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Nasua narica.

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Nasua Storr, 1780

Nasua Storr, 1780:35. Type species *Viverra nasua* Linnæus, by subsequent designation.

Coati Lacepède, 1799:7. Type species *Coati nasua* Lacepède (=*Viverra nasua* Linnæus) by subsequent designation.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Canoidea, Family Procyonidae, Subfamily Procyoninae, Genus *Nasua,* which includes two species: *N. narica* and *N. nasua.* A key to the species (from Decker, 1991) follows:

Palate depressed along midline, nasal bones near parallel, anterior alveolar foramen medial to infraorbital canal, jugal postorbital process absent, baculum not spatulate, white muzzle .... *N. narica*

Palate flat (not concave along midline), nasal bones converging posteriorly, anterior alveolar foramen anterior to infraorbital canal, jugal postorbital process present, spatulate baculum, brown muzzle .... *N. nasua*

Nasua narica (Linnæus, 1766)

White-nosed coati

[*Viverra*] *narica* Linnæus, 1766:64. Type locality "America." Subsequently restricted by Hershkovitz (1951) to "Achotal, Isthmus of Tehuantepec, Vera Cruz."

[*Viverra*] *vulpecula* Erxleben, 1777:490. Type locality "in Mexico."

Nasua narica: Geoffroy Sainte-Hilaire, 1803:86. First use of current name combination.

N[*asua*] *subfusca* Tiedemann, 1808:379. Type locality "im südlichen Amerika." Designated as a synonym of *Viverra narica* Linnæus by Tiedemann.

Nasua solitaria var. *mexicana* Weinland, 1860:191. Type locality "aus dem Staate Veracruz in Mexiko [. . .] in der Nähe der Hacienda Del Mirador, zwanzig span. Leguas von Veracruz, ungefähr 4000 fuβ über dem Spiegel des Golf's von Mexiko."

Nasua nasica Winge, 1895-1896:35. Unjustified emendation of *Viverra narica* Linnæus, 1766.

Nasua nelsoni Merriam, 1901:100. Type locality "Cozumel Island, Yucatan" [=Quintana Roo], Mexico.

Nasua thersites Thomas, 1901:271. Type locality Cozumel Island, Quintana Roo, Mexico.

CONTEXT AND CONTENT. Context same as for genus. Because designation of subspecific status for *N. narica* is hampered by historical dependence on such variable traits as coat color, the synonyms of Hershkovitz (1951) are followed, although he presented only limited analyses. Thus, four subspecies are described as follows (Decker, 1991; Hall, 1981; Hershkovitz, 1951):

N. n. molaris Merriam, 1902:68. Type locality "Manzanillo, Colima, Mexico." (*pallida* Allen and *tamaulipensis* Goldman are synonyms; Hershkovitz, 1951).

N. n. narica Linnæus 1766:64, includes *vulpecula* and *subfusca,* see above. (*bullata* Allen, *panamensis* Allen, *richmondi* Goldman, *isthmica* Goldman and *N. solitaria* var *mexicana* Weinland, are synonyms; Hershkovitz, 1951).

N. n. nelsoni: Merriam, 1901:100, see above. Current name combination first used by Decker (1991:379; *thersites* Thomas is a synonym).

N. n. yucatanica Allen, 1904:52. Type locality "Chichenitza, Yucatan," Mexico.

DIAGNOSIS. *Nasua narica* (Fig. 1) differs from *N. nasua* as follows: pelage on the muzzle is white, and the hairs on the nape of the neck are in the normal posterior position. The palate is depressed along the midline, rather than being flat. The sides of the nasal bones are parallel and not converging posteriorly, and the postorbital process of the jugal bone is absent. A distinctive entoconid on the second lower molar causes the molar to have a well defined talonid, absent in *N. nasua.* The distal tip of the baculum is bilobed rather than spatulate (Decker, 1991).

Much of the taxonomic confusion regarding the recognition of both *Nasua narica* and *N. nasua* versus solely *N. nasua* (e.g., Corbet and Hill, 1986; Eisenberg, 1989) may be traced to errors in interpretations of statements originally made by Cabrera (1957; reviewed by Decker, 1991). The proliferation of pre-1900 *Nasua* species is due to taxonomic splitting based mainly on coat color variation (reviewed by Allen, 1879).

GENERAL CHARACTERS. White-nosed coatis are readily distinguishable from raccoons (*Procyon* sp.) and ringtails (*Bassariscus* sp.) by their long, slender, non-prehensile tail which is equal in length to the head and body and often held vertically erect while foraging. The white-nosed coati also has an elongated rostrum, terminating in a flexible rhinarium that protrudes beyond the end of the lower mandible. The claws are long and the feet are plantigrade with naked soles. Ears are short. The canines are more bladelike than in raccoons, and the premolars and molars have comparatively high crowns with sharp cusps.

FIG. 1. Adult male *Nasua narica* from Barro Colorado Island, Panama.

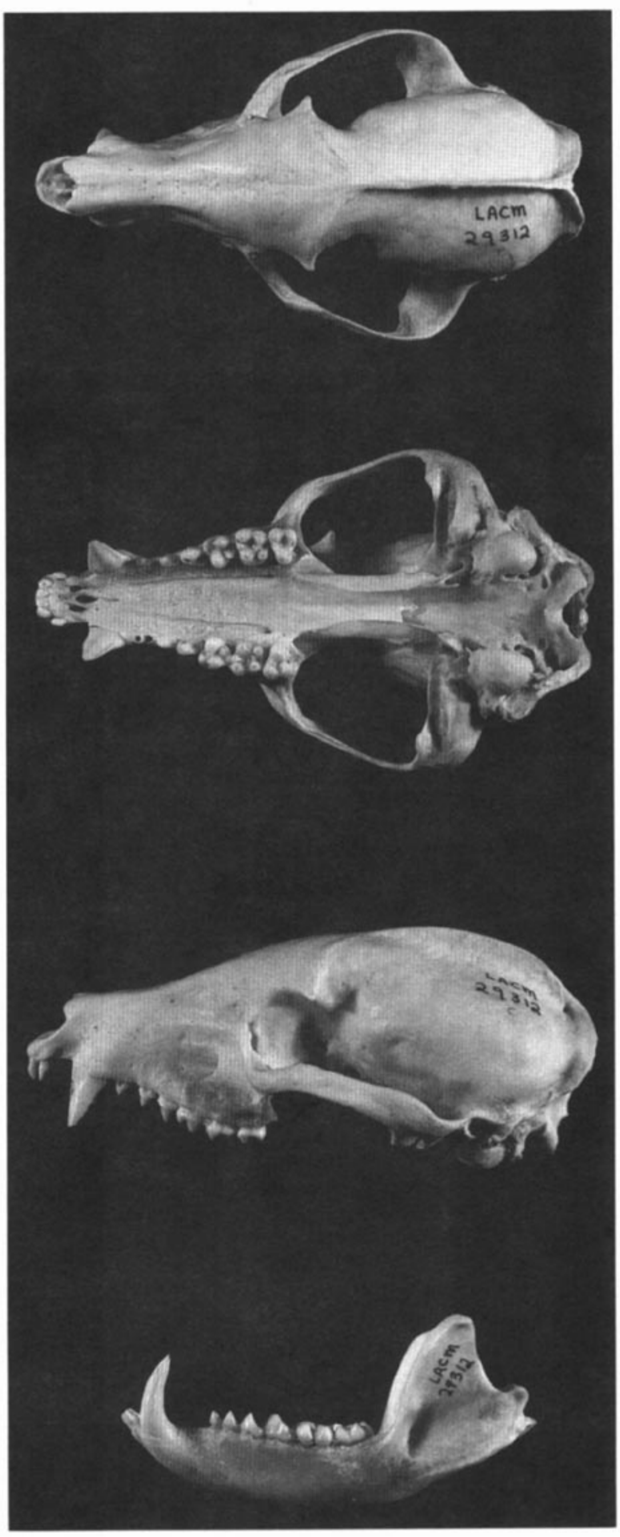

FIG. 2. Dorsal, ventral, and lateral view of skull and lower jaw of adult female *Nasua narica* (Los Angeles County Museum 29312) from Colima, Mexico. Greatest length of skull 132 mm.

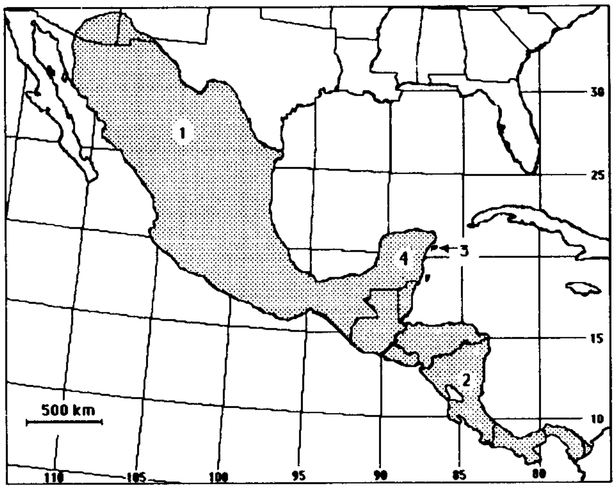

FIG. 3. Distribution of *Nasua narica* (after Decker, 1991; Hall, 1981): 1) *N. n. molaris,* 2) *N. n. narica,* 3) *N. n. nelsoni,* 4) *N. n. yucatanica.* Boundaries between subspecies are not shown because subspecies are not well defined.

Hall (1981) gives external and skull measurements (in mm) of male *N. narica* from throughout North America: total length = 850–1340; length of tail = 420–680; length of hind foot = 95–122; greatest length of skull = 107.2–136.2; condylobasal length = 100.8–128.9; zygomatic breadth = 50.8–74.6. Average measurements of three male and four female *N. n. nelsoni,* respectively, from Cozumel Island, Mexico are: total length = 785, 744; length of tail = 348, 328; length of hind foot = 84, 79. White-nosed coatis from Cozumel Island differ from mainland white-nosed coatis in being smaller and having relatively smaller teeth (Hall, 1981). Lanning (1976*b*) gives measurements (in cm ± *SD*) of adult male (*n* = 6) and adult and subadult female (*n* = 6) white-nosed coatis from the Chiricahua Mountains, Arizona; total length = 114.5 ± 7.1, 102.9 ± 2.4; length of tail = 53.8 ± 6.6, 51.4 ± 1.1; length of hind foot = 11.0 ± 0.5, 10.1 ± 0.6; length of ear = 3.7 ± 0.25, 3.6 ± 0.23; length of upper canine = 0.92 ± 0.04, 0.77 ± 0.08; length of lower canine = 1.63 ± 0.12, 0.87 ± 0.12; body mass (in kg ± *SD*) = 5.9 ± 0.6, 3.5 ± 0.3. The skull is illustrated in Fig. 2.

Extensive variations in pelage coloration are reported throughout the range of *N. narica,* even at the intrapopulation level. Breeding experiments show that even within a litter, coat coloration of individuals may be variable (Burt and Hooper, 1941; Hershkovitz, 1951; Kaufmann, 1962; Pratt, 1962; Risser, 1963; Taibel, 1977). The usual color is pale to reddish or dark brown, to almost black, often overlaid with some yellow or silver. Neck and shoulders are yellow to white; muzzle, chin, and throat are whitish; eyes are masked with pale umber to brown. Thin whitish streaks extend from the muzzle between and over the eyes. Postauricular patches are whitish to yellowish, and the ears are white tipped. Underparts are yellowish to dark brown, and the feet are blackish. Tail is colored like the dorsum and often annulated with yellow and brown. The ring pattern of the tail may be scarcely visible (Hall, 1981; Kaufmann, 1982).

DISTRIBUTION. *Nasua narica* is found from southern Arizona, New Mexico, and Texas southward throughout Mexico and Central America (Fig. 3); Decker (1991) listed three museum specimens from extreme northwestern Colombia (west of the Gulf of Uraba), and Emmons (1990) included the west coasts of Colombia, Ecuador, and northern Peru. Although some authors (e.g., Goldman, 1942; Hall, 1981; Leopold, 1959) excluded the interior highlands of Mexico from the range of *N. narica,* specimens examined by Decker (1991) came from throughout Mexico. *Nasua narica nelsoni* is found only on the island of Cozumel, off the Yucatan Penninsula. In Arizona and New Mexico, white-nosed coatis breed from the Animas Mountains in southwestern New Mexico west to the Baboquivari Mountains in Arizona, and north as far as the Gila River. Marginal records from north of the Gila River are likely from occasional wanderers or released captives. The current distribution and breeding status of white-nosed coatis in Texas is uncertain (Bailey, 1905; Davis, 1966; Jones and Jones, 1992; Kaufmann et al., 1976; Lanning, 1976*b*; Taber, 1940).

FOSSIL RECORD. Fossil *Nasua* are rare, and the fossil record is incomplete. The genus *Paranasua* is represented from Florida and Kansas, and appears closely related to *Nasua* and *Procyon. Nasua* and *Procyon* likely differentiated during the Hemphillian (9.5–4.5 mybp), as first probable records of each are from the late Hemphillian (Baskin, 1982). In North America the genus

Nasua is represented by *N. pronarica* (Dalquest, 1978) from the early Blancan (4.5–2 mybp) of Texas and a possible *Nasua* sp. (Baskin, 1982) from early Miocene of Florida. *Nasua pronarica* is characterized as larger than the modern *N. narica*, with a lower P4 with unreduced hypoconid, protoconid and hypoconid equal in basal diameter, and heel (posterior cingulum) not as well developed as in *N. narica*. It likely inhabited open forests and was omnivorous (Anderson, 1984). Both fossils differ from *N. narica* in having a narrow posterior shelf and a large posterior accessory cusp. Based on the lack of more northern examples of *Nasua*, Dalquest (1978) suggests *N. pronarica* from Texas may have been near the northern limits of the species range. Earliest records of South American *Nasua* are Pleistocene (Lujanian; 0.3 mybp–10,000 yrs bp) fossils from caves in Minas Gerais, Brazil (Berta and Marshall, 1978), and possibly Ensenadan (1.5–0.3 mybp) fossils from Tarija, Bolivia (Marshall et al., 1984).

FORM AND FUNCTION. *Nasua narica* resembles *Procyon lotor* in carotid artery patterns, with the chief difference being the enlarged caliber of the arteries supplying the olfactory apparatus. Arteries to the eyes are small relative to other Procyonidae (Story, 1951). Forearm arteries of *N. narica* are most similar to *Bassariscus*, Ursidae, and Ailuridae, and very different from those of *Procyon* and *Potos* (Davis, 1941). *Nasua narica* is the only member of the Carnivora known to lack collateral ventilation of the lungs; rather it has extremely muscular pulmonary arteries, and a vigorous pulmonary pressor response to acute hypoxia. However, *N. narica* does not develop pulmonary hypertension at high altitudes, thus breaking a cross-species pattern that thick walled pulmonary arteries at low altitude are associated with the development of severe pulmonary hypertension at high altitude (Boggs et al., 1984; Grant et al., 1976; Hanson et al., 1988, 1993; Wagner et al., 1991).

Nasua narica possesses a flexible jaw symphysis and low-cusped cheek teeth. Jaw symphyseal plates are relatively flat, with a few low rugosities that fit loosely into valleys of the complementary plate. This flexible jaw symphysis allows both widening and narrowing of the symphyseal plates, and slight medial or lateral rotations of the mandibular canine. The jaw can be shifted laterally so that buccal cusp ridges of the mandibular posterior teeth lie slightly laterally to those of their maxillary antagonists (Scapino, 1981). The dental formula is i 3/3, c 1/1, pm 4/4, m 2/2, total 40, and teeth are generally smaller than *Procyon* and larger than *Nasuella*. Carnassial blades are reduced in height, and canine shape and inclination is such that gliding contact occurs between upper and lower canines during closure of the jaws (Hollister, 1916; Scapino, 1981). The tongue is notched at the tip, and is relatively long, narrow, and thin, with small conical papillae. The apical fungiform papillae are larger and more prominent in *N. narica* than any other carnivore examined (Sonntag, 1923). *Nasua narica*, like all Procyonidae, does not possess a cecum (Mitchell, 1905).

The ear is short and round, and retains a bursa as a shallow pouch in front of the posterior edge of the pinna. Most of the muscles of the pinna are relatively small and weak (Compton, 1973; Pocock, 1921). The auditory bulla is similar in height and inflation to *Procyon lotor*, but is smaller, and shows differences in caudal entotympanic form (Hough, 1948; Hunt, 1974; Pocock, 1928). Hunt (1974) characterized *N. nasua* and *P. lotor*, but not the red panda *Ailurus fulgens*, as possessing an enlarged bulla (achieved by caudal entotympanic growth) and noted that these species inhabiting warm, arid and open environments possess expanded middle ear activities. The mallei of *N. narica* vary slightly in shape relative to other Procyonidae, but generally resemble the mallei of the Ursidae and Ailuridae (Segall, 1943). The cochlea has six half turns and is medium in size relative to *N. narica* body weight (Pye, 1979).

Organ and gland weights (g) for a 6.25 kg adult male from Guatemala were: brain = 44.17, thyroid = 1.54, adrenal = 0.54, heart = 37.97, liver = 150, eyes = 2.33, and spleen = 5.50 (Crile and Quiring, 1940). The brain of *N. narica* is similar to that of *N. nasua*, but differs from other procyonids. The *N. narica* brain possesses an enlarged sensory cortex region receiving afferent projections from the tip of the snout or rhinarium, and a forepaw reception area strongly biased for joint movement rather than the light contact characteristic of other procyonids. These data are compatible with the long snout and claws of *N. narica* relative to other Procyonidae (Anthony and Botar, 1933; Barker and Welker, 1969; Pubols et al., 1965; Welker and Campos, 1963).

The snout of *N. narica* is greatly enlongated, with the upper edge of the rhinarium extending beyond the nostrils, so that the anterior surface is nearly flat and slopes obliquely down and back. The upper lip is entire, showing no trace of a philtrum. The nostrils are elongated rather than being semicircular as in other procyonids. The internarial septum is long and narrow, and intranarial portions are deep and defined by a groove from the adjoining central portion, which has no median groove. The rostral surface of the rhinarium is densely innervated by sensory receptors, and rhinarial contact with stimuli is made more intimate and varied by the action of numerous extrinsic and intrinsic proboscis muscles, allowing unusually high proboscis mobility (Barker and Welker, 1969; Boas and Paulli, 1908; Compton, 1966, 1973; Pocock, 1921). The proboscis is capable of a large variety of movements, including dorsal and ventroflexion, lateral, dorsolateral and ventrolateral deviation, twisting, and rotational movements, all of which may be of considerable magnitude. Protrusive movements of the base of the rostrum maximize rhinarial contact with surfaces, and deft flicks of the rhinarial tip serve to poke the snout into crevices to pry them apart (Compton, 1973). Coatis curl their snouts above the water surface when drinking (Kaufmann, 1962). *Nasua narica* possesses seven ethmo-turbinal nasal cavities and four sinuses. The maxillo-turbinals resemble those of canids, but are more divided (Anthony and Iliesco, 1926).

Like many arboreal mammals, *N. narica* is able to reverse hind foot posture to descend from trees head first. However, this reversal is not complete; femoral abduction is employed as a means of extending the range of postures. A combination of crurotalar plantarflexion, subtalar inversion, and transverse tarsal supination provide about one-half the excursion possible in the completely arboreal *Potos flavus*. Tarsal structure of *N. narica* and *P. flavus* is similar, with some differences in the posterioral calcaneal facet. Unlike *P. flavus*, no evidence was found that substantial knee rotation contributed to foot reversal. Thus *N. narica* is able to grasp a trunk or vine between both feet, but apparently can neither turn the toes posteriorly nor reverse the plantar surface of the feet (Jenkins and McClearn, 1982, 1984). Shoulder morphology of *N. narica* differs from the generalized carnivore and the more primitive *Bassariscus* in the development of the postscapular fossa and its continuance into a well-defined spiral groove along the axillary border of the scapula, similar to the *Ursus* shoulder (Davis, 1949). The slender, fusiform muscles of *N. narica* usually have narrow fascicle-length distributions, and patterns of fascicle lengths can be largely accounted for by moment-arm lengths and joint-angle excursions (McClearn, 1985). The fore feet contain long, powerful, blunt, and slightly curved claws, with digits webbed up to the proximal ends of the digital pads. The underside of the digits and webs are naked, and the plantar pad is broad, moderately well defined and four-lobed. Above the carpal pad on the ulnar side there is a tuft of carpal vibrissae. Claws of hind feet are somewhat shorter than those of the fore feet, and the plantar pad is naked over the whole of the tarso-metatarsal area as far back as the tip of the calcaneum (Pocock, 1921). The calcaneum of *N. narica* is intermediate in procyonid characteristics and distinguished from that of *N. nasua* by a greater ratio of the length of the posterior articular surface to the total length, by the distinct groves on the edge of the trochlear process and on the outer edge of the body, below and proximal to the posterior articular surface (Stains, 1973). McClearn (1990, 1992*a*) has proposed that the short limbs of the coati are biomechanically suited to their digging activities. *Nasua narica* are excellent diggers and shredders, but have little fine control of digit movements, which with musculoskeletal correlates preclude grasping ability and terminal branch feeding. *Nasua narica* can stand bipedally for short periods of time, but do not normally walk bipedally (McClearn, 1992*a*).

The tip of the baculum is bilobed, with a vestigial third lobe on the ventral surface (Burt, 1960; Chaine, 1925; Decker, 1991; Didier, 1950; Pocock, 1921; Pohl, 1911). Reported length of bacula (mm, $n = 1$ for all) are 76 (Chaine, 1925), 77 mm (Pocock, 1921), 77.5 (Didier, 1950), and 97 (Pohl, 1911). These measurements may not be representative, however, as Decker (1991) notes that baculum size has not been sampled over the entire geographic range. *Nasua narica* has an os clitoris (Layne, 1954). *Nasua narica* anal glands are highly modified, relative to other Carnivora, in having a glandular area situated along the dorsal margin of the anus, consisting of a series of pouches opening by 4 or 5 slits on each side (Mivart, 1885; Pocock, 1921).

Kaufmann (1962) observed molts of solitary males in Panama between June and mid-July. In Arizona, males and non-breeding females molt between June and August. Females with young shed later than males and nonreproductive females, and the molt may not be complete until November. Between 8 and 12 months of age, Arizona juveniles molt the birth coat, which is usually completed by June (Kaufmann et al., 1976; Risser, 1963).

Basal metabolic rates of two *N. narica* from Panama were 335 and 163 kcal/24 h, for 5.1 and 3.2 kg individuals, respectively. These individuals maintained a constant metabolism until the temperature dropped below 20°C, at which point metabolism increased sharply (Scholander et al., 1950*a*; 1950*b*; 1950*c*). These metabolic rates are 133 and 97% of the allometrically predicted value, differ from the lower values of other Procyonidae, and have been questioned based on comparisons to lower values for *N. nasua* (Chevillard-Hugot et al., 1980). *Nasua narica* has a lower minimum resting metabolism, lower minimal thermal conductance, and an intermediate body temperature relative to *Bassariscus sumichrasti* and *Procyon lotor* (Chevalier, 1987). Estimates of average body temperature are 39.1°C (Risser, 1963) and 38.6°C (Chevalier, 1987). *Nasua narica* has two major hemoglobins of approximately equal concentration, including one not found in *N. nasua* (Ahmed et al., 1990; Seal, 1969). Electrophoresis and protein sequencing of the globin chains indicate that the two hemoglobins differ due to an amino acid substitution in the β-chain rather than the α-chain (Brimhall et al., 1977). Although digestive rates have not been quantified, individuals in Los Tuxtlas, Mexico produced an average of 2.5 fecal deposits per 24 h, and a mean fresh weight of 18 g per fecal expulsion (Estrada et al., 1993).

ONTOGENY AND REPRODUCTION. In the relatively few populations examined, *N. narica* breeds synchronously once per year. All mating activity in a population occurs within a 2–4 week period, although this period may shift slightly from year to year. After the mating season, pregnant females eventually separate from the bands to nest and give birth solitarily in a tree or den. The breeding season in Arizona occurs in mid-April, parturition in late June, and females with their new litters rejoin the band in August (Gilbert, 1973; Kaufmann et al., 1976; Pratt, 1962; Risser, 1963). In Mexico, approximate time of birth is June or July in Chihuahua, July in Sinaloa, July, August, or September in Guerrero, and May in Chiapas (Leopold, 1959). Extrapolation of data from Santa Rosa National Park, Costa Rica suggest a parturition date at the beginning of April (Newcomer and DeFarcy, 1985). In Panama, breeding occurs from late January through mid-February, and litters are born in April or early May (Chapman, 1938; Kaufmann, 1962; Russell, 1979, 1982; Smythe, 1970).

Copulation may occur arboreally or terrestrially (Kaufmann, 1962; Russell, 1979, 1982; Sunquist and Montgomery, 1973). In Panama, females have their first breeding opportunity at 22 months of age, although a few females may not breed until 46 months of age. All females may breed, or as few as 20% may breed, depending on ecological conditions such as food availability. Nulliparous females weigh 14% more than parous females (Kaufmann, 1962; Russell, 1979, 1982). Postreproductive females, who are at least 7 years old, continue to participate in normal band activity (Kaufmann, 1962; Russell, 1982). The testes of males descend in the 24th or 25th month of age, at which time males generally become solitary. Males have their first breeding opportunity at 34 months of age, but due to high levels of intrasexual competition, probably do not successfully breed until their 4th or 5th year of life, if ever. More than one male may breed with the females of a given band during a single breeding season. In addition, the consorting male for a given band may vary from year-to-year (Gilbert, 1973; Kaufmann, 1962; Russell, 1979, 1982). In captivity, individuals have reached 17 years of age (Poglayen-Neuwall, 1990).

Gestation period of *N. narica* is 70–77 days (Kaufmann, 1962; Risser, 1963; Smith, 1980). Litter size varies from 1 to 6 (Kaufmann, 1962; Pratt, 1962; Risser, 1963; Smith, 1980), with females in Panama bringing an average of 3.5 juveniles from the nest 5–6 weeks postpartum (Russell, 1982). In captivity, neonates weighed 180 g, with head-body length of 155–165 mm, and length of tail 100–110 mm (Kaufmann, 1962). At 10 days, average measurements of captive born neonates ($n = 4$) were: body mass = 214 g, total length = 305 mm, length of tail = 128 mm (Risser, 1963). At 40 days, when females and their new-born young rejoin the band, juveniles weigh approximately 500 g (Kaufmann, 1962). Young open their eyes after 4–11 days (Kaufmann, 1962; Risser, 1963). Young are born without teeth. Incisors first erupt after 15 days, and canines after 27 days. The milk dentition is complete about 2 months after birth. Young begin to walk and hold their tail erect after 11 days (Kaufmann, 1962). Examination of the oral cavity 98 days after birth revealed deciduous dentition of i 3/3, c 1/1, pm 4/4, m 0/0. The milk canines were about 4 mm long. Adult canines began to break through the gum anterior to the milk canines at about 9 months of age (Risser, 1963). By 9 months of age, males are significantly larger than females, based on body mass, length of head and body, and total length measurements (Risser, 1963; Russell, 1979). Growth rate of *N. narica* is similar to other Carnivora of similar adult female body mass (Gittleman and Oftedal, 1987).

When first brought from the nest, juveniles are small, incompletely developed, and have difficulty keeping up with the band. The band appears to restrict its movements at this time. During the first week after descent from the nest females sometimes leave their young unattended in a temporary nest while they forage (Russell, 1979, 1982). Nursing persists for up to 3 months after band reaggregation, with most nursing occurring during rest periods. Observations of adult females nursing individuals other than their own have been made in field studies (Russell, 1979).

ECOLOGY. *Nasua narica* occupies a diversity of wooded habitats from temperate oak and pine forests to lowland tropical rainforests, and occasionally ranges into deserts and savannas. White-nosed coatis in Arizona concentrate in riparian habitats, primarily in the piñon-oak-juniper woodlands, and are often observed at high altitudes (Kaufmann, 1983; Kaufmann et al., 1976; Lanning, 1976*a*, 1976*b*; Risser, 1963; Wallmo and Gallizioli, 1954). Risser (1963) reported individuals in Arizona from 508 to 2,879 m, with most sightings at intermediate altitudes. Lanning (1976*b*) reports tracking *N. narica* in the snow. In Guerrero, Mexico, *N. narica* is the most common carnivore, preferring heavily wooded canyons with streams, and occupying an altitudinal range up to 2,438 m (Davis and Lukens, 1958). Goodwin (1934) reported sightings of *N. narica* in cloud forests along the upper slopes of volcanoes near Atitlan, Guatemala.

Nasua narica is omnivorous, eating predominantly invertebrates and fruit, although vertebrates and carrion are also consumed when available (Bonaccorso et al., 1980; Delibes et al., 1989; Drummond, 1983; Fowler, 1979; Gilbert, 1973; Howe, 1980; Ingles, 1957; Kaufmann, 1962; Kaufmann et al., 1976; Leopold, 1959; López-Forment, 1979; Rand and Robinson, 1969; Risser, 1963; Russell, 1982; Smythe, 1970; Wallmo and Gallizioli, 1954). Life history events of *N. narica* in Panama are timed to food availability, such that parturition occurs during the period of maximal fruit availability (Smythe, 1970). During the wet season in Panama, 89% of foraging time is spent searching for animal (invertebrate) foods, while in the dry season this proportion drops to 54%; the remainder is spent under fruiting trees (Russell, 1982). Food is generally found by smell rather than sight. Food is initially located by constant sniffing in the litter, and then dug up or extracted from under bark, leaves, or clumps of debris (Chapman, 1938; Kaufmann, 1962). Invertebrate prey are often rolled between the paws, thereby quickly killing animals that have potentially harmful bites or stings, and also removing the various hairs, bristles, and spiny exoskeletal projections that may make the prey distasteful or difficult to eat. Vertebrates are typically pinned under the forepaws, and quickly bitten through the skull. Larger prey may require several bites (Ingles, 1957; Kaufmann, 1962; Kaufmann and Kaufmann, 1963). Fruit is eaten both in trees and on the ground, and long climbs are commonly made to reach the outermost limbs of large trees. In Panama, *Scheelea zonensis*, *Dipteryx panamensis*, *Spondias mombin*, *Ficus insipida*, and *Tetragastris panamensis* are important fruiting species. Individual trees of *Dipteryx* and *Tetragastris* produce so much fruit that a band may restrict its foraging to one or two trees for a period of several days, with only occasional trips to the ground to forage for animals (Bonaccorso et al., 1980; Howe, 1980; Kaufmann, 1962; Russell, 1982).

Reported predators include felids (Currier, 1983; Enders, 1935; Rabinowitz and Nottingham, 1986), raptors (Gilbert, 1973; Kaufmann et al., 1976; Kaufmann, 1982; Risser, 1963), snakes (Janzen, 1970), and primates (Fedigan, 1990; Newcomer and DeFarcy, 1985). Intraspecific predation by adult males on juveniles has also been reported (Russell, 1981). Juveniles have the highest mortality rate, with 90% (20 of 22) of the disappearances of individual juveniles in Panama occuring between May and August (Russell, 1979, 1982).

Endoparasites of *N. narica* include *Trypanosoma cruzi* (Chinchilla, 1966; Lainson, 1965; Petana, 1969), *Toxoplasma gondii* (Jewell et al., 1972), the tapeworms *Dibothriocephalus latum* and *Mesocestoides* sp. (Van Alstine et al., 1974), kidney worm *Dioctophyma renale* (Fyvie, 1971), lungworms *Angiostrongylus cos-*

taricensis, *Parastrongylus costaricensis* and *P. schmidti* (Baskin, 1986; Monge et al., 1978; Slaughter and Ubelaker, 1984), and the nematode *Physaloptera rara* (Neal, 1960). Ectoparasites include the chewing louse *Trichodectes* (=*Neotrichodectes*) *pallidus* (Van Alstine et al., 1974; Wenzel and Tipton, 1966), mites *Sarcoptes scabiei* and *Tur uniscutatus* (Conroy, 1964; Meier, 1976; Wenzel and Tipton, 1966), fleas *Ctenocephalides felis*, *Dasypsyllus gallinulae*, *Hoplopsyllus glacialis*, *Pleochaetis dolens*, *Polygenis klagesi*, *Pulex irritans*, *Rhopalopsyllus australis*, *R. cacicus*, and *R. lugubris* (Neal, 1960; Wenzel and Tipton, 1966), bot fly larvae of the family Cuterebridae (Kaufmann, 1962), chiggers *Euschoengastia tragulata*, *Eutrombicula alfreddugesi*, *E. goeldii*, *Trombicula dunni* (Loomis, 1969; Wenzel and Tipton, 1966), and ticks *Ambylomma ovale*, *A. oblongoguttatum*, *A. naponense*, *A. cajennense*, *A. auricularium*, *Ixodes boliviensis*, *I. rubidus*, and *Haemaphysalis juxtakochi* (Kaufmann, 1962; Wenzel and Tipton, 1966). Mutual grooming may help to control external parasites (Russell, 1983). *Nasua narica* are highly susceptible to a variety of infectious diseases pathogenic to man and other animals (Wallach and Boever, 1983), including tuberculosis *Mycobacterium* (Nóbrega and Reis, 1941), *Salmonellosis* (Pratt, 1962; Risser, 1963), rabies (Kaufmann et al., 1976; Schimmel, 1968), and canine distemper (Appel and Gillespie, 1972; Pratt, 1962; Risser, 1963). The gregarious nature of *N. narica* may facilitate the transmission of canine distemper virus and contribute to rapid population reduction, such as occurred in Arizona during 1960–1961 (Risser, 1963). Carcinoma of the nasal sinus (Lombard and Witte, 1959), and vertebral degenerative disease (Rutkowiak, 1989) have been observed in *N. narica* in zoos.

Because white-nosed coatis are omnivores, many species compete with them for food. In Durango, Mexico *N. narica* is sympatric with coyotes (*Canis latrans*) and grey foxes (*Urocyon cinereoargenteus*). Although all three are generalist feeders, scat analyses revealed resource partitioning such that *C. latrans* eats mainly rodents, *U. cinereoargenteus* fruit, and *N. narica* arthropods, with the least dietary overlap between *N. narica* and *C. latrans*. Of the three species, trophic diversity is smallest in *N. narica* (Delibes et al., 1989). Gilbert (1973) observed a *N. narica* band usurp a deer carcass from a coyote in Arizona. Interactions with armadillos (*Dasypus novemcinctus*), agoutis (*Dasyprocta punctata*), howler monkeys (*Alouatta palliata*), squirrel monkeys (*Saimiri oerstedi*), tapirs (*Tapirus bairdii*), peccaries (*Tayassu tajacu*), and squirrels (*Sciurus granatensis*) are generally nonagonistic (Baldwin and Baldwin, 1972; Kaufmann, 1962). Night monkeys (*Aotus trivirgatus*) and kinkajous (*Potos flavus*) compete with white-nosed coatis for fruit in trees, but since both are nocturnal they rarely encounter *N. narica* (Kaufmann, 1962). White-faced monkeys (*Cebus capucinus*) are direct competitors. White-nosed coatis feeding in fruiting trees return to the ground when *Cebus* arrive, and are often actively chased from a tree. Harassment also occurs on the ground and in trees that are not fruiting. However, *N. narica* will remain under trees where *Cebus* are feeding, eating dropped ripe fruit (Kaufmann, 1962, 1963; Oppenheimer, 1982). White-nosed coatis visiting a water source in Costa Rica accompanied *Cebus* groups 7% of the time (Burger and Gochfeld, 1992).

Population density of *N. narica* is greater in the tropics than in the southwestern United States. Both regions show year-to-year fluctuations in population sizes as a result of disease or food availability. Estimates of densities for Barro Colorado Island, Panama are 26–42 individuals/km^2 (Kaufmann, 1962) and 24 individuals/km^2 (Glanz, 1990), with Kaufmann (1962) noting a 50% decrease over an 8 month period. Densities in Guatemala are 15 individuals/km^2 at Sierra Chame, and 20 individuals/km^2 at Tikal (Glanz, 1990). Vaughan and McCoy (1984) estimate density at Manuel Antonio, Costa Rica to be 70 individuals/km^2 although sample sizes were small. In Los Tuxtlas, Mexico, density is 33 individuals/km^2, a value possibly influenced by hunting pressures (Coates-Estrada and Estrada, 1986). In Arizona, densities are 1.2–2 individuals/km^2, with within-year and between-year sightings so variable as to suggest that *N. narica* in this region may be nomadic or migratory (Kaufmann, 1982; Kaufmann et al., 1976; Lanning 1976*a*, 1976*b*; Pratt, 1962; Risser, 1963; Wallmo and Gallizioli, 1954).

Home range sizes are larger in the more arid northern latitudes than in the tropics. In Panama, home range sizes for three bands (whose group size varied over the course of the study) were 0.45, 0.41, and 0.34 km^2, respectively. Home ranges of neighboring bands overlapped considerably. However, core areas of heavy usage (80% of time) did not overlap, and were 0.20, 0.15, and 0.15 km^2, respectively. The core areas were used consistently throughout the year, but some of the peripheral areas of the home range were only visited when certain fruit crops were available (Kaufmann, 1962). Length of daily movements for the three bands was most often 1500 m–2000 m, with shorter daily movements in the dry season than the wet season. Two solitary adult males had home ranges of 0.36 and 0.46 km^2 (Kaufmann, 1962). Russell (1982) also noted that use of home ranges fluctuated greatly from wet to dry season, with overlap between neighboring bands. During the nesting season, size of home ranges was smallest. In this season, pregnant females foraged alone near their nest for a small fraction of each day (Russell, 1982). In Los Tuxtlas, Mexico, average home range size of bands is 0.8 km^2 (range 0.5–1.10 km^2), with home range overlap of about 5–10% (Estrada et al., 1993). In Arizona, four solitary adult males had overlapping home ranges averaging 1.78 km^2, and bands roamed areas of at least 2–3 km^2 (Gilbert, 1973; Kaufmann et al., 1976; Lanning, 1976*a*).

Nasua narica is an important mammal for subsistence hunters (Hamblin, 1984; Jorgenson and Redford, 1993; March, 1987; Redford and Robinson, 1991), and white-nosed coati densities decline steeply with increased human hunting pressure (Glanz, 1991). Aranda (1991) has reported the selling of coati skins in Mexico. Widespread hunting of *N. narica* for food in northern Mexico has greatly reduced populations, and populations in the United States may now be isolated (Kaufmann, 1987). The *N. narica* population in the Burro Mountains, New Mexico, was greatly reduced by poisoning during an indiscriminate predator control campaign in the 1970s. Coatis are now legally protected in New Mexico (Kaufmann, 1987; King and Schrock, 1985). In Honduras *N. narica* is protected under the Convention on International Trade in Endangered Species Appendix III (Emmons, 1990).

BEHAVIOR. *Nasua narica* is highly gregarious, with several adult females and their offspring of ≤ 2 years old forming bands of up to 25 individuals, and occasionally more. These are not harem groups, as all adult males are generally solitary. While groups as large as 200 individuals have been reported, these figures are likely exaggerated due to congregation of bands at food sources, and the noisy dispersal of startled white-nosed coatis through dense underbrush (Kaufmann, 1962; Kaufmann et al., 1976; Risser, 1963; Russell, 1979). Band size is highly variable within a population, and from year-to-year within a band. Field studies of white-nosed coati bands in Panama report sizes of 5–18 individuals (n = 6 bands; Russell 1979), 2–15 individuals (n = 5 bands; Kaufmann, 1962), and 6–26 individuals (n = 3 bands; Gompper and Krinsley, 1992). In one study, average band size varied from 11.5 to 7.1 individuals within years, with most of this variation resulting from mortality and birth of juveniles (Russell, 1982). At Palo Verde, Costa Rica, mean band size (n = 106 observations) was 5.4 ± 0.9, although this included observations of subgroups and solitary males (Burger and Gochfeld, 1992). In Los Tuxtlas, Mexico, mean band size was 22.5 (n = 8), with a range of 10–25 individuals (Estrada et al., 1993). Bands contain mostly closely related individuals, although unrelated members have been observed (Gompper and Wayne, in press; Russell, 1979, 1983). New bands may form by fission or fusion of existing bands. Migration of individuals between bands also occurs. The net effect of migration on population size is likely small (Kaufmann, 1962; Russell, 1979, 1982). Evolutionary explanations for gregariousness of white-nosed coati bands include reduction of feeding niche overlap between males and females (Smythe, 1970), anti-predator behavior (Burger and Gochfeld, 1992), and more specifically, the protection of juveniles from predation by adult males (Russell, 1979, 1981).

Males gradually become increasingly independent from the band, and soon after 24 months of age are generally completely solitary (Kaufmann, 1962, 1963). Occasional long-term associations between males and bands have been reported outside of the breeding season in both Arizona (Gilbert, 1973; Kaufmann et al., 1976; Wallmo and Gallizioli, 1954) and Panama (Gompper and Krinsley, 1992). Males consorting with bands may gain such benefits as lower ectoparasite loads, protection from potential predators, and protection from other adult males. Fighting between adult males is common, especially during the breeding season, and 30% of males display bite wounds or canine damage (Gaumer, 1917; Gompper and Krinsley, 1992).

Nasua narica has a wide range of social behavior, including cooperative grooming, nursing, vigilance, and aggressive anti-predator behavior (Janzen, 1970; Kaufmann 1962; Russell 1979, 1981, 1983; Smith, 1980). Bands are usually slightly agonistic to other bands when they meet. However, peaceful interactions also occur, and are occasionally characterized by inter-group grooming sessions (Kaufmann, 1962, 1963; Russell, 1979). Adult males that approach bands are generally aggressively chased away by one or several band members, including juveniles and subadults. Females often groom one another in an excited manner following such chases (Russell, 1979, 1981). Both kin selection and reciprocal altruism likely play a role in these behaviors (Janzen, 1970; Russell, 1979, 1983; Wilkinson, 1988). During the breeding season males are submissive to females and immatures, and occasionally groom them (Russell, 1981). However, dominance hierarchies do not occur among band members, and bands often break into subgroups for several hours or occasionally 1–2 days (Kaufmann, 1962, 1963; Russell, 1979).

White-nosed coatis do not voluntarily share food, nor do they store it. However juveniles are tolerated by foraging adults, and juveniles can often be seen sniffing the muzzles of feeding adults. This behavior may enhance the rate by which juveniles learn characteristics of food (Russell, 1982). While foraging, bands typically assume an elliptical outline, with subadults and adults forming the periphery, and juveniles aggregated in the center. Animals on the periphery protect juveniles through specialized vigilance behavior, cooperative attacks on potential predators, and assuming protective positions during flight from alarming stimuli. However, when parous females leave the group during the nesting season, bands assume a rank formation, a spatial organization efficient for foraging, but not for defense (Russell, 1979, 1982, 1983). Attacks by adult males on juveniles may increase during this period (Russell, 1981). Vigilance levels of individuals are highest in small bands and lowest in large bands. In addition, when observed at a waterhole, larger bands remained longer and each member drank longer than individuals in small bands or solitary individuals (Burger and Gochfeld, 1992; Russell, 1979, 1983). When frightened, white-nosed coatis flee on the ground rather than into the trees, and even if startled in large trees, will often leap to the ground to escape (Leopold, 1959).

White-nosed coatis are primarily diurnal and, in undisturbed tropical habitats, sleep at night in trees. In Arizona, rocky ledges and dens are often used. Juveniles are usually in the center of the band during rest and sleep periods, with adults on the perimeter (Gilbert, 1973; Kaufmann, 1962; Kaufmann et al., 1976; Russell, 1979). In populated areas of tropical America where they are hunted for food by humans, white-nosed coatis have become more nocturnal (Kaufmann, 1983, 1987). Rest periods of up to 2 h are often taken during the daylight hours, with this being more frequent in Panama during the dry season when fruit is abundant (Kaufmann, 1962).

During heavy rains white-nosed coatis in Panama become quite nervous, with the band grouping tightly together and young remaining close to their mothers. Invariably the band runs for cover, such as in tree buttresses, under palm fronds, or in dense brush piles and tree tops. After the rain ceases, white-nosed coatis return to normal activities. During light rains, *N. narica* bands show little discernable reaction, although sometimes they may travel at an increased pace, with juveniles often giving chitter vocalizations (Kaufmann, 1962).

Nasua narica is both arboreal and terrestrial, and easily descends or ascends small trees and vines. It has more difficulty climbing the smooth trunks of large trees, and normally descends or ascends by moving out to the end of a limb and transferring to nearby branches of the same tree (Ingles, 1957; McClearn, 1992*a*). The tail is not prehensile, but does serve as a balancing tool during arboreal activity (Ingles, 1957). White-nosed coatis spend about 90% of their daytime hours foraging, and at least 90% of that foraging time is spent on the ground (Kaufmann, 1962; Russell, 1982). Terrestrial running speed may reach 27 km/h (Kaufmann, 1962), and Goodwin (1934) noted that *N. narica* can run for 3 h when driven by hounds. The white-nosed coati is a strong swimmer, although it does not generally enter water voluntarily (Enders, 1935; Kaufmann, 1962).

Nasua narica is highly vocal, with a rich repertoire of specific vocalizations for aggression, appeasement, alarm, and maintaining contact between individuals. Certain vocalizations are only given by specific age or sex classes, with band members generally much more vocal than solitary adult males (Gompper and Krinsley, 1992; Kaufmann, 1962, 1987; Krinsley, 1989; Russell, 1979; Smith, 1980). Spectrographic and aural analyses indicate that the vocalizations of individual animals are distinctive (Krinsley, 1989). Visual signals are also used, and include nose-up, head-down, and tail-switching displays (Kaufmann, 1962; Krinsley, 1989; Smith, 1980). Scent marking in *N. narica* involves a perineal drag, usually on trees, logs, and vines. Although males scent mark year round, females perform this behavior most frequently just prior to the mating season. Perineal sniffing of adult females by adult males has been observed both in the wild and in captivity (Kaufmann, 1962; Russell, 1982; Smith, 1980).

Comparative studies of captive and free-ranging *N. narica* have shown that while specific communicative signals were displayed in the correct context by captive individuals, major differences existed in social relationships and in feeding behavior. Captive adults of both sexes could sometimes be kept together, were observed to allogroom outside of the breeding season, and were observed to sleep together, although the quantity and quality of these behaviors varied greatly between studies. Captives often showed little interest in many live prey enthusiastically eaten in the wild (Kaufmann and Kaufmann, 1963; Krinsley, 1989; Smith, 1980).

Coatis have been observed to eat the ticks from coats of tapirs (*Tapirus bairdi*) in Panama. This mutualistic behavior may have arisen when coatis and tapirs were in close proximity at a feeding station, and is likely culturally transmitted (McClearn, 1992*b*; Overall, 1980). An additional learned behavior is self-grooming and allogrooming with the resin of *Trattinnickia aspera* (Burseraceae). This behavior is also likely acquired and maintained through cultural transmission, and may serve some pharmaceutical purpose (Gompper and Hoylman, 1993).

GENETICS. The diploid (2n) chromosomal compliment of *N. narica* is 38, including 30 metacentrics and submetacentrics, and 6 acrocentric autosomes. Sex chromosomes are a relatively large submetacentric X and an acrocentric or small submetacentric Y (Hsu and Arrighi, 1966; Hsu and Benirschke, 1970; Todd et al., 1966). *Nasua narica* differs from the karyotype of a male *N. nasua*, by having one additional acrocentric pair and one less metacentric pair (Wurster and Benirschke, 1968). Verleye et al. (1987) examined a zoo colony of *N. narica* and *N. nasua* by G-banding, and noted hybridization resulting from complex chromosome rearrangements.

Pauly and Wolfe (1957) utilized *N. narica* in an examination of the serological relationships of species of Carnivora. In Carnivora hemoglogin systematic studies that have included *Nasua narica* (Brimhall et al., 1977; Seal, 1969; Stenzel and Brimhall, 1977), the two hemoglobins of *N. narica* are distinct from the single types of *N. nasua* and *Procyon lotor*. The small number of differences between the two *N. narica* hemoglobin β-chains suggest a relatively recent divergence (Stenzel and Brimhall, 1977).

REMARKS. Confusion over the status of solitary males led early researchers to designate separate species names (*N. solitaria* [Schinz, 1821] and *N. sociabilis* [Schinz, 1821]) for adult males and for gregarious band members of *N. nasua* from Brazil, and many of the common names still used in North and South America perpetuate the confusion (Hensel, 1869; Kaufmann, 1962, 1983). Common names for *N. narica* include gato solo (Panama), pizote and pizote solo (Costa Rica, Honduras), chic and sis (Mayan), quash (Belize), tejon and tejon solo (Mexico), and in the United States, chulo, chulo bears, coati and coatimundi (Emmons, 1990; Gilbert 1973; Leopold 1959). The common name coati is of Tupian Indian origin, referring to the coati's habit of sleeping with the nose tucked on the belly. Although coati monde from the Brazilian vernacular properly refers to solitary males, it is often used to denote all coatis. Through usage the spelling has become coati mundi (Kaufmann, 1962).

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