed in the same karyotype pattern group as the caracal, Asian golden cat (*Catopuma temmincki*), *F. chaus*, *F. silvestris*, black-footed cat (*F. nigripes*), Eurasian lynx (*Lynx lynx*), serval (*Leptailurus serval*), clouded leopard (*Neofelis nebulosa*), lion (*Panthera leo*), jaguar (*P. onca*), leopard (*P. pardus*), tiger (*P. tigris*), African golden cat (*Profelis aurata*), and snow leopard (*Uncia uncia*).

CONSERVATION

Felis margarita is the least threatened of the wild cats and has been listed in the International Union for Conservation of Nature and Natural Resources *Red List of Threatened Species* as “Near Threatened” since 2002 (Mallon et al. 2011). This listing reflects concern over potentially low population size and declining numbers. *F. margarita* is also listed on the Convention on International Trade of Endangered Species (CITES) Appendix II (Nowell and Jackson 1996). The Pakistani subspecies (*F. m. schefeli*) is listed on CITES Appendix I and in the United States Endangered Species Act as endangered (Wilson and Mittermeier 2009). Hunting of *F. margarita* is prohibited in Algeria, Iran, Israel, Kazakhstan, Mauritania, Niger, Pakistan, and Tunisia (Nowell and Jackson 1996). No legal protection exists in Egypt, Mali, Morocco, Oman, Saudi Arabia, and United Arab Emirates (Nowell and Jackson 1996). No Information is available for Iraq,

Jordan, Kazakhstan, Qatar, Turkmenistan, Uzbekistan, Western Sahara, and Yemen. Additional fine-scale distribution studies, including estimates of home range size and population density, are needed to determine whether or not the precautionary listing of “Near Threatened” is warranted (Mallon et al. 2011).

Habitat degradation appears to be the major threat to *F. margarita*. Although this species is recorded from protected areas scattered across its range, arid ecosystems are being degraded by human activity and settlement, especially by conversion for agriculture and livestock grazing (Mendelsohn 1989; Allan and Warren 1993; Abahussain et al. 2002; Al-Sharhan et al. 2003). Periodic droughts and desertification also threaten the mammalian prey populations that *F. margarita* relies upon (Sunquist and Sunquist 2002). Because *F. margarita* populations already occur at low densities, these cats could disappear quickly from a disturbed desert environment. Monitoring population abundance and protecting suitable habitat are important conservation strategies (Belousova 1993; Mallon et al. 2011).

Additional localized threats include the introduction of feral and domestic carnivores, which may serve as predators, competitors, and vectors for disease transmission (Nowell and Jackson 1996). *F. margarita* may be accidentally killed by trapping targeted at disease prevention (e.g., plague), control of other species (e.g., foxes and jackals), or in retaliation for killing poultry. This cat is not considered a poultry threat by some oasis residents and is protected by religious tradition in some areas (Heptner and Sludskii 1992; Dragesco-Joffé 1993; Amr 2000). *F. margarita* may also be hunted for sport or their pelts in some parts of their range (Sausman 1997b; Ostrowski et al. 2003). International commerce in *F. margarita* products is strictly regulated. Nevertheless, this species may be a target for the illegal pet trade, but the magnitude of this activity is not known (Sausman 1997b; Mallon and Budd 2011).

In Saudi Arabia, the primary threat facing wild cats throughout their range is hybridization with *F. catus* (Nowell and Jackson 1996). *F. catus* is beginning to encroach into habitat occupied by *F. margarita* (Ostrowski et al. 2003) and represents a potential epidemiologic risk to *F. margarita* in these areas. Additionally, in central Saudi Arabia, individual *F. margarita* has died because it was caught in diamond mesh fences (Sher Shah and Cunningham 2008).

Conservation scientists speculate that the possible effective population size of *F. margarita* might be below 10,000 breeding individuals with no subpopulation having an effective size greater than 1,000 (Mallon et al. 2011). A declining trend is hypothesized due to habitat degradation and an eroding prey base. If these perceived trends persist, or if better documentation of species status and range becomes available, *F. margarita* may qualify as “Vulnerable.” Understanding the natural history of *F. margarita* and documenting its distribution should be priorities (Nowell and Jackson 1996). *F. margarita* is one of the most widespread cats, but one of the rarest and least well known.

Historically, the skins of *F. margarita* were used in the fur industry in central Asia (Heptner and Sludskii 1992). Between

1954 and 1958, 805–2,098 skins of this species were processed in Turkmenistan; 917 were processed in Uzbekistan in 1958. Heptner and Sludskii (1992) also report that this species was caught in the hundreds in Kazakhstan. Populations of *F. m. scheffeli* in Pakistan apparently declined because of exploitation by commercial animal dealers from 1967 to 1972 (Nowell and Jackson 1996). A number of these animals were also captured and sent to private collectors and zoos in Europe and North America, leading to an expanded representation in zoos and an increase in captive breeding (Roberts 1997).

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