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Caracal caracal (Carnivora: Felidae)

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Abstract: *Caracal caracal* (Schreber, 1776) is a felid commonly called the caracal. It is a slender, medium-sized cat (5.8–22 kg) characterized by a short tail and long ear tufts. *C. caracal* has a wide distribution and is found throughout Africa, north to the Arabian Peninsula, the Middle East, central and southwest Asia into India; its habitat includes arid woodlands, savanna, scrublands, hilly steppes, and arid mountainous regions. It is globally listed by the International Union for Conservation of Nature and Natural Resources as "Least Concern" despite population trends unknown across most of its geographic distribution. The Convention on International Trade in Endangered Species of Wild Fauna and Flora lists Asian populations under Appendix I and African populations under Appendix II.

Key words: Africa, African lynx, Asia, caracal, carnivore, feline, mesocarnivore, rooikat

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Caracal Gray, 1843

Felis: Schreber, 1776:pl. 110. Part, not *Felis* Linnaeus, 1758.
Caracal Gray, 1843:46. Type species *Caracal melanotis* Gray, 1843 (= *Felis caracal* Schreber, 1776), by monotypy.
Caracala Gray, 1843:XX, 202. Nomen nudum; incorrect original spelling of *Caracal* Gray, 1843 that appears in the table of contents (p. XX, before the appearance of *Caracal*) and index (p. 202).
Urolynchus Severtzov, 1858:389. Type species *Lynchus (Urolynchus) caracal* auct. ("of various authors;" presumably = Schreber, 1776), by monotypy; described as a subgenus of *Lynchus* Jardine, 1834 (= *Lynx* Kerr, 1792).

CONTEXT AND CONTENT. Order Carnivora, suborder Feliformia, family Felidae, subfamily Felinae. The genus *Caracal* includes the following two species: *Caracal aurata* (formerly *Profelis aurata*) and *C. caracal* (Kitchener et al. 2017).

Fig. 1.—Subadult *Caracal caracal* from Anysberg Nature Reserve, South Africa. Photograph by Marine Drouilly.

Caracal caracal (Schreber, 1776)

Caracal

Felis caracal Schreber, 1776:pl. 110. Type locality "Vorgebirge der guten Hofnung," restricted to "Table Mountain, near Cape Town, South Africa," by J. A. Allen (1924:281).

Felis caracal Müller, 1776:30. Type locality "Arabia" (but probably near Constantine, Algeria). Preoccupied by, but not, *Felis caracal* Schreber, 1776; see discussion in J. A. Allen (1924:281).

Felis caracal algiricus J. B. Fischer, 1829:210. No type locality specified.

Felis caracal nubica J. B. Fischer, 1829:210. No type locality specified, designated as "Meroe, Nubia [Sudan]," by J. A. Allen (1924:281).

Felis caracal bengalensis J. B. Fischer, 1829:210. No type locality specified; preoccupied by *Felis bengalensis* Kerr, 1792.

Felis caracal var. *algira* J. A. Wagner (in M. Wagner), 1841: vol. 3, 76, atlas, Tab IV. Type locality "Algeria."

Caracal melanotis Gray, 1843:46. Replacement name (unnecessary) for *Felis caracal* Schreber, 1776; see above."

Lynx lucani Rochebrune, 1885:87. Type locality "Landana," northern Angola.

Caracal caracal: Matschie, 1892:114. First use of current name combination.

Caracal berberorum Matschie, 1892:114. Type locality "Nordafrika. (Constantine…) [Constantine, Algeria];" corrected to "Staouely, Algeria," by Matschie 1912.

Felis (*Caracal*) *berberorum spatzi* Matschie, 1912:61. Type locality "zwischen Feriana und Tebessa in den Aleppokiefernwaldungen zwischen Bir bou Haya und Ain bou Dries gesammelt hat [between Fériana and Tébessa, in the Aleppo pine forests between Bir Bou Haya and Ain Bou Dries]," Aleppo, Tunisia.

C[*aracal*]. *berberorum medjerdae* Matschie, 1912:62. Type locality "Tunis," Tunisia.

Felis (*Caracal*) *nubicus corylinus* Matschie, 1912:63. Type locality "Tangiers," Morocco.

Felis (*Caracal*) *caracal schmitzi* Matschie, 1912:64–65. Type locality "Ain ed dschuheijir nordwestlich des Toten Meeres [Ain Dcherer, northwest of the Dead Sea, Palestine = Israel]."

Felis (*Caracal*) *caracal aharonii* Matschie, 1912:66. Type locality "Einmündung des Chabur in den Euphrat [at the confluence of the Khabur and the Euphrates]," Syria.

Caracal caracal poecilotis Thomas and Hinton, 1921:3. Type locality "Mt. Baguezan, Asben, 5,200 feet [=Mont Idoukal-n-Taghès (Mt. Bagzane), Asben, Air, Niger, 1,600 m]."

Caracal caracal coloniæ Thomas, 1926:181. Type locality "Deelfontein, central Cape Colony, South Africa."

Lynx caracal roothi Roberts, 1926:247. Type locality "Elandshœk, Drakensberg, Barberton district," Transvaal, South Africa.

Lynx caracal limpopoensis Roberts, 1926:248. Type locality "Nijellele River, north of Zoutpansberg and near the Limpopo River," Northern Transvaal, South Africa.

Lynx caracal damarensis Roberts, 1926:248. Type locality "Quickborn, Okahandja, S.W.A. [=Namibia]."

Felis (*Caracal*) *caracal michaëlis* Heptner, 1945:310. Type locality Bokurdak, Turkmenistan.

[*Caracal caracal*] *melanotix* Wozencraft, 2005:533. Nomen nudum.

Context and Content. Context as for genus. The number of subspecies reported from different authors varies, mainly due to a lack of recent morphological and molecular studies that examine geographical variation in this species (Kitchener et al. 2017). Wozencraft (2005) recognized eight subspecies of *Caracal caracal* based on Smithers (1971); *algira*, *caracal*, *damarensis*, *limpopoensis*, *lucani*, *nubica*, *poecilotis*, and *schmitzi*. Sunquist and Sunquist (2009) recognized *C. c. michaelis* (Heptner 1945) as a ninth subspecies. The latest taxonomic revision of the Felidae proposes the possibility of as few as three subspecies, *caracal*, *nubica*, and *schmitzi* but suggests the need for further research to elucidate the geographical variation within *C. caracal* (Kitchener et al. 2017). The following are the eight subspecies presented by Wozencraft (2005):

C. c. algira (Wagner, 1841). See above; *berberorum* Matschie, 1892; *corylinus* Matschie, 1912; *medjerdae* Matschie, 1912; and *spatzi* Matschie, 1912 are synonyms.

C. c. caracal (Schreber, 1776). See above; *coloniae* Thomas, 1926; *melanotis* Gray, 1843; and *roothi* (Roberts, 1926) are synonyms.

C. c. damarensis (Roberts, 1926). See above.

C. c. limpopoensis (Roberts, 1926). See above.

C. c. lucani (Rochebrune, 1885). See above.

C. c. nubica (J. B. Fischer, 1829). See above.

C. c. poecilotis (Thomas and Hinton, 1921). See above.

C. c. schmitzi (Matschie, 1912). See above; *aharonii* Matschie, 1912; *bengalensis* Fischer, 1829; and *michaelis* Heptner, 1945 are synonyms.

Nomenclature Notes. Though originally classified under the genus *Felis* (Roberts 1951; Groves 1982; Meester et al. 1986; Heptner and Sludskii 1992), caracals have since been reclassified under a separate genus, *Caracal*. Early on *Caracal caracal* was aligned with the lynxes due to its prominent ear tufts and short tail, both characteristics shared with the Canadian lynx (*Lynx canadensis*), the bobcat (*Lynx rufus*), the Iberian lynx (*Lynx pardinus*), and the Eurasian lynx (*Lynx lynx*). However, *C. caracal* belongs to a much older lineage that diverged from the ancestral felid line more than 1 million years before the lynx evolved (Johnson et al. 2006). *C. caracal* is most closely related to the African golden cat (Janczewski et al. 1995; Johnson and O'Brien 1997; Johnson et al. 2006). A phylogenetic analysis indicated that the caracal lineage (serval, caracal, and African golden cat) diverged from other felids about 8.5 million years ago (Janczewski et al. 1995; Pecon-Slattery and O'Brien 1998). The serval diverged about 5.6 million years ago, and the African golden cat and *C. caracal* bifurcated about 1.9 million years ago (Johnson et al. 2006). Some authors continue to keep two

different lineages for *C. caracal* and the African golden cat (*Profelis aurata*—Rolland et al. 2015); however, a more recent classification groups the caracal and African golden cat in the genus *Caracal* (*C. caracal* and *C. aurata*, respectively), and places the serval in the monotypic genus *Leptailurus* (*Leptailurus serval*—Kitchener et al. 2017).

Buffon (1761) chose the name caracal in reference to its Turkic name "Karrah-kulak" or "Kara-coulac," meaning cat with black ears. Other vernacular names for *C. caracal* are African lynx, caracal lynx, desert lynx, karakal, red cat, red lynx, and rooikat (Kenmuir and Williams 1975; Stuart 1982).

DIAGNOSIS

Caracal caracal is a slender, medium-sized cat characterized by a short tail and long ear tufts (Hoath 2003; Fig. 1); no other African felid has distinct ear tufts. The body color is a uniform reddish brown in southern Africa (Hufnagel 1972) but can be sable in Asia and the Arabic peninsula (Kingdon and Hoffmann 2013). These distinct physical characteristics help to distinguish *C. caracal* from the other six felids of southern Africa. *C. caracal* is sympatric with the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), serval, African wild cat (*Felis lybica*), and black-footed cat (*Felis nigripes*) in southern Africa (Caro and Stoner 2003). *C. aurata* is sympatric with *C. caracal* in portions of their respective geographic ranges, which can generate some confusion for identification. However, *C. aurata* selects for different habitat types than *C. caracal* and is found only in the humid equatorial rainforests (Furstenburg 2010).

The key to distinguishing these two species is a combination of coat pattern and color, body size, shape of the ears, and the pattern, color, and carriage of the tail. *C. caracal* has triangular, black-backed ears with long (ca. 50 mm) black tufts on the tip. *C. aurata* has shorter ears (ca. 53 mm) that are solid black (Kingdon and Hoffmann 2013). The tail of *C. caracal* is sandy-red to golden-red throughout, and dangles nearly straight down when the cat is standing, not reaching the hocks. The tail of *C. aurata* is black-tipped, and when the animal is standing, the tip of the tail curves away from the body with the lowest part of the tail reaching the hocks (Kingdon and Hoffmann 2013).

GENERAL CHARACTERS

Classified as a medium-sized felid, head and body lengths for *Caracal caracal* are 61–106 cm with the largest individuals inhabiting South Africa and the smallest occurring in Israel and the Sahara Desert (Smithers 1971; Stuart 1981; Nader 1984; Sunquist and Sunquist 2002; Furstenburg 2010). The hindquarters are set slightly higher than the forequarters (Hufnagel 1972), with the height of the shoulders about 46 cm (Hufnagel 1972). *C. caracal* has a relatively short (18–34 cm), robust tail compared to most cats, roughly one-third of the body length and it dangles straight down (Kingdon and Hoffmann 2013). Most individuals have furry paws; individuals from the Karakum Desert in Turkey have stiff bristle hair under the paws (Furstenburg 2010). Both front and hind paws of adults have four toe cushions and are typically 50–60 mm long and 40–50 mm wide (Furstenburg 2010). Weights vary between 5.8 and 22 kg across its geographic range. Adult males can weigh anywhere between 8 and 20 kg (average 12.7 kg), while females range between 6.2 and 15.9 kg (average 10.1 kg—Smithers 1971; Roberts 1977; Pringle and Pringle 1979; Smithers and Wilson 1979; Smithers 1983; Nader 1984; Weisbein and Mendelssohn 1990; Heptner and Sludskii 1992; Sunquist and Sunquist 2002; Sunquist and Sunquist 2009).

Caracal caracal body color is uniform golden or a rufous brown that explains the Afrikaans name of "rooikat" meaning "red cat"; the underbelly is cream with orange or brown spots, with the inner legs being pale (Kingdon and Hoffmann 2013). Intraspecific color variation is slight, with females generally lighter in color (Sunquist and Sunquist 2002). Animals from areas with low rainfall tend to be paler than those from higher rainfall regions (Kingdon and Hoffmann 2013). Melanistic individuals have been recorded in Kenya and Uganda (Rosevear 1974). Guard hairs are 15–30 mm and seasonal variation can occur in coat thickness providing effective insulation from extreme temperatures (Pocock 1939; Smithers 1983).

The head is rather angular and strikingly marked. The eyes are commonly brilliant green or yellow, and occasionally blue in color, contoured by a distinctive dark line, which runs from above the eye down along the tear line and down the nose. *C. caracal* exhibits a lowered upper eyelid and black tear streaks around the eyes, which are likely protective adaptations against the sun's glare (Sunquist and Sunquist 2002). White fur covers the chin, throat, upper lips, and around the eyes. The eyes and lips are often lined with black (Hufnagel 1972). The large, pointed ears measure up to 80 mm long including the tufts. These conspicuous ear tufts have been suggested to play a role in intraspecific communication (Nowell and Jackson 1996).

DISTRIBUTION

Caracal caracal has a very wide distribution, one of the most expansive of extant carnivores, ranging from the southern tip of the African continent, north to the Arabian Peninsula, the Middle East, and Turkey, eastwards to central India and northwards to Kazakhstan and Turkmenistan (Fig. 2; Stuart 1984; Nowell and Jackson 1996; Sunquist and Sunquist 2002; Hoath 2003). It is widely distributed on the African continent, with the exception of the equatorial rainforests and the Sahara interior (Ray et al. 2005). *C. caracal* is distributed across the drier regions of central Asia, and southwest Asia and India as well (Avgan et al. 2016). It is present in the montane massifs of the Sahara Desert and its fringes, including the Adar des Iforas in northeastern Mali (Sidiyéne and Trainer 1990), Hoggar and

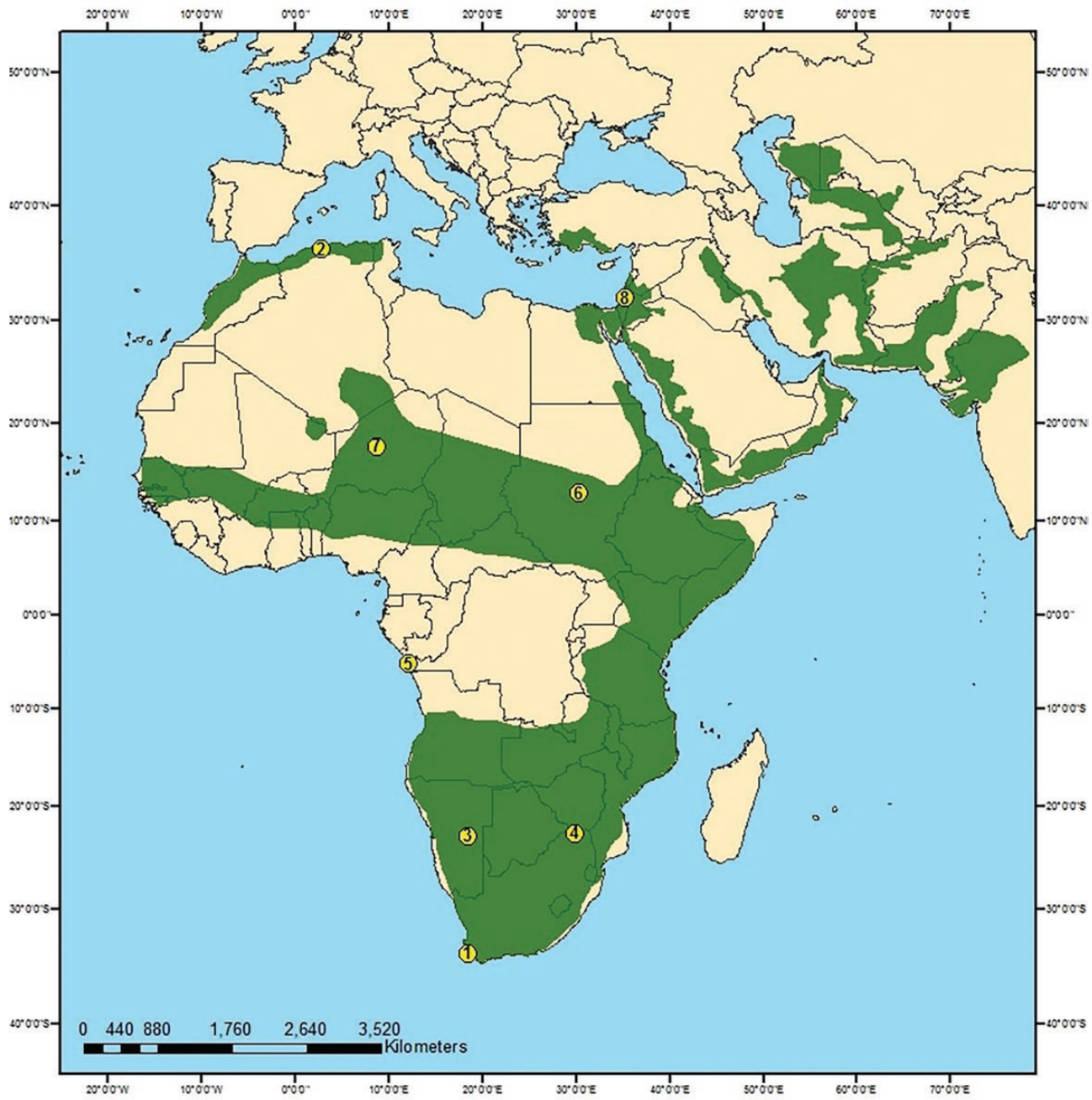

Fig. 2.—Geographic distribution of *Caracal caracal*. Map redrawn from IUCN Red List of Threatened Species. The type locality for each subspecies is indicated within the historic range of *C. caracal*: 1) *C. c. caracal*; 2) *C. c. algira*; 3) *C. c. damarensis*; 4) *C. c. limpopoensis*; 5) *C. c. lucani*; 6) *C. c. nubica*; 7) *C. c. poecilotis*; 8) *C. c. schmitzi*.

Tassil mountains of southeastern Algeria and the Saharan Atlas (De Smet 1989; Kowalski and Rzebik-Kowalska 1991), the Air of Niger (Dragesco-Joffé 1993), edges of the great sand areas of the Eastern Great Erg, and Tanzania (Pettorelli et al. 2010). In Egypt, *C. caracal* is recorded only from the Eastern Desert and north and southwestern Sinai (Hoath 2003). In Turkey, it is present in the southwest of the country, specifically in Datça and Bozburun peninsulas (Ilemin and Gürkan 2010); in Iran *C. caracal* is present in central and eastern areas of Iran (Farhadinia et al. 2007; Ziaie 2008). The presence of *C. caracal* is equivocal in the savanna regions of the Congo basin (Pettorelli et al. 2010), north of the Congo River, and in central Sinai (Hoath 2003).

Sunquist and Sunquist (2009) reported distinct geographical areas for all nine of the subspecies described in the literature. *C. c. caracal* (Schreber, 1776) is in eastern and southern Africa, *C. c. algira* (Wagner, 1841) in northern Africa, *C. c. damarensis* (Roberts, 1926) throughout Namibia, *C. c. limpopoensis* (Roberts, 1926) north of the province Transvaal, *C. c. lucani*

(Rochebrune, 1885) in the grasslands of southeastern Gabon (Coetzee 1977), *C. c. michaelis* (Heptner, 1945) in desert regions of the Caspian Sea Region and east to Amu Darya River, *C. c. nubica* (Fischer, 1829) eastern Cameroon and north to the Nubian Desert, *C. c. poecilotis* (Thomas and Hinton, 1921) in western Africa, and *C. c. schmitzi* (Matschie, 1912) in Turkey, Palestine, Iran, and India.

Caracal caracal is still widely distributed throughout its historic range in Africa; however, there have been substantial losses along the peripheries. In northern and western Africa in particular, *C. caracal* has been locally extirpated from areas with high land conversion rates to livestock areas (Ray et al. 2005). In Africa, it is estimated to have lost 37.7% of its historical distribution (Ray et al. 2005), occurring less frequently and in patchily distributed pockets of drier habitat (Nowell and Jackson 1996). However, *C. caracal* is most abundant in South Africa and Namibia, where its range is expanding (Stuart and Wilson 1988; Nowell and Jackson 1996), possibly due to local extirpation of the black-backed jackal *Canis mesomelas* by farmers (Pringle and Pringle 1979; Stuart 1982; Nowell and Jackson 1996). In Asia, *C. caracal* remains patchily distributed and limited by harsh winters with the Himalayas acting as a natural barrier preventing expansion further north (Nowell and Jackson 1996; Furstenburg 2010)

FOSSIL RECORD

The subfamily Felinae comprise the common ancestor of all living cats and the Felidae family originated near the end of the Eocene (Werdelin et al. 2010). Modern felids arose in Asia 10.8 million years ago before the progenitor of the caracal lineage arrived in Africa between 8.5 and 5.6 million years ago (Johnson et al. 2006). The earliest record of the caracal lineage is from about 4 million years from eastern and southern Africa (Werdelin et al. 2010).

Based on molecular ages of lineages, the specimens from the caracal lineage group into two distinct size classes, large, represented by the stem containing the *C. caracal* and *C. aurata* lineage, and small represented by the serval stem (Werdelin et al. 2010). However, whether these fossils are conspecific with extant species in the caracal lineage remains unclear. Available materials, mostly isolated teeth and fragmented jaws prevent further clarification of this (Werdelin et al. 2010). "*Felis*" *issiodorensis*, a species that is generally placed in the genus *Lynx*, may be placed in the *Caracal* genus (Morales et al. 2003) based upon biometric analyses that show similarities to caracal specimens, a possibility deserves further study (Werdelin et al. 2010).

FORM AND FUNCTION

Caracal caracal is part of the subfamily Felinae, the conical tooth cats, due to the presence of a rounded canine cross-section (Werdelin et al. 2010) and relatively large, well-enameled teeth (Smithers 1983). The second upper premolars are typically absent in *C. caracal* (Skinner and Chimimba 2006) and in a sample of 100 skulls, P2 was present in only eight (Skinner and Chimimba 2006). The dental formula of *C. caracal* is I 3/3, C 1/1, P 3/2, M 1/1, total 30 (Skinner and Chimimba 2006). The diastema on the upper jaw and small lower incisors allows for the upper canines to sink to full depth into prey (Pringle and Pringle 1979). *C. caracal* has relatively large canines; Christiansen and Adolfssen (2005) reported an upper canine length of 18.4 mm and lower canine length of 17.0 mm for an adult specimen while Pringle and Pringle (1979) reported upper canine lengths up to 20 mm. The skull and dentition of *C. caracal* may have evolved to handle relatively large prey in proportion to its body size (Pringle and Pringle 1979).

Among extant felids, *C. caracal* is characterized by relatively large morphological features with a rounded, blunt rostrum (Fig. 3; Sicuru 2011). The sagittal crest is distinctive, providing extra surface area for jaw muscle attachment indicating a powerful bite force. Additional leverage for muscles involved in closing the jaw is provided by a thick mandible with a tall coronoid process (Smithers 1983). Orbital sockets and auditory bullae are relatively large, indicating keen senses of vision and hearing (Smithers 1983). From the posterior most part of occipital to anterior most extension of nasals, total skull length was 103.52 mm for a typical female specimen collected from Sudan. Furstenburg (2010) reported a total skull length of 150 mm, width of 113 mm, and bite width of 37 mm, which the author measured based on adapted methodology from Smithers (1983).

Muscle fibers of *C. caracal* are considered three times more powerful than those found in humans (Neils 2018). Powerful hindquarters enable *C. caracal* to leap vertically ≥ 3 m in the air to capture avian prey (Furstenburg 2010; Kohn and Noakes 2013). Relatively large paws with stiff guard hairs on the underside may be advantageous for moving thorough soft substrate such as sand (Heptner and Sludskii 1992) and provide protection from extreme midday heat in more arid environments (Furstenburg 2010). The forepaw has an additional fifth digit, a sturdy dewclaw used for hunting (Grobler 1981).

ONTOGENY AND REPRODUCTION

Kittens are born blind, opening their eyes at 6–10 days. Ears will lie flat on the head at birth and only become erect after 30 days when the tufts on ear tips are about 10 mm long (Furstenburg 2010). Cubs will begin to hunt with the mother 4–6 months after weaning and their canines erupt (Sunquist and Sunquist 2009). Juveniles may leave the natal range by 9–10 months or may remain with the mother for about a year (Sunquist and Sunquist 2009).

Caracal caracal females reach sexual maturity between 7 and 12 months and males between 9 and 14 months (Bernard and Stuart 1987). However, males likely do not begin mating until they are between 18 and 20 months due to older, dominant males controlling higher quality territories (Furstenburg

Fig. 3.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult female *Caracal caracal* (FMNH [Field Museum of Natural History] 105607) collected by H. H. Hoogstraal (collector # 13919) on 9 December 1972 at Africa, Sudan, Kassala, Ethiopian: Kassala, Abu Gamal. Total skull length is 103.52 mm. f8e611ef-14e0-431f-acd8-8955c8521c97 Field Museum of Natural History (Zoology) Mammal Collection. https://collections-zoology.fieldmuseum.org/catalogue/2604376.

2010). Females likely do not begin mating until 14 months of age and can remain reproductive until 18 years of age (Furstenburg 2010). Females are polyestrous and estrus cycles last anywhere from 1 to 6 days (Nowell and Jackson 1996). Estrus depends on female nutritional status, which may be why spermatogenesis in males is aseasonal with a reduction in reproductive activity in the winter (Bernard and Stuart 1987). Reproduction is timed with the phenology of prey species, peaking when vegetation, and therefore prey, production is highest. Thus, timing of reproduction varies by geographic location with usually only a single litter produced each year (Bernard and Stuart 1987). However, for captive *C. caracal*, births can occur throughout the year with a pronounced peak in the summer (Bernard and Stuart 1987). Copulation tends to be short and gestation period averages 78–81 days. Births are typically separated by 1 year (Bernard and Stuart 1987) but consecutive litters can be spaced approximately 10 months apart (Furstenburg 2010). Litters average 2–4 kittens (Bernard and Stuart 1987) but up to six kittens may be born (Sunquist and Sunquist 2009).

There has been a greater awareness that many felid species are at risk of extinction, which has led to exploration of the possibility of using assisted reproductive technology for captive breeding programs (Pope et al. 2006). Several studies have been conducted on the reproductive biology of captive *C. caracal* to gain insights for breeding programs. In fecal samples, progesterone levels increased in pregnant females and estradiol levels peaked near estrus (Graham et al. 1993). Additionally, sexual behaviors were positively correlated with an increase in fecal estradiol while progesterone only rose after mating or during pregnancy (Graham et al. 1995). Fecal PGFM (13,14-dihydro-15-keto-prostaglandin F2α) levels increased 41 days after mating until parturition, then returned to basal levels postparturition (Dehnhard et al. 2012). Many felids have difficulty producing offspring in captivity and with advancements of in vitro fertilization (IVF) systems for the domestic cat (*Felis catus*), preliminary studies have been conducted to test the viability of these systems for captive wild felids, including *C. caracal* (Goodrowe et al. 1991). Female *C. caracal* responded positively to pregnant mare's serum gonadotropin (PMSG) treatments and mature oocytes could be collected using laparoscopic techniques (Goodrowe et al. 1991). Two live kittens were produced from females that received auto-transferred day-4 or day-5 embryos (Pope et al. 2006). *C. caracal* embryos were successfully cryopreserved before thawing and transferring to recipients on days 5 or 6. This had a 33% success rate for establishing pregnancies which led to a total of three kittens being born (Pope et al. 2006).

ECOLOGY

Population characteristics.—*Caracal caracal* has an average life span of 10 years in the wild but captive individuals can live up to 19 years (Nowell and Jackson 1996; Livingston 2009). Male to female ratios and overall population density are dependent on prey availability, habitat type, and the degree of persecution by humans (Avenant 1993). However, in general,

small felids, like *C. caracal*, tend to exhibit a male-biased adult sex ratio (Anile and Devillard 2018). In semiarid habitat of Western India about 4.8 individuals occurred per 100 km^2 (Singh et al. 2015). *C. caracal* occurs throughout South Africa with high densities occurring in the south and west (Stuart 1981) with 38.5 individuals/100 km^2 (Grobler 1981). Avenant and Nel (1998) estimated a density of 23–47 individuals/100 km^2 in Postberg Nature Reserve in the Western Cape of South Africa, whereas Moolman (1986) estimated a density of 38 individuals/100 km^2 for Mountain Zebra National Park in the Eastern Cape Province of South Africa. The Beydaglari Mountains of Turkey harbor only 1.7 individuals/100 km^2 (Albayrak et al. 2012). *C. caracal* is estimated to have an average annual population growth of 8–15% in southern Africa (Furstenburg 2010).

Space use.—*Caracal caracal* occupies a wide variety of landscapes and habitat types across its geographic distribution at elevations ranging from sea level to 3,300 m, with highest elevations reported in Ethiopia and Lesotho (Grobler 1981; Sunquist and Sunquist 2009). However, *C. caracal* space use was found to decrease as elevation increased and preferred areas at elevations of < 1,200 m (Ramesh et al. 2017).

Over its distribution range, *C. caracal* appears to be associated more with woodlands or riparian vegetation of savannas than forests (Skinner and Chimimba 2006; Hanekom and Randall 2015). One study in Garden Route National Park, South Africa found that *C. caracal* was one of the most widely distributed species across various forest types. However, it was detected less frequently in large forest complexes than in smaller patches of forest and may use forests as refuges while feeding in adjacent, more open areas (Hanekom and Randall 2015).

In general, habitat for *C. caracal* includes arid woodlands, savanna, scrublands, hilly steppes, and arid mountainous regions (Sunquist and Sunquist 2009; Fig. 4). Specifically, in arid or semiarid areas, it is found most often in thick brush and vegetation on rocky slopes (Avenant and Nel 1998) and in riverine habitat (Drouilly et al. 2018a), where rodent abundance is high. In southwestern Turkey, *C. caracal* occurs in highly heterogeneous pine woodlands (Ilemin and Gürkan 2010). *C. caracal* generally avoids open sandy deserts and tropical forests throughout its distribution range (Farhadinia et al. 2007; Sunquist and Sunquist 2009).

Caracal caracal uses vegetation for cover while hunting (Farhadinia et al. 2007; Singh et al. 2015) and will often use trees for refuge (Heptner and Sludskii 1992). Vegetation offers valuable shade throughout the day, and *C. caracal* often rests beneath shrubs or within rock crevices during the day. It may use open areas more during nocturnal activity and stick to thicker shrub during daylight hours (Sunquist and Sunquist 2009).

Though *C. caracal* is primarily nocturnal, activity levels are bimodal and depend on ambient temperature rather than photoperiod (Avenant and Nel 1998). Movement rates tend to increase more during nocturnal periods than the daytime (Ramesh et al. 2017). It prefers temperatures below 20°C and diurnal activity increases on cool, overcast days. Male *C. caracal* wandered 5–15 km daily, whereas females moved 2.5–10 km per day (Weisbein and Mendelssohn 1990). *C. caracal* in Namibia and other sub-Saharan African countries range over large areas with no seasonal effects on home range size (Marker and Dickman 2005). Males travel further distances and at a greater pace than females, reaching almost twice the distance during an active cycle. Females may move slower when cubs are present (Avenant and Nel 1998).

Fig. 4.—Typical *Caracal caracal* habitat on sheep farmland in the Central Karoo, Western Cape Province, South Africa (top). Typical *C. caracal* habitat in the Cederberg mountains, Western Cape Province, South Africa (bottom). Photographs by Marine Drouilly.

Vegetation productivity has cascading effects on mammalian prey, which can affect home range size of *C. caracal*. Home range size and population density for *C. caracal* were dependent on spatial and temporal productivity of vegetation with high variation throughout its distribution. Large home ranges are thought to result from lower productivity and prey abundance in arid environments (van Heezik and Seddon 1998). In the Western Cape Province of South Africa, male home ranges were about 26 km^2 (Avenant and Nel 1998) to 65 km^2 (Norton and Lawson 1985) and females patrolled home ranges of roughly 7 km^2 (Avenant and Nel 1998). In contrast, a male in Saudi Arabia ranged over 1,116 km^2 during winter months (van Heezik et al. 1998), whereas males in Israel had an average yearly home

range of 220 km^2 and females had an annual average of 57 km^2 (Weisbein and Mendelssohn 1990).

Home range size of *C. caracal* differs between the sexes, with males exhibiting larger home ranges than females (Avenant and Nel 1998; Neils 2018). Reproductive status also impacts home range size. In the Western Cape Province of South Africa, female home ranges contracted from 7 km^2 on average to as little as 3 km^2 while raising young (Norton and Lawson 1985; Avenant and Nel 1998). Females in South Africa exhibited 0–19% overlap, whereas overlap was 81–99% between males and females, with male home ranges encompassing one or two female territories (Avenant and Nel 1998). Female *C. caracal* in Israel showed 27% overlap (Weisbein and Mendelssohn 1990) and males in Namibia showed 19% overlap in home range (Marker and Dickman 2005), which again demonstrates the variability in space use.

Agricultural areas influence *C. caracal* space use in certain portions of its range. Home ranges of males were larger than those of females in fragmented agricultural areas in South Africa (Ramesh et al. 2017). Additionally, under conditions of low prey availability in Namibia during the cold season, *C. caracal* moved closer to agricultural lands to prey on small livestock (Melville and Bothma 2006). *C. caracal* will adapt to using areas of higher human activity that have higher prey availability (Ramesh et al. 2017), possibly due to reduction of apex carnivores. In the Western Cape of South Africa, *C. caracal* had a higher relative abundance on small-livestock farms devoid of apex carnivores than on a neighboring nature reserve where leopards occur (Drouilly and O'Riain 2019) and similar to the pattern observed on fenced ranches relative to a national park in Kenya (Kinnaird and O'Brien 2012).

Diet.—*Caracal caracal* preys on a variety of species, with small mammals, antelope, and birds forming a majority of its diet (Smithers 1971; Grobler 1981; Skinner and Chimimba 2006; Drouilly et al. 2018b). Diet analysis showed that small mammals compose up to 89% of its diet in sub-Saharan Africa (Nowell and Jackson 1996; Mukherjee et al. 2004; Neils 2018). Mammalian prey, which included lagomorphs, rock hyrax (*Procavia capensis*), and springhare (*Pedetes capensis*) composed approximately 95% of the diet of *C. caracal* in the southern Free State of South Africa (Pohl 2015). Rodents were identified as the most likely prey for *C. caracal* in Iran's Kavir National Park (Mousavi 2010) and scat analyses from Karoo National Park, South Africa, identified rodents as its most common prey (Palmer and Fairall 1988). Grey rhebuck (*Pelea capreoulus*) and rock hyrax made up a significant portion of *C. caracal* diets beyond small mammals in the Karoo (Palmer and Fairall 1988). Palmer and Fairall (1988) estimated an individual *C. caracal* kills approximately 15–16 hyrax per year. *C. caracal* is known for its exceptional ability to catch birds by leaping high into the air to knock them down (Nowell and Jackson 1996). Occasionally, *C. caracal* will take larger prey, including adult gazelle and springbok (*Antidorcas marsupialis*—Nowell and Jackson 1996). Despite weighing only 8–20 kg, *C. caracal* regularly kills prey more than twice its own body mass from a variety of taxa (Grobler 1981; Sunquist and Sunquist 2002). The dietary niche breadth of *C. caracal* in the Western Cape Province of South Africa was higher on farmland than in a nearby protected area (Levin's measure = 6.7 and 4.2, respectively—Drouilly et al. 2018b); which can be an asset for adapting to changes in land use when more prey is available and *C. caracal* is less vulnerable to dietary competition and prey fluctuation on farmlands.

The diet of *C. caracal* is highly dependent on its distribution within the broader geographic range and prey availability. In the Western Cape Province of South Africa and Namibia, *C. caracal* diets, as determined by scat analysis, were largely (94–100%) composed of mammals (Skinner and Chimimba 2006; Drouilly et al. 2018b, Neils 2018). In coastal areas that have been heavily influenced by anthropogenic modifications such as plantations and farms, *C. caracal* diet was composed mostly of rodents with native ungulates commonly eaten as well (Braczkowski et al. 2012). Average food consumption is about 1 kg per day (Grobler 1981). Rarely *C. caracal* will scavenge on carrion (Skinner 1979; Nowell and Jackson 1996). As a hypercarnivore, it does not need to consume large amounts of water (Kingdon 1990).

A major source of human conflict with *C. caracal* comes from depredation of livestock, which has been reported across its range, particularly in southern Africa (Nowell and Jackson 1996; Ramesh et al. 2017; Drouilly et al. 2018b). Consumption of livestock by *C. caracal* has been linked to substantial economic losses to farmers (Ramesh et al. 2017). *C. caracal* is thought to be responsible for between 9% (in Mpumalanga, South Africa) and 36% (in the Western Cape Province, South Africa) of small-stock predations (van Niekerk 2010) and 11% of cattle calf predation in the North West Province (Badenhorst 2014). In Namibia, livestock accounts for 2–3% of *C. caracal* diets (Neils 2018). On small-livestock farms in the Western Cape Province of South Africa, the frequency of occurrence of domestic ungulates in *C. caracal* scats represents more than 34% (Drouilly et al. 2018b). Despite that, *C. caracal* on farms showed strong prey preference for wild mammals rather than for goats or sheep. Predation on small stock and introduced springbok was seasonal when alternative wild prey was scarce (Avenant and Nel 1998) in sub-Saharan Africa. In South Africa's Mountain Zebra National Park where wild prey was abundant, no livestock were found in 200 *C. caracal* scats (Grobler 1981). Similarly, out of 80 *C. caracal* scats collected in Anysberg Nature Reserve in the Little Karoo region of South Africa, only one contained goat remains (Drouilly et al. 2018b).

Diseases and parasites.—Most research of diseases and parasites for *Caracal caracal* has been conducted in captive settings. Feline panleukopenia virus (Lane et al. 2016), cystine calculi (Jackson and Jones 1979) and cystine urolithiasis (Tordiffe et al. 2012), and *Toxoplasma gondii* (de Camps et al. 2008) were noted in captive *C. caracal* in South Africa

and the United States. More recently a respiratory nematode (*Aelurostrongylus abstrusus*) was found in South Africa despite no previous infections in wild felids (Di Cesare et al. 2016). A wild *C. caracal* from west of the Kalahari exhibited FIV [feline immunodeficiency virus]-like infection based on seropositive results for the virus (Thalwitzer et al. 2010). A variety of ticks (~11 species) have been documented on wild *C. caracal* across its geographic range (Iori and Lanfranchi 1996; Horak et al. 2010) and several species of fleas (Horak et al. 2004). A recent study on the epidemiology of tick-borne pathogens affecting *C. caracal* in three areas of South Africa (i.e., Namaqualand farmland, Central Karoo farmland, and the Cape Peninsula) found *Hepatozoon felis*, *Babesia felis*, *Babesia leo*, and a potentially undescribed *Babesia* species, genetically similar to *Babesia venatorum*, an emerging zoonosis, in *C. caracal* (Viljoen 2017). An *Anaplasma* species previously described in domestic dogs (*Canis lupus familiaris*) from South Africa was also found in urban *C. caracal* from the Cape Peninsula (Viljoen 2017). In comparison to farmland *C. caracal*, these urban *C. caracal* displayed substantially higher rates of tick-borne pathogen coinfection and greater pathogen diversity. Every *C. caracal* (n = 57) examined was infected with at least one tick-borne pathogen (Viljoen 2017).

Interspecific interactions.—*Caracal caracal* competes with other carnivores for resources, with main competitors documented to be the black-backed jackal and the leopard (Ramesh et al. 2017; Drouilly et al. 2018b). On farmland in the Central Karoo of South Africa, the dietary niche overlap between black-backed jackal and *C. caracal* was 69.8% compared to 64.7% in a nearby protected area (Drouilly et al. 2018b). *C. caracal* and the leopard only had a dietary niche overlap of 53.3% in a protected area in the Western Cape Province of South Africa, due to the consumption of different prey size categories (Drouilly et al. 2018b). Interestingly, dietary overlaps with black-backed jackal and leopard were higher between farmland than reserve *C. caracal*, highlighting the high dietary flexibility of *C. caracal* between land-use types. *C. caracal* and the black-backed jackal had a high niche overlap in rural areas of the southern Free State of South Africa and moderate to small niche overlap with Cape grey mongoose (*Galerella pulverulenta*) and yellow mongoose (*Cynictis penicillata*—Pohl 2015).

Caracal caracal is expanding its distribution in South Africa and Namibia linked to local extirpation of the black-backed jackal (Nowell and Jackson 1996; Drouilly et al. 2018c). The serval overlaps *C. caracal* in portions of its African distributions (Macdonald et al. 2010), but probably does not compete for resources with *C. caracal* as it selects for different habitat types. Based on a literature review of diet and habitat overlap, *C. caracal* shares some portion of its geographic range in Africa with 67 other mammalian carnivores and was vulnerable from nine of those species when stealing prey (Caro and Stoner 2003) which indicates the relative importance of exploitative competition and interspecific killings for *C. caracal* in Africa. *C. caracal* kills and feeds on small carnivores such as African wildcat (*Felis lybica*), Cape gray mongoose, small-spotted genet (*Genetta genetta*), bat-eared fox (*Otocyon megalotis*—Drouilly et al. 2018b), and vulnerable species such as the black-footed cat (*Felis nigripes*—Wilson et al. 2016). Adult *C. caracal* can be killed by leopard and spotted hyena (*Crocuta crocuta*—Skinner 1979), whereas kittens will be predated by these carnivores and jackals if found (Furstenburg 2010; Bothma 2012).

HUSBANDRY

Caracal caracal generally does well in captivity and is prevalent in households and zoos. Though common as house pets, domestic settings are rarely adequate to fulfill the needs of *C. caracal*. Natural behaviors, including hunting, leaping, and scent-marking, make it an undesirable pet with large space requirements. Enclosures must include enrichment opportunities that encourage physical and mental stimulation. Like other felids kept in captivity, *C. caracal* may exhibit stereotypic behaviors, such as pacing, excessive grooming, or long periods of inactivity. Providing small forms of enrichment, such as hiding food throughout the day, can reduce stereotypy and increase natural behaviors (Livingston 2009).

A proper diet is imperative to meet energy and nutrition requirements and prevent future health problems. *C. caracal* nutritional requirements have not been studied; thus, standards follow that of a domestic cat (*Felis catus*—Livingston 2009). Namely, diets must be meat-based for cats to obtain vitamin A and niacin requirements (Morris and Rogers 1982). Arachadonic acid (Livingston 2009), vitamin D (Ullrey and Bernard 1999), and taurine must also be added to the diet (MacDonald et al. 1984). Commercial diets for domestic cats should fulfill the necessary requirements for *C. caracal*; however, some North American zoos also sell appropriate diets (Livingston 2009). Food should be handled with care to prevent bacterial contamination (Livingston 2009). In captivity, *C. caracal* typically eats 400–500 g of a meat-based diet daily and is offered bones one to three times weekly (Livingston 2009); however, appropriate food amounts depend on diet composition and frequency of feeding, body size, activity, and metabolism. Caretakers should provide healthy diets low in carbohydrates and adequate exercise opportunities to prevent obesity and Type II diabetes (Rand et al. 2004). Additionally, under-supplemented diets that do not provide enough calcium, phosphorous, and vitamin D can lead to metabolic bone disease (Turk 2011). This is a concern especially during periods of growth and reproduction. In general, grain-based diets are linked to higher pH and increased crystal formation, whereas meat products lower urine pH. An ideal pH of 6.0 or 6.5 is maintained in felids to prevent crystal formation (Livingston 2009). Cysteine calculi occur in captive *C. caracal*, but dietary information was unfortunately not provided (Jackson and Jones 1979; Tordiffe et al. 2012).

Caracal caracal is common in zoos and is successfully bred in captivity. Both American and European Zoo Associations manage breeding programs supervised by Felid Taxon Advisory Groups. To initiate mating, males are placed in the same enclosure as females after sexual maturity is reached. Mating will occur several times in a manner similar to that of other cats. The male is typically removed from the enclosure when the female shows signs of pregnancy (Gowda 1967; Kralik 1967; Cade 1968). During pregnancy, the female's appetite will increase until the day preceding birth, in which the female may not feed. Mothers create nests out of hair and feathers of prey and spend increasing amounts of time in their shelters. Successful breeding requires minimal disturbance both before and after birth (Mellen 1991). For small felids, mothers that were hand-reared were less successful at raising their own young than maternally reared females; thus, hand-rearing should be avoided when possible (Mellen 1991). If young cannot be reared by the mother, milk replacements are commercially available. Kitten Milk Replacer and Zoologic Milk Matrix 33/40 (Pet-Ag Inc., Hampshire, Illinois) products have been used successfully with *C. caracal* (Livingston 2009). These products are already adequately supplemented with taurine, calcium, phosphorus, etc., and do not require additional supplementation. During weaning appropriate mineral ratios must be maintained (Livingston 2009). A 50 g daily weight gain is expected for *C. caracal*; small felids should be fed between 15% and 20% of their body weight per day, with six to eight feedings a day (Livingston 2009).

BEHAVIOR

Grouping behavior.—*Caracal caracal* is quite elusive and often persists in low densities; therefore, it is a difficult subject for behavioral studies. It is solitary and only rarely are two adults observed move together (Stuart 1981; Schütze 2002). Eight individuals were seen at a fishpond in Israel (Hoath 2003). Females have been seen accompanied by their offspring. Additionally, home ranges overlap both within and between sexes. Males exhibit marking behavior by moving paws through dampened sand after urination or spray-marking by lifting the tail vertically and spraying urine on vegetation and logs around their territory (Stuart 1981). Females also exhibit marking behavior, though not as frequently as males (Norton and Lawson 1985; Bothma and LeRiche 1994; Livingston 2009). Both sexes use "scratching trees" to mark their territories (Stuart and Wilson 1988).

Reproductive behavior.—*Caracal caracal* is promiscuous and females often mate with more than one male. Before approaching females, males will examine urine spray sites to ensure female receptivity, avoiding nonreceptive females (Bernard and Stuart 1987). Males may fight each other for access to receptive females. In Israel, females copulated with multiple males in succession, in which mating order is determined by age and weight (Sunquist and Sunquist 2009). Once a mate is chosen, males and females travel together for 3 or 4 days before separating, copulating multiple times (Bernard and Stuart 1987). Males do not take part in any rearing of the young and are reported to kill young kittens (Stuart 1981), likely to induce estrus in females. Females retract home ranges before birth, which may be in part due to a switch in prey source from rodents to antelope or livestock (Avenant and Nel 1998). Females nest in old porcupine burrows, trees, brush, or rock crevices and line beds with feathers and hair (Schütze 2002). Birth can occur year-round; however, timing of birth depends on the female's nutritional status and is dependent on prey availability. In the Western Cape Province of South Africa, *C. caracal* exhibits birth peaks between December and March (Avenant and Nel 1998) and birth peaks occur between October and February in the Eastern Cape Province (Bernard and Stuart 1987). Males disperse 60–90 km away from natal ranges, whereas females remain and may occupy home ranges overlapping with their mother's (Weisbein and Mendelssohn 1990).

Communication.—*Caracal caracal* has a good sense of sight, hearing, and smell and relies on all three to communicate (Schütze 2002). It is suspected that the prominent ear markings are used for intraspecific communication (Nowell and Jackson 1996). When threatened, *C. caracal* flicks, twists, and turns the ear. It reacts to aggressive encounters between conspecifics or other threats by approaching slowly with head held below shoulder level. Ears are cocked and turned outwards and the tail twitches. At a higher threat level, it holds an open-mouthed gape with teeth bared and ears pinned back, hissing or spitting (Schütze 2002).

Caracal caracal is known to exhibit a range of vocalizations, including purrs, growls, hisses, barks, chirrups, and meows (Guggisberg 1975). Guggisberg (1975) additionally mentions a cry similar to that of a leopard emitted on occasion by adults. Contact calls are largely composed of barks, chirrups, and meows. Young kittens emit a shrill call resembling that of a Cape Sparrow (*Passur melanurus*—Grobler 1982). In captivity, pregnant females and adjacent males communicate using barking signals (Kralik 1967). A hiss-bark has also been reported upon the introduction of new animals into an enclosure or inappropriate mounting by subadult males. It also communicates with chemical signals via urine spraying and scent-marking. *C. caracal* has cheek, chin, anal, and digital scent glands (Schütze 2002) that enable individuals to mark territories and advertise receptivity.

Miscellaneous behavior.—*Caracal caracal* exhibits typical feline hunting behavior, including stalking and pouncing with a killing bite to the nape of the neck or throat, depending on prey size (Kenmuir and Williams 1975; Pringle and Pringle 1979; Stuart 1981). Small to mid-size prey are killed with a bite to the back of the neck while larger prey items are killed with a bite to the throat. *C. caracal* is said to be the fastest felid of its size and can run down prey for short distances (Skinner 1979; Kingdon and Hoffmann 2013). If excess food is left over, it may cache food in a tree or dense bush for later. *C. caracal* is greatly admired for their precision in bird hunting, attributed to

their remarkable ability to lunge up to 4 m into the air and catch birds with their forepaws or knock several out of the air at one time (Heptner and Sludskii 1992). *C. caracal* was traditionally used as hunting cats by royalty in Iran, India, Egypt, and Syria (Heptner and Sludskii 1992). Ancient Egyptians attached some religious significance to this felid by mummifying a few dead animals (Heptner and Sludskii 1992).

GENETICS

Johnson and O'Brien (1997) conducted a phylogenetic reconstruction of Felidae and found that based on mutations to the 16S rRNA and NADH-5 genes, *Caracal caracal* and *C. aurata* form a separate clade from other felid lineages consistent across minimum evolution, maximum parsimony, and maximum likelihood methods. The caracal lineage first diverged from other felids approximately 8.5 million years ago and speciated into *C. caracal*, *C. aurata*, and *Leptailurus serval* (Johnson et al. 2006; Werdelin et al. 2010). The split from the caracal clade occurred approximately 5 million years (Werdelin et al. 2010).

The genetics of *C. caracal* at a local scale are poorly known. Recently, mitochondrial and microsatellite markers revealed a high level of genetic diversity in *C. caracal*, with all individuals belonging to a single nuclear genetic cluster in the Karoo region of South Africa (Tensen et al. 2018). Whether subspecies are genetically distinguishable from each other is unknown. Genetic profiles are largely lacking for the nine previously recognized subspecies. Though two proposed subspecies, *C. c. michaelis* and *C. c. schmitzi*, were thought to occur in Iran, a genetic analysis of 24 tissue samples taken throughout Iran showed very little variation in mitochondrial DNA (Hassan-Beigi 2015). The author found that only four of eight tested domestic cat loci produced success results. Further genetic analysis of subspecies that tests additional feline primers, in addition to a broader array of sample specimens, may yield greater insight into whether subspecies are genetically distinct. Mountain chains and wide roads or highways may pose as significant barriers to gene flow for the caracal (Hassan-Beigi 2015).

CONSERVATION

Caracal caracal is globally listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources because it is relatively common across a broad distribution, particularly in southern and eastern Africa (Macdonald et al. 2010). However, range losses have occurred in north and west Africa and *C. caracal* is of conservation concern in most of the Asian range (Avgan et al. 2016). It is most abundant in South Africa and Namibia (Nowell and Jackson 1996).

The status of *C. caracal* in individual countries varies, ranging from "common" to "extremely rare." *C. caracal* is found throughout much of Africa and northward into Israel (Visser 1976) and these populations are listed under Appendix II (CITES 2020). Asian populations are listed under Appendix I (CITES 2020), however, and are thought to be nearly extinct in India (Sunquist and Sunquist 2009; Singh et al. 2015). Although *C. caracal* is protected by law in countries including Israel, Iran, Afghanistan, and Turkey, across its geographic distribution, widespread habitat destruction for agricultural or road development, poaching for fur or meat, culls due to human–wildlife conflict, exotic pet trade, and road collisions threaten its populations (Habibi 1977; Serez 1992; Nowell and Jackson 1996; Giannatos et al. 2006; Ghoddousi et al. 2009; Hassan-Beigi 2015). Populations are decreasing and conservation status is rare or endangered in a majority of their range, especially North Africa, Arabia, and Turkey (Nader 1984; Giannatos et al. 2006). Asian populations are particularly threatened resulting from overexploitation for fur or meat (Sunquist and Sunquist 2009; Hassan-Beigi 2015).

Caracal caracal that inhabits farmland can prey on livestock, causing intense conflict with locals that often leads to culling and poisoning (Grobler 1981; Nowell and Jackson 1996; Farhadinia et al. 2007; Hassan-Beigi 2015; Neils 2018). In Iran, 12–18% of livestock losses are attributed to *C. caracal*, despite few accounts of direct observation of such attacks. The majority of livestock depredations occur in poorly secured barns at night. Many locals attempt to remove the problem animal by culling or poisoning nearby *C. caracal*. Since it is a protected species in Iran, these killings are often unreported (Hassan-Beigi 2015).

Though culling may result in population declines in Asian and some African populations (Hassan-Beigi 2015; Singh et al. 2015), *C. caracal* continues to increase and expand into agricultural areas in South Africa and Namibia (Avenant and Du Plessis 2008; Drouilly et al. 2018c). In these locations, it is common, often seen as vermin, and thus unprotected by the law (Nowell and Jackson 1996; Avenant and Nel 1998; Avenant et al. 2016). *C. caracal* is heavily persecuted and Stuart (1982) reported an average of 2,219 *C. caracal* per year were killed in control operations in South Africa's Karoo ecosystem from 1931 to 1952. Similarly, Namibian farmers responding to a government questionnaire reported killing up to 2,800 *C. caracal* in 1981 (Joubert et al. 1982). The annual persecution rate reported by farmers in the North West Province was 1.1 individuals/100 km^2 (Thorn et al. 2012), which compares to the estimation for the Cape Province of 1.6 individuals/100 km^2 (Brand 1989).

Beyond culling, there are additional threats to *C. caracal* populations living in urban and agricultural areas. *C. caracal* is sometimes used as bushmeat and consumed by communities in South Africa and Namibia (Avenant et al. 2016). Beyond intended poisoning of livestock carcasses by farmers, *C. caracal* is exposed frequently to anticoagulant rodenticides; *C. caracal* presents a very high exposure (92%, $n = 28$) to anticoagulant rodenticides in the Greater Cape Town region of South Africa, the most important risk factor being their proximity to vineyards (Serieys et al. 2019).

Caracal caracal response to anthropogenic pressures remains unclear (Du Plessis et al. 2015). Agricultural lands alter *C. caracal* feeding ecology by providing reliable, abundant, year-round food sources in the form of small livestock, meanwhile wildlife management may cause social and reproductive behavior to shift. *C. caracal* can shift prey preference to livestock when natural prey density is low (Melville et al. 2004; Melville and Bothma 2006; Ramesh 2017). This phenomenon occurs in *C. caracal* that inhabits natural habitat in parks and reserves and in human-modified landscapes. Knowledge regarding how *C. caracal* alters hunting behavior between seasons can provide insight into when and why it is targeting domestic livestock and when management practices may be best applied (Melville et al. 2004). Studies investigating differences in spatial ecology between *C. caracal* populations in rangelands versus those in preserves are also vital to understand complex human–wildlife relations. In some areas, *C. caracal* feeds preferentially on natural prey (Drouilly et al. 2018b; Minnie et al. 2018). The effect of livestock provisioning on *C. caracal* home ranges is unclear, and home ranges may be larger on livestock farms due to reduced density of preferred prey (Minnie et al. 2018). In some cases, increased hunting pressure, low natural prey availability, and highly fragmented habitat in human-modified landscapes can result in larger home ranges (Marker and Dickman 2005).

Management strategies that implement culling lack a sound scientific basis and the response of *C. caracal* populations is unknown. Compensatory reproduction in *C. caracal* is unknown and little research on the effects of lethal management on reproduction has occurred (Minnie et al. 2018). The increase in *C. caracal* numbers despite heavy persecution suggests that these strategies are ineffective (Nowell and Jackson 1996) and *C. caracal* often repopulates areas soon after extirpation (Visser 1976). Tensen et al. (2018) hypothesized that high population turnover due to lethal management on farmlands may promote compensatory dispersal in *C. caracal*. As an example, in South Africa, Conradie and Piesse (2013) used hunting club data from the 1980s and found that farms where *C. caracal* hunted experienced worsening problems over time, suggesting that lethal control may have been counterproductive and unsustainable (Conradie and Piesse 2013; Neils 2018). Improvements to livestock safety and infrastructure, as well as educational outreach that encompasses traditional values and emphasizes the benefits of carnivore presence may be more viable management options (Hassan-Beigi 2015).

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