MAMMALIAN SPECIES No. 340, pp. 1–9, 3 figs.

Panthera onca.

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Published 26 October 1989 by The American Society of Mammalogists

Panthera onca (Linnaeus, 1758)

Jaguar

[*Felis*] *onca* Linnaeus, 1758:42. Type locality "America meridionali;" restricted to Pernambuco, Brazil by Thomas (1911).
Felis nigra Erxleben, 1777:512. Type locality "Brasilia et Guiania."
Felis panthera Schreber, 1778: pl. 99. No type locality given.
F.[*Felis*] *jaguar* Link, 1795:90. Renaming of *F. onca* Linnaeus, 1758.
Leopardus hernandesii Gray, 1857:278. Type locality "Mazatlan."
Panthera onca: Fitzinger, 1869:211. First use of current name combination.
Felis jaguarete Liais, 1872:451. Renaming of *F. onca* Linnaeus, 1758.
Felis jaguapara Liais, 1872:451. Renaming of *F. onca* Linnaeus, 1758.
Felis jaguatyrica Liais, 1872:459. Renaming of *Felis nigra* Erxleben, 1777.
Felis centralis Mearns, 1901:139. Type locality "Talamanca, Costa Rica."
Felis paraguensis Hollister, 1914:169. Type locality "Paraguay."
Felis notialis Hollister, 1914:170. Type locality "San Jose, Entre Rios, Argentina."
Felis ramsayi Miller, 1930:14. Replacement name for *Felis paraguensis* Hollister, 1914.

CONTEXT AND CONTENT. Order Carnivora, Family Felidae, Subfamily Pantherinae. The genus *Panthera* includes four living species, *P. leo, P. onca, P. pardus,* and *P. tigris*. See Hemmer (1966) for a key to the species of the genus. Eight subspecies are recognized (largely following Pocock, 1939, and not Cabrera, 1957):

P. o. arizonensis Goldman, 1932:144. Type locality "near Cibecue, Navajo County, Arizona."
P. o. centralis (Mearns, 1901:138), see above.
P. o. goldmani (Mearns, 1901:142). Type locality "Yohatlan, Campeche, Mexico."
P. o. hernandesii (Gray, 1857:278), see above.
P. o. onca (Linnaeus, 1758:42), see above (*major* and *minor* Fischer, *mexianae* Hagmann, *coxi, boliviensis, ucayalae,* and *madeirae* Nelson and Goldman are synonyms).
P. o. paraguensis (Hollister, 1914:169), see above (*notialis* Hollister, *ramsayi* Miller, *milleri* and *paulensis* Nelson and Goldman are synonyms).
P. o. peruviana Blainville, 1843:186. Type locality "Pérou."
P. o. veraecrucis Nelson and Goldman, 1933:236. Type locality "San Andres Tuxtla, Vera Cruz, Mexico."

DIAGNOSIS. The jaguar is the largest felid in the New World. It is similar in appearance to the leopard (*P. pardus*), but differs as follows: larger average size (length of head and body, 1.12 to 1.85 m compared to 0.91 to 1.67 m for the leopard, although the leopard may reach 1.91 m); shorter and more tapering tail (length, 0.45 to 0.75 m compared to 0.58 to 1.10 m); heavier, more compact and powerfully built body (mass, 36 to 158 kg compared to 28 to 90 kg); more robust head and larger foot pads that are more evenly rounded especially on the forefoot (Nelson and Goldman, 1933; Nowak and Paradiso, 1983). The jaguar has relatively larger lower canines, smaller p3, and shorter m1 when compared to other pantherines, especially the leopard (Werdelin, 1983); it also has relatively shorter canines, the lower canines barely reaching the plane of the lower border of the anterior nares (in the leopard they reach well above this plane). Canine longitudinal grooves may be absent or obsolescent (well developed in the leopard; Nelson and Goldman, 1933). Skull with tubercle of variable size in the middle of the inner side of the rim of the orbit (also called lacrimal eminence). This tubercle is usually larger than in the other pantherines. Rosettes are similar to those of the leopard, however the rosettes on the flank tend to enclose one or more small black spots (usually absent in the leopard). There is so much variation in their pelts that it is not always possible to separate *P. onca* from *P. pardus* (Neff, 1986). The karyotype of the jaguar is almost identical to that of the leopard (Hsu, 1962).

GENERAL CHARACTERS. Body structure corresponds to the general form of the Felidae. Jaguars are muscular with relatively short massive limbs, a deep-chested body, and a relatively large, rounded head (Fig. 1). Total length of adults varies greatly among subspecies, but generally ranges from 1.57 to 2.19 m for females and 1.72 to 2.41 m for males, the longest recorded being 2.7 m; overall average is 1.82 m (Hall, 1981; Perry, 1970). Females usually are 10 to 20% smaller than males (Rich, 1976; Seymour, 1983). The jaguar is smaller than the lion (*P. leo*) or tiger (*P. tigris*) and slightly larger than the leopard. The tail is not longer than one-third of the head plus length of body (Guggisberg, 1975). Shoulder height is about 0.68 to 0.75 m (Rich, 1976). Ears are small, rounded, and black on the back with small white or buff central spots, as in the tiger (Cabrera and Yepes, 1960). Hair is rather short and bristly. The throat, chest, belly, and interior parts of the feet have longer fur (Canevari, 1983). Condylobasal length of the adult skull may exceed 275 mm, but is usually between 190 and 260 mm; it rarely is <180 mm. The following skull measurements (in mm, $n = 112$) were taken by the author from a sample of males and females representing all subspecies (mean, range): condylobasal length, 218.2, 177 to 276; bizygomatic breadth, 165.2, 129 to 212; rostral breadth, 67.8, 55.4 to 89.8; interorbital breadth, 46.1, 33.8 to 68.1; length of upper canine, 18.2, 14.0 to 23.5; length of upper fourth premolar, 27.1, 23.0 to 32.3; length of lower canine, 17.5, 13.2 to 23.5; length of lower first molar, 20.1, 16.5 to 24.8.

The skull is robust, relatively short, broad in the rostrum (more so in males than females), and wide in the zygomatic arches (Fig. 2). The sagittal crest may become well developed, especially in males and older individuals. The permanent dental formula is: i 3/3, c 1/1, p 3/2, m 1/1, total 30; for the deciduous dentition: i 3/3, c 1/1, p 3/2, total 26. In Venezuela, average mass for females is 56.3 kg ($n = 3$) and 95.0 kg for males ($n = 9$; Mondolfi and Hoogesteijn, 1986), while in Brazil the average mass for females is 77.7 kg ($n = 3$) and 94.8 kg for males ($n = 6$; Schaller and Vasconcelos, 1978). Six males from Belize averaged 57.2 kg (Ra-

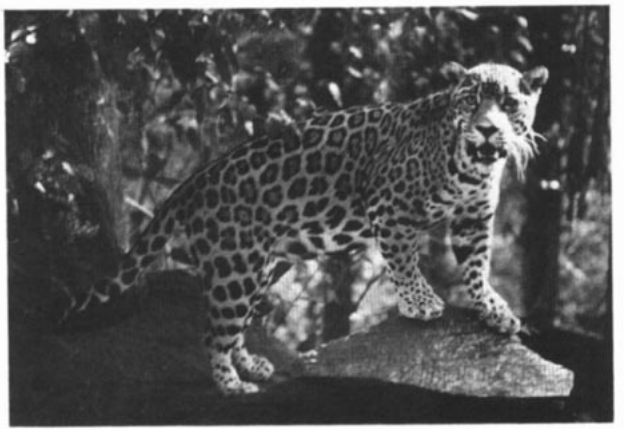

FIG. 1. Adult female *Panthera onca goldmani* in Belize. Photograph by E. M. Watt.

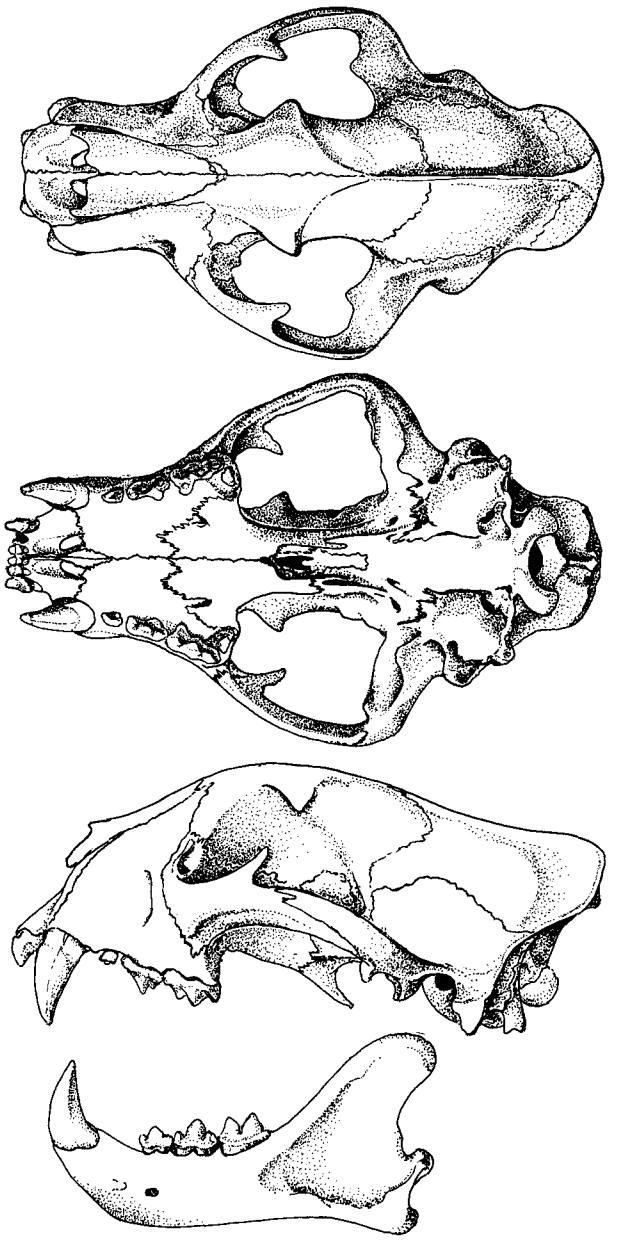

FIG. 2. Ventral, dorsal, and lateral views of cranium and lateral view of mandible of a female *Panthera onca paraguensis*. Academy of Natural Sciences Philadelphia 13948, from the state of Mato Grosso, Brazil. Condylobasal length of cranium is 227 mm. Drawn by S. Poray-Swinarski.

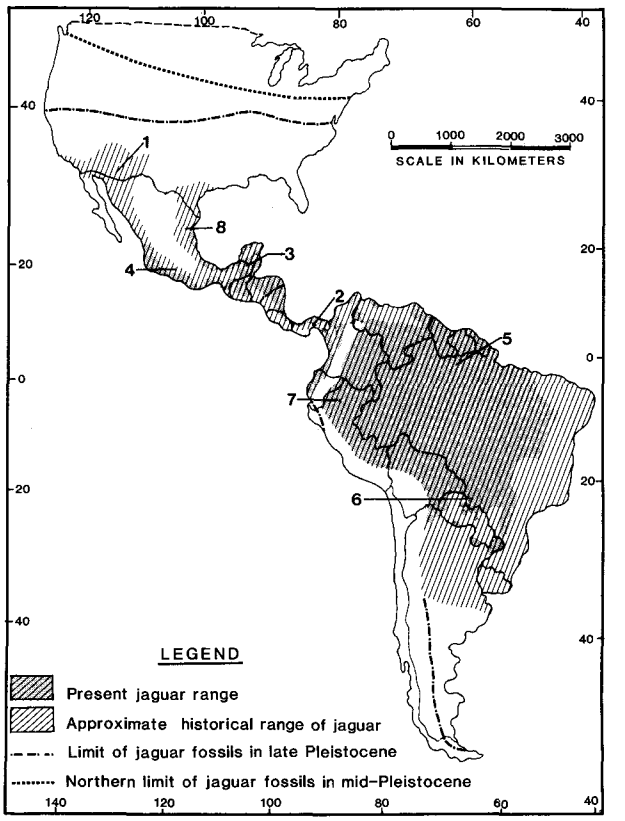

FIG. 3. Distribution of *Panthera onca*: 1, *P. o. arizonensis*; 2, *P. o. centralis*; 3, *P. o. goldmani*; 4, *P. o. hernandesii*; 5, *P. o. onca*; 6, *P. o. paraguensis*; 7, *P. o. peruviana*; 8, *P. o. veraecrucis*. Boundaries between subspecies are not shown because subspecies are not well defined. Adapted from Nowak (1975), Seymour (1983), and Swank and Teer (1989). Drawn by S. Poray-Swinarski.

binowitz, 1986*a*). Individuals weighing 130 kg to 158 kg occasionally are reported (Guggisberg, 1975; Perry, 1970).

Overall, coloration varies from pale yellow to tan or reddish yellow. On any one individual the color is nearly uniform over the median-dorsal area, although it pales to buff or white on the cheeks, side of neck, throat, outer surfaces of legs, and lower parts of the flanks (Nelson and Goldman, 1933). Color is generally whitish on the throat, belly, and insides of limbs. Jaguars are profusely spotted at all ages; spots on the sides frequently form rosettes that enclose one or several dots (Nowak and Paradiso, 1983). Along the middle of the back the spots elongate and tend to merge. The spots often form more or less longitudinal rows on flanks, roughly parallel to the median stripe. However, the spotting is extremely variable and often is not the same on right and left sides of an animal (Nelson and Goldman, 1933). The spots are solid on the head and neck and on the belly turn into large blotches. The tail is white underneath, with two or three black rings near the end and the tip is usually black (Cabrera and Yepes, 1960).

DISTRIBUTION. The distribution of the jaguar (Fig. 3) once extended from the southwestern United States (Brown, 1983) to southern Argentina (Lehmann-Nitsche, 1907). However, hunting pressure and habitat destruction have caused its extirpation from much of its former range (Thornback and Jenkins, 1982). It is now extirpated from the United States (Brown, 1983), El Salvador, Uruguay (Koford, 1975), and the developed areas of the Brazilian coast (Thornback and Jenkins, 1982). It has a limited range in Mexico, Guatemala, and Argentina (Thornback and Jenkins, 1982; Arra, 1974). It is not mentioned as presently occurring in Chile (Koford, 1976) or Nicaragua and is endangered in Bolivia, Panama, Costa Rica, and Honduras (Thornback and Jenkins, 1982). It is also considered rare in much of Peru, Colombia, and Venezuela (Mondolfi and Hoogesteijn, 1986; Paradiso, 1972).

The largest remaining population now occurs in the Amazonian rainforest in Brazil, but jaguars are difficult to census due to their secretive nocturnal habits and dense forest cover (Thornback and Jenkins, 1982). The jaguar is mainly tropical in distribution, usually selecting dense cover near water, although it has been reported from a diversity of habitats (Perry, 1970). They rarely are found at altitudes over 1,000 m (Grimwood, 1969), however there are records of jaguars at 2,000 m in Venezuela (Mondolfi and Hoogesteijn, 1986), 2,100 m in northern Peru (Osgood, 1914), and 2,700 m in Bolivia (Guggisberg, 1975). Scant records exist to suggest its possible presence in eastern North America since the arrival of Europeans (Daggett and Henning, 1974; Nowak, 1975; Simpson, 1941*b*).

FOSSIL RECORD. Fossil jaguars in North America date back to the middle Pleistocene, or Irvingtonian Land Mammal Age (Schultz et al., 1985). Kurtén and Anderson (1980) suggested that these earliest jaguars may have been conspecific with the middle Pleistocene *P. gombaszoegensis* of Eurasia (see Hemmer, 1971) that probably migrated across the Bering land bridge to reach North America at that time. Fossil finds of pre-Wisconsinan jaguars (that is, middle Rancholabrean Land Mammal Age or earlier) range as

far north as the states of Washington, Nebraska, and Maryland, while the Wisconsinan finds do not range as far north, reaching approximately Nevada, Missouri, and Tennessee (Fig. 3; Kurtén, 1973). In Recent times, the jaguar ranged only as far north as Arizona, New Mexico, and Texas (Brown, 1983; Lange, 1960; Nowak, 1975). This range reduction, from the middle Pleistocene to the Recent demonstrates that the living species can be considered to be a relict population of a once more widely distributed Holarctic form (Kurtén and Anderson, 1980). The fossil form is commonly called *P. onca augusta* and is 15 to 20% larger than most of the living subspecies. It underwent a size reduction during the Pleistocene in which its limbs, and especially its metapodials, became relatively shorter (Kurtén, 1973). There are over 60 late Pleistocene and 13 middle Pleistocene fossil finds in North America, whereas only 18 late Pleistocene finds have been reported from South America (Seymour, 1983).

FORM AND FUNCTION. As in other pantherines, the short hairs on the nose spread almost to its anterior margin so that in dorsal view none or only a narrow part of the hairless rhinarium is visible (Hemmer, 1966; Pocock, 1917). The shape of the rhinarium is the same as in other *Panthera* (Pocock, 1917). The cervical whorl of hairs (Mähenwirbel) is found, as in other pantherines, at the base of the shoulders or the sides of the neck, rather than immediately below the back of the ears as in the Felinae and *Uncia* (Hemmer, 1966; Leyhausen, 1950). Albinistic jaguars were reported by Rengger (1830) and Sanderson (1955); Fitzinger (1869) even attempted to base a subspecies on an apparently albinistic color phase from Paraguay, but no specimens are known. Melanism is more common in the jaguar than in other felids, except perhaps the leopard (Loxton, 1973). Melanistic jaguars have been reported to outnumber the spotted in drier areas of northeast Brazil (Bates, 1875), and to be more common in hot, humid forests than in higher, drier areas, thus following Gloger's Rule (Searle, 1968; Severtzov, 1858).

The pupil is round (Gray, 1867) and the iris color is golden to reddish yellow (Cabrera and Yepes, 1960). There are four mammae. The os penis is a cylindrical or conical rod that is little ossified and quite variable. Measurements are 8.0 to 8.3 mm long, 2.0 to 2.2 mm high, and 1.5 to 2.0 mm wide at the proximal end (Didier, 1949; Kratochvíl, 1976). The clavicle is 5 cm in length and functionless (Martin, 1832).

Skull function and features are similar to those of other pantherines (Haltenorth, 1936, 1937). An elastic ligament is interposed between the ceratohyal and the upper bones of the hyoidean apparatus as in other *Panthera*, although the epihyal is largely retained in contrast to other pantherines (Pocock, 1916*a*). Although Pocock (1916*a*) suggested that this enabled the pantherines to roar, Peters (1978) believed there was no evidence for this supposition. The auditory bulla has a small outer chamber and large inner chamber as in the other pantherines (Pocock, 1916*b*). For one jaguar, the length of the cochlear duct was 33.3 mm, the cochlea had 2.75 turns and there were 16,340 hair cells in the organ of Corti (Burda et al., 1984). These hair cells atrophy with age (Ülehlová et al., 1984). Jaguars have a stiff mandibular symphysis that allows recruitment of more muscle for mastication (Scapino, 1981).

The spinal column consists of 7 cervical, 13 thoracic, 7 lumbar, 3 sacral, and about 19 caudal vertebrae. The percentage of intervertebral discs relative to length of vertebral column is greater in the jaguar than in domestic cats; this presumably correlates with greater flexibility of the spine in the jaguar (Lohse and Baba, 1982).

The tongue is flattened at the tip, with the upper surface covered by sharpened papillae that are reflected backwards; these diminish in size to the base of the tongue (Hemmer, 1966; Martin, 1832). The most posterior papillae are separated from the epiglottis by a smooth mucous surface (Sonntang, 1923). The papillae function to clean the fur and to remove the remnants of flesh from bones (Rabinowitz, 1986*b*).

The deciduous carnassial pair is formed by dP3/dp4 while the adult pair is P4/m1. The P2 tends to be lost prematurely; the alveolus often closes (Cabrera and Yepes, 1960). The canines serve to hold and kill larger prey by crushing their bones (Rabinowitz, 1986*b*). Six of 92 skulls examined had one or more canines broken, and in one case all canines were broken and worn to stubs, apparently testifying to the animal's survival after the loss of its canines (Nelson and Goldman, 1933). The maximum gape was reported as 131 ± 7.8 mm (Kiltie, 1984), or an angular gape of approximately 65 to 70° (Emerson and Radinsky, 1980).

In the lungs of one female jaguar there were three lobes on the left and four on the right, as well as 34 rings in the trachea. The liver had five lobes, the small intestine was 4.2 m long, the large intestine 0.76 m long, and a caecum was present (Martin, 1832). The mass of organs (in g) for one captive female were: body mass, 34.47 kg; eyes, 17.28; heart, 186; brain, 147; lungs, 576; liver, 894; spleen, 62.12; kidney, 164.5; adrenal, 7.46; thyroid, 1.72 (Crile and Quiring, 1940). One female jaguar had a rapid turnover of iodine in the thyroid (Joasoo et al., 1975).

The morphology of the elbow (Gonyea, 1978) and body proportions (relatively shortest forelimbs and hind limbs of all the pantherines, especially noticeable in the proportions of the tibia and third metatarsal) correlate with its usual habitat of dense forests and therefore reduced cursorial behavior (Gonyea, 1976). The feet are digitigrade and typically pantherine in structure (Pocock, 1917). There are five toes on each forefoot, the pollex or first toe is smaller and set above the others. Each hind foot has four toes, the first toe being represented only by a tiny vestigial metatarsal bone. Each digit including the pollex has a sharp retractile claw. Claw retraction, as in other Felidae, is a function of the dorsal elastic ligaments attaching to the middle and distal phalanges and not of the forearm extensor muscles; claw protrusion requires contraction of both forearm flexor and extensor muscles (Gonyea and Ashworth, 1975).

The adult male pugmarks are apparently larger, rounder in shape, and have a greater spread of the toes compared to the adult female (Schaller and Crawshaw, 1980). On a sample of nearly 70 jaguars, the forefoot pugmarks averaged 9 cm long by 10 cm wide and those of the hind foot averaged 9 cm long by 9 cm wide (Rabinowitz, 1986*b*). The width of the forefoot was given as 12 cm and the width of the hind foot as 7.5 cm by Murie (1974).

Feces are cylindrical in shape, although they vary greatly. They primarily consist of hair and bones of prey animals (Aranda, 1981).

The body size of jaguars changes with latitude (Cabrera and Yepes, 1960; Simpson, 1941*a*). However, size differences correlate to some extent with prey size and not latitude (Kiltie, 1984; McNab, 1971).

Captive animals average 10.8 h of sleep/night with single sleeps of 50 to 113 min being common (Zepelin, 1970). Aserinsky (1977) reported a range of 2.5 to 12.5 h of sleep/night with mean Rapid Eye Movement sleep of 1.10 ± 0.42 h and mean non-Rapid Eye Movement sleep of 7.03 ± 2.98 h.

ONTOGENY AND REPRODUCTION. The average length of intercourse (n = 40) is 9 s (range, 2 to 35 s; Stehlik, 1971). However, Hill et al. (1976) observed an average of 2 to 3 s. Gestation period varies from 91 to 111 days, the average being 101 days (Hemmer, 1979). Cubs are born in a sheltered place such as in a cave, under an uprooted tree, in a thicket, among rocks, or under the bank of a river (Guggisberg, 1975). One to four young are born, usually two (Canevari, 1983). In Belize, 52% of 23 sightings of mother and cubs involved two cubs, 35% one cub, and 13% three cubs (Rabinowitz, 1986*b*). In captivity, births have been recorded in every month of the year (for example, Zuckerman, 1953); this may also hold true for wild animals, especially those living in tropical areas such as southern Venezuela (Mondolfi and Hoogesteijn, 1986). However, in more northerly and southerly parts of its range there is evidence for a breeding season. Births are more common in Paraguay from November to December (Rengger, 1830), in Brazil from December to May (Crawshaw, 1987), in Argentina from March to July (Crespo, 1982), in Mexico from July to September (Leopold, 1959), and in Belize from June to August (Rabinowitz, 1986*b*). In Belize, the young are usually born during the rainy season when prey is more abundant (Rabinowitz, 1986*b*), hence a distinct seasonality in births in other parts of its range could be linked to prey availability.

The young are usually born with their eyes closed, opening after 3 to 13 days, averaging 8 days (Hemmer, 1979). However, Stehlik (1971) reported that four of five cubs born in captivity opened their eyes on the first day. Young have a long, coarse, woolly pelage, pale buff in color, and heavily marked with round black spots that may have pale-colored centers (Perry, 1970). The cubs also have black stripes on their faces at birth (Ricciuti, 1979). Cubs are about 40 cm long at birth and mass is 700 to 900 g, averaging 800 g (Hemmer, 1979; Perry, 1970). They gain mass at an average of 48 g/day for the first 50 days, ranging from 34 to 69 g/day (Seifert, 1964). The lower incisors erupt at 9 to 19 days, the upper incisors at 11 to 23 days, the upper canines around 30 days, and

the lower canines at 36 to 37 days (Stehlik, 1971). The permanent teeth erupt in the same sequence as other Felidae, that is: upper teeth—P2, M1, P4, P3; lower teeth—ml, p4, p3 (Slaughter et al., 1974). The young first walk at about 18 days (Hemmer, 1979) and may begin to take meat around 10 to 11 weeks, although suckling may continue for 5 to 6 months (Hunt, 1967; Stehlik, 1971). They begin to follow their mother at approximately 6 weeks although they may remain in the den for 2 months (Canevari, 1983; Guggisberg, 1975). They take adult coloration around 7 months and remain with the mother for 1.5 to 2 years (Guggisberg, 1975; Mondolfi and Hoogesteijn, 1986). Sexual maturity ranges from 2 to 2.5 years to just over 3 years for females (Hemmer, 1979; Leal, 1979) and 3 to 4 years for males (Mondolfi and Hoogesteijn, 1986). The age of last reproduction is about 8 years (Eisenberg, 1986). Captives have lived to 22 years of age (Nowak and Paradiso, 1983). In Belize, Rabinowitz (1986*b*) found few wild jaguars over 11 years of age.

Variation occurs in length of estrous cycle. The following data (average heat length, range, *n*, interestrous length, range, *n*) give lengths of estrous cycles for four captive jaguars: 6.8, 6 to 8, 9, 29.5, 14 to 58, 8; 8.8, 5 to 11, 4, 22, 13 to 38, 3 (Stehlik, 1971); 12.9, 6 to 17, 10, 42.6, 26 to 60, 8 (Sadleir, 1966); 12, 11 to 13, 7, —, —, — (Wildt et al., 1979). The total length of cycle for this last jaguar (from first day of heat of first cycle to first day of heat of second cycle) was (average, range, *n*): 47,2, 41 to 53, 6 (Wildt et al., 1979).

The major cause of mortality is hunting by man. Young are reported to be preyed upon by other jaguars (Mondolfi and Hoogesteijn, 1986; Ricciuti, 1979), crocodilians, and large snakes (Wrigley, 1986). Accidental death in the wild may occur when an adult jaguar loses a contest with an intended prey species such as puma (*Felis concolor*), anaconda (*Eunectes*), or a herd of peccaries (*Tayassu*; Perry, 1970); venomous snakes probably also take a minor toll.

ECOLOGY. As implied by their original extensive geographic distribution, jaguars apparently are tolerant of a variety of environmental conditions. They are most commonly found in areas with considerable plant cover, a water supply, and sufficient prey. They have been reported from the following habitat types: rainforest, low-scrub jungle, lowland semi-deciduous forest, open tree and shrub woodland, swampy savanna, lagoons, marshland, floating islands of vegetation, thorn scrub, pampas/llanos, and deserts (Guggisberg, 1975; Leopold, 1959; Mares et al., 1981*a*, 1981*b*; Mondolfi and Hoogesteijn, 1986; Perry, 1970). In Brazil, jaguars utilize all vegetational types (Schaller, 1983).

In Brazil, there was an estimated density of 1/12.5 to 25 km² with 4/137 km² (Schaller, 1983; Schaller and Crawshaw, 1980). Using radio-telemetry, it was found that one female ranged over 25 to 38 km² and a male ranged more than 90 km². The range of neighboring females overlapped, and the range of the male included the ranges of all the females (Schaller and Crawshaw, 1980). In Belize, it was estimated that 25 to 30 jaguars were present in about 250 km². Radio-telemetry studies revealed that of four males, ranges varied from 28 to 40 km² with an average of 33.4 km². Two females had ranges of 10 and 11 km², respectively. The home range of the two females did not overlap, but those of the males extensively overlapped (Rabinowitz, 1986*b*). They often remained within small areas of their range (2.5 ± 0.6 km²; $n = 16$) for 4 to 14 days (average, 7) before shifting to another part of their range (Rabinowitz and Nottingham, 1986). Estimates of home range vary from 2 to 5 km² in Mexico (Leopold, 1959) to 100 km² (Koford, 1976) and even 390 km² in Brazil (Doughty and Myers, 1971). About 4,000 km² may be needed to ensure annual production of several young (Koford, 1976).

More than 85 prey species have been reported. Diurnal terrestrial mammals with a body mass >1 kg are the chief prey, although other mammals, reptiles, and birds are important components (Emmons, 1987). Jaguars are particularly fond of peccaries (*Tayassu tajacu* and *T. pecari*), capybaras (*Hydrochoerus*), pacas (*Agouti paca*), agoutis (*Dasyprocta*), armadillos (*Dasypus*), caimans (*Caiman*), and turtles (*Podocnemis*; Emmons, 1987; Guggisberg, 1975; Mondolfi and Hoogesteijn, 1986; Perry, 1970; Watt, 1987). In contrast to the puma, jaguars rarely take deer (*Odocoileus*), although they take brocket deer (*Mazama*) and marsh deer (*Blastocerus dichotomus*; Schaller and Vasconcelos, 1978; Watt, 1987). Other prey include: opossums (*Didelphis*), monkeys, (*Alouatta seniculus, Aotus trivirgatus*), otters (*Lutra*), ocelots (*Felis pardalis*), skunks (*Conepatus*), kinkajous (*Potos flavus*), tapirs (*Tapirus*), sloths (*Bradypus, Choloepus*), anteaters (*Myrmecophaga, Tamandua*), porcupines (*Coendu*), coypus (*Myocastor coypu*), anacondas (*Eunectes murinus*), boas (*Boa constrictor*), tortoises (*Geochelone*), iguanas (*Iguana iguana*), anhingas (*Anhinga anhinga*), herons (*Ardea cocoi*), storks (*Jabiru mycteria, Euxenura maguari, Mycteria americana*), currassows (*Crax*), catfish (*Pseudoplatystoma fasciatum, Phractocephalus hemiliopterus*), frogs (Ranidae), and crabs (Decapoda; Canevari, 1983; Emmons, 1987; Guggisberg, 1975; Husson, 1978; Leopold, 1959; Mondolfi and Hoogesteijn, 1986; Perry, 1970; Rabinowitz, 1986*a*; Rabinowitz and Nottingham, 1986; Schaller and Crawshaw, 1980; Schaller and Vasconcelos, 1978; Watt, 1987). They also eat grass and apparently are fond of avocados (van der Pijl, 1982). They are opportunistic feeders, especially in rainforests, and their diet varies according to prey density and ease of prey capture (Emmons, 1987; Rabinowitz and Nottingham, 1986; Watt, 1987). Most species are taken in about the ratio of occurrence although jaguars in Peru tend to prey on peccaries more frequently than expected (Emmons, 1987). In Belize, the diet of jaguars was more varied in the dry season than in the rainy season (Watt, 1987). Individual jaguars are known to develop a preference for certain livestock such as cattle, horses, pigs, or dogs (Brock, 1963; Husson, 1978; Leopold, 1959; Mondolfi and Hoogesteijn, 1986). When these particular jaguars are removed from an area, livestock losses cease even though there are other jaguars in the vicinity (Leopold, 1959; Rabinowitz, 1986*a*). The majority of problem jaguars in Belize had suffered previous injuries, especially shotgun wounds (Rabinowitz, 1986*a*). In Brazil, jaguar predation on cattle accounted for only a small percentage of livestock deaths even though untended livestock could become the major food of a healthy jaguar (Schaller, 1983).

Parasites reported from the jaguar include the protozoans *Hammondia pardalis, Isospora* sp., and *Toxoplasma*-like organisms (Patton et al., 1986), the trypanosome *Trypanosoma evansi* (Sen and Chowdhuri, 1968), and the trematode lung fluke *Paragonimus* sp. (Patton et al., 1986). Tapeworms include *Diphyllobothrium* (Carneiro et al., 1972), *Echinococcus oligarthrus* (Thatcher and Sousa, 1967), *Spirometra* sp. (probably *Spirometra mansanoides*; Watt, 1987), *Taenia macrocystis* (Verster, 1969), *Toxascaris, Toxocara cati* (Patton et al., 1986), and *Toxocara mystax* (McClure, 1933). Also reported are the acanthocephalan *Oncicola oncicola* (Thatcher and Nickol, 1972), the hookworms *Ancylostoma tubaeformae* and *A. pleuridentatum* (Thatcher, 1971), Strongylida, probably *A. brasiliensis* (Watt, 1987), and *Aelurostrongylus* sp. (Patton et al., 1986), the spiruriid nematode *Physaloptera anomala* (Ortlepp, 1924), and the whipworm *Capillaria* (Patton et al., 1986). External parasites are the screwworm *Cochliomya homnivorax* (Rawlins et al., 1983), warble fly larvae *Dermatobia hominis* (Jobsen, 1974), and the fungus *Trichophyton* (Schönborn, 1970). In captive animals, various types of tumors have been reported (Bossart and Hubbell, 1983; Kollias et al., 1984; Ladiges et al., 1981; Lohse and Baba, 1982; Port et al., 1981; Rasheed and Gardner, 1981), as well as anthrax (Abdulla et al., 1982), pox virus (Marennikova et al., 1977), and diabetes (Kollias et al., 1984).

Pumas and jaguars are known to have overlapping ranges and have little interaction; indeed they seem to mutually avoid one another (Emmons, 1987; Rabinowitz, 1986*b*; Rabinowitz and Nottingham, 1986; Schaller and Crawshaw, 1980). This is not the case for jaguar and ocelot (Emmons, 1987). When the ranges of pumas and jaguars overlap, pumas are more abundant in drier areas and jaguars select wetter areas (Emmons, 1987; Schaller and Crawshaw, 1980).

In 1973, the jaguar was placed on Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and is presently classified as vulnerable by the International Union for Conservation of Nature and Natural Resources (IUCN). This means that trade in it or its products is subject to strict regulations by ratifying nations and trade is banned for commercial purposes (Thornback and Jenkins, 1982). However, not all nations in which the jaguar lives are presently ratifying nations, most notably Mexico. Nevertheless, the jaguar is legally protected in Mexico, Brazil, Venezuela, Colombia, Peru, and Belize (Hornocker, 1971; Koford, 1974; Lemke, 1981; Mondolfi and Hoogesteijn, 1986). Legal protection is difficult to enforce in most countries and there is still a black market for jaguar skins. Prior to CITES protection in 1973, large numbers of jaguar pelts were shipped from South America, primarily to the United States, England, and West Germany (Doughty and Myers, 1971). For example, during 1968,

13,516 jaguar skins reached the United States (Nowak and Paradiso, 1983).

A few large parks in Bolivia, Brazil, Colombia, Peru, and Venezuela protect some jaguars; others are essentially protected on large, privately owned ranches in Brazil and Venezuela (Thornback and Jenkins, 1982). The world's first nature preserve created specifically for the protection of the jaguar was created in Belize on 2 December 1984 (Rabinowitz, 1986*b*). To afford adequate protection for the remaining populations and their habitat, it was suggested that assessment of population sizes and habitat evaluation, as well as control of hunting, are necessary (Mondolfi and Hoogesteijn, 1986).

Jaguars are kept in many zoos and breed well (Leal, 1979). It is also possible to hand-rear newborn jaguars (Seifert, 1964).

Several methods for hunting jaguars, as used by both sportsmen and native hunters, are: waiting in ambush at, or following vultures to, a fresh kill; attracting them by grunting into a hollow gourd (coroteo); tracking them unaided or with trained dogs; poisoning a carcass; and setting up a shotgun trap (Mondolfi and Hoogesteijn, 1986). These last two methods commonly are employed to eliminate problem jaguars. The trained-dog method is perhaps the most commonly used (Roosevelt, 1914; Siemel, 1965). Live jaguars can be trapped in cages and radio collared as described by Rabinowitz (1986*b*). However, this method sometimes proves too dangerous; the animals tended to break their canines on the bars of the cage.

BEHAVIOR. Movements are similar to other members of the Pantherinae except jaguars sometimes appear more clumsy than the leopard. Their strides are about 50 cm long, and their tail is often carried in an upwardly curved position as in the leopard. They climb trees quite well, but they do not do so as often as does the puma. Jaguars like water and can swim exceedingly well, usually with their head and spine out of the water. They hunt and play in water perhaps even more frequently than the tiger. When emerging from the water they shake the body and each of the paws separately (Guggisberg, 1975). Many times they have been seen swimming between islands and the shore (Perry, 1970). Postures, in general, are the same as in the other Pantherinae (Hemmer, 1966). Eating is done usually in a squatting or crouching position, frequently with paws on the kill (Guggisberg, 1975). Sleeping posture, often on the back, may be explained as a functional correlation of body size and proportions (Hemmer, 1966, 1972).

Jaguars usually catch and kill their prey by stalking or ambush and by biting through the nape as do most Felidae (Leyhausen, 1979). For larger prey, such as cattle, they jump on the victim from the back or side, reach one paw over to grip the head and pull it around, so the animal unbalances and falls to the ground. The neck is usually broken in the fall; the usual bite does not break the neck (de Almeida, 1976). Sometimes they bite through the skull (Rabinowitz, 1986*b*) or occasionally through the neck vertebrae of large prey (Brock, 1963; Mondolfi and Hoogesteijn, 1986). They rarely kill by biting the throat or by asphyxiation as do the tiger or leopard, respectively. The jaguar has developed a special bite for killing capybara. It bites from above or below, with its head at right angles to the victim and cracks the skull like a nutshell, sometimes inserting one upper and one lower canine into an ear of the victim (Leyhausen, 1979; Schaller and Vasconcelos, 1978). Most capybara taken by jaguars are young individuals, 4-years old or younger (Schaller et al., 1984). Jaguars also are fond of turtles and will flip them onto their backs before proceeding to scoop out the entire insides. They are remarkably adept at consuming whole turtles (*Podocnemis*) or tortoises (*Geochelone*) in this fashion without breaking the shell. Jaguars also may break turtle shells to ease their consumption. To consume caimans, they turn them over and eat the unprotected underparts first; they may not eat the head, tail, and feet. Smaller prey species may be killed with one blow of the paw to the head (Mondolfi and Hoogesteijn, 1986).

Two eyewitness accounts as well as legends attest to the jaguar using its tail to attract fishes to the surface, whereupon it scoops them out of the water with a paw (Gudger, 1946). Jaguars do capture fish in this manner; whether the tail is consciously used to attract fish is still a matter of conjecture.

Jaguars sometimes move their kill to a more secluded or protected place, rarely in a tree; this may mean dragging large prey >2 km (Mondolfi and Hoogesteijn, 1986; Roosevelt, 1914). For 11 kills, an average distance of 87 m was recorded. Jaguars drag their prey while straddling it with their forelegs, with the carcass in their mouth, as does the tiger (Schaller and Vasconcelos, 1978). They will cross rivers with their prey (Perry, 1970). Jaguars often consume the whole animal, even the skin, bones, hooves, and claws (Emmons, 1987; Rabinowitz and Nottingham, 1986; Watt, 1987). They tend to consume the tongue, neck, and foreparts (brisket) of large animals first; often the rear end is not touched (Brock, 1963). They also like to eat the internal organs (heart, liver, spleen) but not the intestines, which they sometimes will move for some distance without breaking them (Schaller and Vasconcelos, 1978). If disturbed, and prey is abundant, they will abandon their prey without eating it. They may return to the kill a few hours later, or as many as 3 days later (Schaller and Crawshaw, 1980). They usually make no attempt to hide their kill as do tigers (Schaller, 1967) and pumas (Hornocker, 1970).

The jaguar is the least likely of the pantherines to attack man and is virtually undocumented as a maneater. Two cases were documented by Roosevelt (1914); other possible cases are recorded in Perry (1970) and Guggisberg (1975), but such occurrences are difficult to verify. There is no record of a jaguar systematically hunting man for food, as the tiger, lion, and leopard occasionally will do (Mazák, 1981). Scavenging is rare, but has been reported (Koford, 1975).

Although several jaguars may frequent the same area, they usually are solitary, except during mating or when the young are still dependent on their mothers (Perry, 1970). Young sibling pairs sometimes travel together (Emmons, 1987). Jaguars use a land-tenure system (Rabinowitz and Nottingham, 1986) similar to that used by tigers (Sunquist, 1981), leopards (Schaller, 1972), and pumas (Seidensticker et al., 1973). Land tenure seems to be based on a "first come" system; when one animal dies,the ranges of the others shift (Rabinowitz and Nottingham, 1986).

Jaguars primarily hunt at night and on the ground (Rabinowitz, 1986*a*). One female in Brazil was active for two-thirds of the day and inactive for the remaining one-third (Schaller and Crawshaw, 1980). Her activity pattern tended to be as follows: rest, 0030 to 0300 and 0930 to 1200; travel, 0330 to 0600 and 1830 to 2100; transition, 0630 to 0930, during which time she was locally active. Thus, this animal was almost equally active during both day and night, and the 24-hour activity pattern was quite variable; the distance travelled in any 1 day varied from 2 to 5 km and occasionally >18 km. Male jaguars in Belize behaved in a similar fashion (Rabinowitz and Nottingham, 1986).

Jaguars are not known to migrate regularly, although lone males have been known to roam hundreds of kilometers (Perry, 1970). Local adjustments of range may take advantage of seasonal changes in habitat (Husson, 1978). When pursued they may travel 65 km in one evening (Perry, 1970). Jaguars are known to use dens, especially when rearing young, although non-breeding adults also have been known to make dens in caves (Guilday and McGinnis, 1972; Mondolfi and Hoogesteijn, 1986), canyons (Guggisberg, 1975), and ruins of ancient civilizations (Loxton, 1973).

Young captive jaguars display "threat and attack" behavior as well as "neck snapping"; these are more or less ritual forms of fighting, but probably form part of the learning process for the young (Leyhausen, 1979). The first few months of vocalization consist solely of bleating; gurgling develops next, and then mewing, which replaces gurgling at 3 to 6 months. The pitch of calls lowers with age; 1-year old jaguars have gained the full repertoire, with the exception of some structured call sequences exclusively associated with reproductive behavior (Peters, 1978). Prusten is well developed in jaguars; it consists of an atonal, low-intensity, short (<1 s) snorting sound composed of several pulses, usually <10, divided by phases of decreasing intensity (Peters, 1978, 1984). These vocalizations are unique to jaguars, tigers, snow leopards (*Uncia uncia*), and clouded leopards (*Neofelis nebulosa*; Hemmer, 1972; Peters, 1978). By the end of the second year jaguars develop a structured call sequence; these calls develop without learning from conspecifics (Peters, 1978). The most noted vocalization in the adult is the "grunt" sometimes described as a hoarse barking cough (Pocock, 1916*a*) consisting of five or six gutteral notes (Guggisberg, 1975). These vocalizations are done by both male and female and may serve for communication, especially during mating periods (Crawshaw, 1987).

Scraping, urination, scent marking, deposition of feces, and tree raking may function in communication or as territory markers (Perry, 1970; Wemmer and Scow, 1977). In Belize, only scraping and feces deposition were recorded; these signs were noted partic-

ularly in areas of territory overlap (Rabinowitz and Nottingham, 1986). These scrapes averaged 37 cm long (n = 26; range, 18 to 58 cm) and 10 cm wide (n = 21; range, 7 to 19 cm). Peruvian jaguars of both sexes go through periods of intense scraping (Emmons, 1987). The aforementioned signs were rarely noted in Brazil (Schaller and Crawshaw, 1980). Jaguars in Brazil select the morcequeira tree (*Andira inermis*) for tree raking, probably because of its thick trunk and rough bark (de Almeida, 1976). The bolletrie (*Manilkara bidentata*) is selected in Suriname (Husson, 1978). Tree scraping may only serve to remove loose claw sheaths as in the puma (Seidensticker et al., 1973) and may not serve any communication function (Mondolfi and Hoogesteijn, 1986). Jaguars have been observed spraying urine backwards in the typical felid fashion (Fiedler, 1957). Urine spraying has been noted for the male jaguar, but not for the female. Head-rubbing and claw-raking also have been noted as scent-marking behavior (Wemmer and Scow, 1977).

Mating behavior is as in other Felidae. During mating the female growls and the male licks the nape of her neck. When finished, the male bites her neck and jumps away while the female continues to roll around. Afterwards the male often drinks, urinates, or licks his genitals (Stehlik, 1971). During mating periods, fighting over a female is not common, although more than one male may follow a female (Mondolfi and Hoogesteijn, 1986). During estrus there is a marked change in the female's behavior. Although her appetite does not decrease, she growls, rubs against objects, and rolls on the ground more frequently. The female will not let the male near her cubs as he may eat them (as tigers sometimes do; Sunquist, 1981). Up to weaning, the female will eat the feces of cubs (Stehlik, 1971).

Jaguars are sensitive to catnip (*Nepeta cataria*) even though the two are allopatric in the wild. Reproductive-aged adults are more sensitive than either aged or immature individuals (Hill et al., 1976).

GENETICS. The jaguar has 19 pairs of chromosomes as do the majority of felids. Seventeen pairs are metacentric or submetacentric and two are acrocentric or submetacentric. The total number of chromosome arms is 36; this pattern is the most common among the felids (Robinson, 1976). The X chromosome is medium and metacentric and the Y chromosome is small and subtelocentric (Hsu et al., 1963).

Melanism is inherited as monogenic dominant to the normal colored form (Dittrich, 1979). Previous literature (Carvalho and Yonenaga, 1972; Rich, 1976; Ricciuti, 1979) assumed that melanism was inherited recessively as is true for the leopard (Robinson, 1969, 1970).

In captivity, jaguars and leopards have been successfully crossed a number of times and even backcrossed (Fitzinger, 1855; Gray, 1972; Severtzov, 1858). The offspring are called leguars or jagopards depending on whether they are descendants of a male leopard and female jaguar or vice versa, respectively (Peters, 1978). Female hybrids can be fertile (hence successful backcrosses); male hybrids are reported as healthier and stronger than leopard or jaguar cubs, but fertility is unrecorded (Windischbauer, 1968). A hybrid between a male lion and a female hybrid of a jaguar and leopard has been reported (Hemmer, 1968).

REMARKS. The generic name *Panthera* Oken, 1816 frequently has been used in the general zoological literature as well as in specialized taxonomic publications (Mazák, 1981); recently it has been more commonly used for the jaguar than has *Felis* or *Leo* (Neff, 1986). Hemmer (1966) demonstrated that the pantherines are behaviorally and morphologically distinct from the felines and hence should not be placed in the genus *Felis*. Although Oken's (1816) publication has been ruled unavailable for nomenclatural purposes by the International Commission on Zoological Nomenclature, this same Commission has ruled that *Panthera* Oken, 1816 is available (Tubbs, 1985).

Subspecific synonymies used here are from Pocock (1939). Although he did not have access to enough specimens to critically evaluate all subspecies, his comments implied that *P. o. goldmani* could be synonymized with *P. o. centralis*, and likewise *P. o. peruviana* with *P. o. onca* and *P. o. arizonensis*, *P. o. centralis*, and *P. o. veraecrucis* with *P. o. hernandesii*. If these changes were to be made, only three subspecies would remain: *P. o. hernandesii*, *P. o. onca*, and *P. o. paraguensis*; subspecific synonymies made by Cabrera (1957) would be in accordance with this except that he placed *P. o. boliviensis* into *P. o. palustris* and not into *P. o. onca*. Since *P. o. palustris* was based upon a fossil, it should probably not be used for the description of a living subspecies. Even though Pocock (1939) and Cabrera (1957) used this name, I follow Nelson and Goldman (1933) and use *P. o. paraguensis* instead.

The jaguar was worshipped by various South and Central American cultures such as the Aztecs, Mayas, Olmecs, Toltecs, Zatopecs, and Nahualistas. There is a temple to the jaguar god in Tikal, Guatemala. The Olmecs reportedly deformed their heads to resemble this cat (Perry, 1970). In Paraguay, the celestial jaguar of the Guaraní is believed to cause eclipses (Cadogan, 1973). The importance of the jaguar in the arts and myths of North American cultures probably has been underestimated (Daggett and Henning, 1974).

The name jaguar is apparently borrowed from one of the Tupi-Guaraní languages; it was originally "yaguara" which means "wild beast that overcomes its prey at a bound" (Guggisberg, 1975). The Portuguese names for the jaguar are "onça verdadeira" and "onça pintada." The Spanish name is "el tigre." Native names for the jaguar include: yaguareté, yaúi, zauat, uturuncu, nahuel, and acangusú (Cabrera and Yepes, 1960). Native names for melanistic jaguars include: kuchí kudáu, ming shá, and yaguaretehú (Ambrosetti, 1894).

I thank P. Purves for typing the manuscript, E. M. Watt for helpful discussions and references, S. Poray-Swinarski for drafting the figures, and P. Trunks for locating many of the older papers.

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