



Martes martes (Carnivora: Mustelidae)

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Abstract: *Martes martes* (Linnaeus, 1758), commonly called the European pine marten, is a small predator widespread in western Eurasia. In almost all its geographic distribution, it is autochthonous. It is as a secondary consumer but, a predator with omnivorous traits. *Martes martes* inhabits forests with varied tree compositions, but in recent decades, it has spread to forest-steppe and agricultural areas. It is hunted in some areas, mainly in winter. In some countries during the 20th century, it experienced significant declines in numbers, but at present, it is “Least Concern” (LC) on the International Union for the Conservation of Nature’s Red List of Threatened Species.

Key words: carnivore, Eurasia forest-dweller, European pine marten, furbearer, mustelid

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Martes martes (Linnaeus, 1758)

European Pine Marten

Mustela martes Linnaeus, 1758:46. Type locality “sylvia antiquis;” restricted to “Upsala,” Sweden, by Thomas (1911:139).

Mustela sylvestris Oken, 1816:1029. Unavailable name (International Commission on Zoological Nomenclature 1956; Opinion 417).

Martes vulgaris Griffith, 1827:123. Type locality “Northern parts of Europe and Great Britain.”

Martes sylvatica Nilsson, 1847:41. Type locality “Scandinavia.”

Martes abietum Gray, 1865:104. Type locality “Europe, England and France, Russia.”

Martes martes latinorum Barrett-Hamilton, 1904:389. Type locality “Sardinia Isle,” Italy.

Martes martes var. *notialis* Cavazza, 1912 [1911]:181. Type locality “southern Italy.”

Martes martes lorenzi Ognev, 1926:47. Type locality “Storozhevaya (vicinity),” Kuban province, Russia.

Martes martes ruthena Ognev, 1926:49. Type locality “Dmitrovsk vicinity,” Moscow province, Russia.

Martes martes ruthena borealis Kuznetzov, 1941:126. Type locality “Shenkursk district,” Arkhangelsk province, Russia.

Martes martes uralensis Kuznetzov, 1941:126. Type locality “Miass vicinity,” southern Urals, Russia.



Fig. 1.—Adult female *Martes martes* from Lapland State Reserve, Russia. Photograph by Olga Natalskaya used with permission.

- Martes martes borealis*: Bobrinskoy (in Bobrinskoy et al. 1944:121). Name combination.
- Martes martes sabaneevi* Jurgenson, 1947:147, 179. Type locality “Pechora River” (territory of Pechoro-Ilychskii Reserve), Northern Urals, Russia.
- Martes martes kuznetsovi* Pavlinov and Rossolimo, 1987:61. Replacement name for *Martes martes ruthena borealis* Kuznetsov, 1944.
- Martes martes minoricensis* Alcover, Delibes, Gosálbez, and Nadal, 1986:331. Type locality “exceptionally on the Menorca Isle,” Spain.

CONTEXT AND CONTENT. Order Carnivora, family Mustelidae, subfamily Mustelinae, tribe Mustelini, genus *Martes*, subgenus *Martes* (Anderson 1970; Pavlinov and Rossolimo 1987; Wozencraft 2005). No subspecies are currently recognized (Larivière and Jennings 2009; Burgin et al. 2020; see “Nomenclatural Notes”).

NOMENCLATURAL NOTES. Ten nomenclaturally valid subspecies, including the nominal *martes*, have been named in the scientific literature. Two to 10 subspecies have been recognized: two subspecies by Ognev (1931), five by Heptner et al. (1967, 2001) and Aristov and Baryshnikov (2001), six by Gromov et al. (1963), seven by Ellerman and Morrison-Scott (1951) and Grakov (1981), eight by Wozencraft (2005), nine by Abramov and Khlyap (2012), and 10 by Pavlinov and Rossolimo (1987). Given recent concern about the validity of subspecific taxonomy (e.g., Patton and Conroy 2017; Schiaffini 2020), an evaluation of subspecies of *Martes martes* with contemporary techniques and analyses is needed, which might be challenging because *M. martes* is considerably variable across its extensive geographic distribution (Heptner et al. 1967, 2001; Grakov 1981; Larivière and Jennings 2009).

DIAGNOSIS

Martes martes is a small carnivorous mammal about the size of a domestic cat. It is very similar morphologically to *M. zibellina* (sable—Monakhov 2011), *M. foina* (stone marten—Stubbe 1993), *M. americana* (American marten—Clark et al. 1987), and *M. melampus* (Japanese marten—Hagmeier 1961; Anderson 1970). Pelage is lush and soft, without brilliance and grayness typical of *M. zibellina*. Coloration of *M. martes* is monotonous yellowish brown to pale yellow, rarely dark brown (Kusnetzov 1941; Stubbe 1993; Heptner et al. 2001). The head has the same color as the back, whereas in *M. zibellina* and *M. melampus* the head is lighter, and in *M. flavigula* (yellow-throated marten) and *M. gwatkinsii* (Nilgiri marten) it is darker. Paws are brown to black, finger-pads, unlike *M. foina*, are densely furred in winter, same as in *M. zibellina*, and claws are blonde. A yellow, or slightly orange, elongated “bib” almost always occurs on the neck and between and extending to the base

of the front legs (Fig. 1); it is rarely whitish (as in *M. foina*—Pavlinin 1963). Nose tip, unlike *M. foina* (flesh-colored), is black (Görner and Hackethal 1988). The bushy tail is relatively long (>19 cm in females and >22 cm in males), measuring one-half to two-thirds of the body length, and approximately the same color as the back, with fluffy hair and a dull brown hue; the end is pointed (Fig. 1), which differs from the shorter tail of *M. zibellina* (<17.2 cm in females and <19 cm in males; up to one-half of the body length—Aristov and Baryshnikov 2001) with its blunt, rounded end (Novikov 1956). Several features of the skull can be used to distinguish *M. martes* from *M. zibellina* and *M. foina*. Compared to *M. zibellina*, *M. martes* has relatively elongated auditory bullae and there is a greater distance between the bullae; the processus mastoidei only slightly protrudes beyond the edges of the auditory foramen in *M. martes* (Ognev 1931). Oral edge of palatine arch, unlike *M. zibellina*, has a clear outgrowth in *M. martes* (Pavlinin 1963). Nasal bones unlike those of *M. foina* have a slight narrowing in the middle part (Ognev 1931; Novikov 1956). Unlike *M. foina*, distance between mental foramina of *M. martes* is greater than diameter of lower canine (Fig. 2; Novikov 1956); length of inner lobe of M1 is more than 70% of its width (Monakhov 2011). The massive postorbital constriction of *M. martes* is proposed as distinguishable from the smaller postorbital constriction of *M. foina* (Altuna 1973) and *M. zibellina* (Monakhov 2020). Bacula of *M. martes* are 39–46 mm (Aristov and Baryshnikov 2001), curved at the distal end (Novikov 1956) with closed ring (Fig. 3), which differs morphologically from *M. zibellina* (forked end forms an unclosed ring—Pavlinin 1963; Monakhov 2011). A key to the species of *Martes* can be found in Monakhov (2011).

GENERAL CHARACTERS

Martes martes is a small-sized, terrestrial, carnivore. It has an elongated body with a small triangular head. It is semiplantigrade and has relatively short, five-fingered paws: hindlegs are longer than the front legs. When walking and jumping, the back is arched up. *Martes martes* has marked sexual dimorphism: the male is 10–15% larger than the female (Pavlinin 1959); therefore, size characteristics are given for males and females separately.

Body masses (kg) of males and females, respectively, were: 1.2–2.4 and 0.8–1.4 (Görner and Hackethal 1988), 1.18–1.78 and 0.97–1.33 (Stubbe 1993), 1.14–1.89 and 0.84–1.33 (Ansorge 1988), 1.0–1.6 and 0.73–1.1 (Danilov and Tumanov 1976), 0.76–1.63 and 0.56–1.1 (Polezhaev 1998), and 1.13–1.94 and 0.88–1.44 (Stier 2012). Head–body lengths (cm) for males and females, respectively, were: 44.5–49.0 and 42.0–50.0 (Stubbe 1993), 42.0–52.2 and 41.0–49.0 (Ansorge 1988), 39.5–57.0 and 37.5–44.0 (Danilov and Tumanov 1976), 38.0–46.7 and 34.5–42.0 (Polezhaev 1998), and 38.9–52.2, 36.1–46.1 (Stier 2012). Tail lengths (cm) for males and females, respectively, were: 22.5–30.0 and 19.0–26.0 (Stubbe 1993), 21.6–30.0 and 21.5–28.0 (Ansorge 1988), 20.0–24.0 and 19.0–23.5 (Danilov and Tumanov 1976), 18.4–24.5 and 17.6–25.0 (Polezhaev 1998),

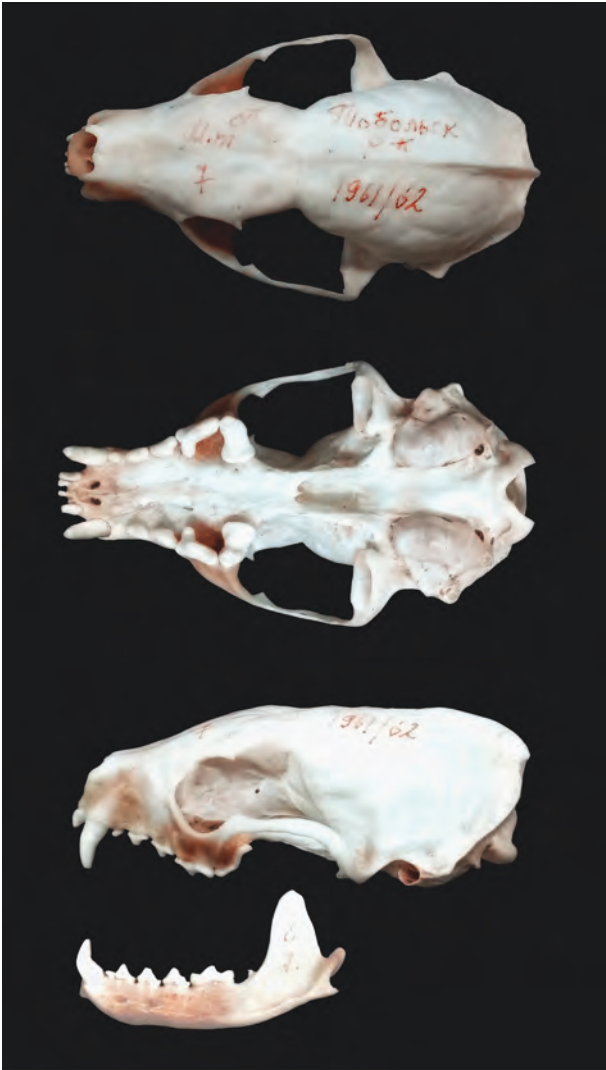


Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Martes martes*. Specimen No. 789083 (from Tobolsk district, Tyumen province) housed in the Zoological Museum, Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, Yekaterinburg, Russia. Greatest length of skull is 87.2 mm. Photograph by V. Monakhov.

and 19.1–28.2 and 20.8–26.9 (Stier 2012). Ear lengths (cm) for males and females, respectively, were: 3.7–5.2 and 4.0–4.8 (Stubbe 1993), 3.0–5.0 and 3.0–4.3 (Ansorge 1988), 4.5–4.7 and 4.3–4.6 (Pavlinin 1959), and 3.0–5.4 and 3.0–4.7 (Stier 2012). Height at the withers is about 15 cm (Lemke 1981).

Skull measurements of adult *M. martes* (mm; mean \pm SE; males and females, respectively) were: Balearic Islands (21 males and 17 females—Lopez-Martin et al. 2006), condylobasal length (CBL) 87.8 ± 0.31 and 79.9 ± 0.24 , mastoid width (MW) 36.40 ± 0.37 and 35.60 ± 0.29 ; Denmark (23 males and 10 females—Reig 1989), CBL 87.1 ± 0.31 and 79.2 ± 0.51 , MW 42.1 ± 0.21 and 37.5 ± 0.63 ; Finland (37 males and 27 females—Lansink et al. 2019), CBL 85.61 ± 0.41 and 78.90 ± 0.41 , MW 39.75 ± 0.24 and 36.25 ± 0.21 ; Karelia (72 males and 30 females—Danilov and Tumanov 1976), CBL 83.0 ± 0.24 and 76.8 ± 0.26 ; eastern Germany (38 males and 15 females—Monakhov and Hamilton 2020), CBL 86.41 ± 0.30 and 79.83 ± 0.30 , MW 41.48 ± 0.17 and 38.36 ± 0.24 ; Caucasus (33 males and 34 females—Monakhov and Hamilton 2020), CBL 85.36 ± 0.32 and 78.37 ± 0.25 , MW 39.53 ± 0.16 and 36.56 ± 0.13 , and Kirov Oblast, Russia (32 males and 31 females—Monakhov and Monakhova 2014), CBL 80.80 ± 0.30 and 73.58 ± 0.27 , MW 34.67 ± 0.13 and 33.04 ± 0.15 . Thus, *M. martes* with the largest sizes live in the west and those with the smallest sizes in the east in Europe (Reig 1989; Monakhov 2021).

Little attention has been given to the size and structure of the baculum of *M. martes* (Fig. 3). Stubbe (1993) provided data on the os penis (minimum–average–maximum): length, excluding age, was 38.9–42.3–45.7 mm and mass was 0.20–0.29–0.35 g. Vercillo and Ragni (2011) reported that baculum length of adult *M. martes* in Italy was 42–51 mm, and they, like Abeleantsev (1968) and Pavlinin (1963), argued that this trait can be used to distinguish *M. martes* and *M. foina*. Length of baculum for *M. martes* of western Ukraine was 37–44.6 mm (Abeleantsev 1968) and in the upper reaches of the Pechora River basin, was 37.0–41.26–45.0 mm (minimum–average–maximum—Polezhaev 1998). Size of the baculum depends on age (Jurgenson 1947). Dimensions (mm; minimum–average–maximum) of the os penis for juveniles were 35.1–37.0–38.3 and



Fig. 3.—Lateral views of bacula of adult *Martes martes* (left) and *Martes zibellina* (right); specimens from Zoological Museum, Institute of Plant and Animal Ecology, Ekaterinburg, Russia. Photograph by V. Monakhov.

adults 38.9–42.3–45.7 (Novikov 1956). Ranges reported for baculum were: 32.4–36.1–41.0 mm for 64 juvenile males and 38.9–42.8–46.4 mm for 67 adults from the Urals (measurements taken by VM). Some researchers consider it possible to estimate age (juveniles versus adults) based on characteristics of the baculum (Popov 1943; Walton 1968; Malecha et al. 2009).

Pelage of *M. martes* is monotonous from light brown to chestnut with a yellow, rarely almost white or creamy, oblong throat patch. Tail is fluffy and dense more than one-half the body length and darker at the tip (Stubbe 1993). Fur is practically devoid of the gray hairs and gloss that are characteristic of *M. zibellina*. The difference in coloration of the body and head is almost negligible (Pavlinin 1963). Summer fur is darker than winter fur. *Martes martes* with albino (Fig. 4), melanistic (Fig. 5), or anomalously colored pelts are rarely captured (Stubbe 1993). Pavlinin (1965) described the case of catching an individual with black skin in the south of the Perm region. Voipio (1962) believed that variation in the general color of fur and throat patch happened independently and irrespective of age. He identified three color variations in *M. martes*, the frequencies of which were “light” 9.5%, “medium” 50.8%, and “dark” 39.7% ($n = 398$). There were statistically more females with a dark pelt (49.5%) than males (30.2%—Voipio 1962). Davletov (2013) reported that there are four color categories for *M. martes* skins used in international trade: “dark blue,” “blue,” “dark sand,” and “sand.”



Fig. 4.—Albino *Martes martes* from the vicinity of Baikalovo village, Sverdlovsk region, Russia. The mount and photograph by Igor Glukhov used with permission.

Color and shape of the throat patch (bib) of *M. martes* has been studied more extensively than coat color. The throat patch (Fig. 1) does not extend to front feet (Grimmberger 2014). According to Grakov (1969), only 2.6% of 5,624 pelts lacked a throat patch, and only 1.8% of the patches were white. Throat patches are yellow, orange, or white. For example, Cavazza (1912) stated that *M. martes* of Sardinia was characterized by a yellow-orange patch, whereas individuals in the Alps and the northern part of the peninsula had a light-yellow patch. According to Grakov (1974), the ratio of groups of skins with one of the three variants of throat patches in some populations of *M. martes* in Russian was (% yellow, orange, and white, respectively, $\pm SE$): Novgorod region, 25.8 ± 3.9 , 54.7 ± 4.4 , and 19.5 ± 3.5 ; Arkhangelsk region, 78.2 ± 2.2 , 18.4 ± 1.9 , and 2.7 ± 1.5 ; Pechora River, 59.1 ± 4.4 , 26.1 ± 4.7 , and 2.2 ± 3.7 (no spots 12.7 ± 3.5); Kirov region, 43.0 ± 4.0 , 57.0 ± 4.0 , and 0.0 ; Bashkir Republic, 58.2 ± 3.7 , 39.5 ± 3.7 , and 2.3 ± 1.1 ; and Chelyabinsk region 9.6 ± 6.4 , 90.4 ± 6.4 , and 0.0 .

In summer, there are 190–250 guard hairs/1,000 down hairs on the skin of *M. martes*; guard hairs are 23–27 mm in length with a diameter of 100–150 μm and downy hairs are



Fig. 5.—Melanistic *Martes martes* collected in the Omsk region, Russia, in 2014. Photograph by Igor Glukhov used with permission.

11–12 mm and 15–16 μm , respectively (Grakov 1978). In winter on the skin, there are 63–83 guard hairs/1,000 down hairs; and guard hairs are 36–38 mm in length with a diameter of 75–90 μm whereas the downy hairs are 22.0–22.5 mm long and 14.0–14.5 μm (Grakov 1978). Pavlinin (1965) obtained the following average values of hair size in *M. martes* (10 males and 11 females) of the Lower Ob: length of guard hairs was 40.7 and 43.1 mm, downy hairs were 23.7 and 23.8 mm in length; guard hairs had diameters of 101.0 and 101.6 μm and downy hairs 17.1 and 17.1 μm . Molting lasts from late April to early July in spring and summer and August to November in autumn. Hunters typically harvest *M. martes* in November–February when it has the most valuable fur. Molt in spring occurs first on the head and gradually extends to the tail; it is reversed in autumn (Stubbe 1993).

Color of the fur on the head is almost always the same as that on the back. Tip of the nose is dark or black (Lemke 1981; Görner and Hackethal 1988). Dense vibrissae occur on upper lips. Ears have a pale-yellow border.

DISTRIBUTION

Martes martes inhabits mature mixed and coniferous forests of the temperate zone of central and western Eurasia (Anderson 1970) from the Atlantic Ocean to the foothills of Altai Mountains (Fig. 6). The area occupied by *M. martes* covers about 11 million km^2 of the western Palearctic: almost all of Europe, the Caucasus, Asia Minor, Iran, and a part of Western Siberia. The Russian part of its distribution area is 5.05 million km^2 (46%). Overall, the distribution is 6,800 km from west to east and 4,600 km from south to north.

Martes martes is native in Albania (east), Armenia, Austria, Azerbaijan (north), Belarus, Belgium (south), Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Greece (north), Hungary, Iran, Ireland, Italy (with islands), Kazakhstan, Latvia, Liechtenstein, Lithuania, Luxembourg, Moldova, Montenegro, the Netherlands, North Macedonia, Norway (central and south), Poland, Portugal (north), Romania, Russian Federation, Serbia,



Fig. 6.—Geographic distribution of *Martes martes* following Herrero et al. (2016) with changes in the eastern part of the range based on Monakhov et al. (2020).

Slovakia, Slovenia, Spain (north; Balears—introduced from continent), Sweden, Switzerland, Turkey, Ukraine, and United Kingdom (north, west—Proulx et al. 2004; Herrero et al. 2016).

Martes martes is autochthonous throughout its distribution (for exceptions see “Conservation”). Distribution of *M. martes* is wide and generally continuous, without significant isolated areas. The latter include (except for islands) the population in Wales and that in the lower reaches of the Ural River (Atyrau region, Kazakhstan). *Martes martes* occurs at elevations up to about 2,300 m in the Pyrenees Mountains and Spain (Herrero et al. 2016), and at 2,200–2,400 m in the Caucasus (Bakeev 1973).

FOSSIL RECORD

The genus *Martes* is poorly differentiated among mustelids and dates to the Miocene and probably from the late Pleistocene of central and western Europe. After the Last Glacial Maximum, it entered Scandinavia (Stubbe 1993; Sommer and Benecke 2004). Anderson (1970, 1994) considered *M. laevidens* Dehm, 1950 from lower Miocene deposits in Bavaria, Germany, to be the earliest known marten ancestor, and the line of phylogeny imagined as *Martes laevidens*–*M. wenzensis*–*M. vetus* (intermedia *M. foina*)–*M. martes*. It was a small marten with thin jaws and four premolars in each side of the jaw. Later, near Lodz, Poland, remains were found of a similar but larger *M. wenzensis* Stach, 1959, from the early Villafranchian horizon (3.5–1.0 Ma), and a similar *Martes* from Greece and Romania (Anderson 1994). Nevertheless, it has recently been found that *M. laevidens* does not belong to the true marten group based on anatomical features, and *M. wenzensis* should be considered the ancestor of true martens (Sato et al. 2003). In the middle-to-late Pleistocene, *M. martes* and *M. zibellina* became distinct species (Anderson 1994). Ancestors of *M. martes* and *M. zibellina* (*M. vetus*), morphologically like modern species, are known from several Riss-Wurm deposits from the Pleistocene in central Europe (England [Kent and Devon], Austria, Germany [Westphalia and Weimar], Czech Republic, Poland, Hungary, and the Netherlands) and Holocene from Norway, Denmark, Switzerland, Belgium, Bulgaria, France, Italy, and Romania (Anderson 1970). Sato et al. (2003) estimated divergence of *M. martes* and *M. zibellina* at 0.43 Ma, but others estimated this separation at about 2 Ma (Bininda-Emonds et al. 1999; Hosoda et al. 2000).

The earliest unquestioned find of *M. martes* belongs to the last interglacial period, the Eemian (Wolsan 1993; Anderson 1994; Van Kolfschoten 2000), about 120,000 years ago. Fossils that might represent *M. martes* have also been found in deposits extending as far back as 400,000 years ago (Wolsan 1993). Sommer and Benecke (2004) published a study on glacial refugia in southern Europe, summarizing fossil findings of mammals, including *M. martes*. For the late glacial, there are 20 *M. martes* localities with the northernmost record in Denmark. The Iberian and Italian peninsulas and Carpathians (Moldova) are considered glacial refuges for *M. martes*, and the Balkans and North Pontic region as possible refugia (Sommer and Benecke 2004).

Fossil remains of *M. martes* are also known from the layers of the middle-to-upper Pliocene near Odessa in Ukraine (Gromova 1962), on the territory of Moldova (Svistun et al. 1989), near Pavlodar, Kazakhstan, the Caucasus, and Crimea (Gromova 1962; Baryshnikov et al. 1981). Numerous Holocene samples have been described from localities near the cities of Vinnitsa, Kiev, Poltava, Khmelnytsky, Chernivtsi, and Chernigov (Abeletsev 1968). In the Southern Urals (near Magnitogorsk and Ufa), *M. martes* was recorded in Pleistocene horizons in mountainous areas with ages of 11,000–35,000 years BC and throughout the Holocene in mountains and on the plains (Kosintsev and Bachura 2013). *Martes martes* entered the Central Urals in the middle Holocene and into the Northern Urals in the late Holocene (Kosintsev et al. 2016). Based on samples from the Subboreal period (2,600–4,000 years BC), *M. martes* is thought to have spread to the right bank of the Yenisei, and its distribution moved west near the right bank of the Ob in the modern Tomsk region (Devjashin et al. 2016).

Huges (2012) drew an updated scheme of the phylogeny of *Martes* that added new fossil finds related to older ancestors. For example, she included species such as *M. munki*, *M. filholi*, *M. burdigaliensis*, *M. collongensis*, *M. sainjoni*, and others with age estimates of 15–18 Ma from France, Spain, and Austria. It confirmed Anderson’s (1970, 1994) scheme for the ancestors of true martens of the Miocene (*M. wenzensis*) and the Pleistocene (*M. vetus*), although their relationship was disputed by Kurten (1968), and general conformity with new genetic data (Huges 2012). A new fossil species *M. crassidens* from the early-to-middle early Pleistocene horizon from the vicinity of the city of Dalian (China) was recently described by Jiangzuo et al. (2021) who concluded that this marten was closely similar (even more than *wenzensis* and *vetus*) to the *martes*–*zibellina*–*melampus*–*americana* group (Holarctic marten group). They believed that they found a true ancestor (including *M. martes*) of the Holarctic marten group that originated in this region of Asia and spread almost throughout the Holarctic (Jiangzuo et al. 2021).

Many mammals of Eurasia are representatives of migratory faunas at different periods of their species history, and Anderson (1970) referred the genus *Martes* to the same category. During the long phylogenesis of *M. martes*, alternate periods of increase and decrease in body size occurred (Paaver 1965; Smirnov 1975). By analyzing (radiocarbon dating) subfossil samples, the time of translocation of *M. martes* to the island of Mallorca was proposed. Valenzuela and Alcover (2015) examined two samples and determined a date range of 87–330 AD (i.e., translocations took place during the Roman Empire).

FORM AND FUNCTION

Form.—Structural features and size of the skull can be used to determine age of *M. martes* (Ansorge 1988, 1992; Reig and Ruprecht 1989; Helldin 1997, 1999). Tooth wear, developing masticatory muscles of the skull, development of the tibia epiphysis, size of the baculum, and other features that have been described for the fisher (*Pekania pennanti*) and *M.*

americana (Marshall 1951; Poole et al. 1994), and have been used to separate young individuals from older ones. To estimate age of adult *M. martes*, Helldin (1997, 1999) counted annual layers in cementum of canine teeth as described for the fisher (Strickland et al. 1982). Similar methods to estimate the age of *M. zibellina* and *M. martes* were used earlier in the Soviet Union (Stroganov 1937; Timofeev and Nadeev 1955; Jurgenson 1956; Maldzhiunaite 1957; Smirnov 1960; Ryabov 1962; Grakov 1963; Klevezal and Kleinenberg 1967; Pavlinov 1976).

Dentition of *M. martes* is very similar to that of *M. zibellina* and *M. americana* (Clark et al. 1987). Dental formula is i 3/3, c 1/1, p 4/4, m 1/2, total 38. Length of upper toothrow (mm; 47 males and 30 females, mean \pm SE) in *M. martes* from eastern Germany was 30.5 ± 0.19 and 28.6 ± 0.18 , and length of lower toothrow was 35.1 ± 0.18 and 32.8 ± 0.20 (Ansoerge 1988). Mean length of upper molar (mm; 29 males and 20 females) was 6.5 and 5.8, and its width was 8.6 and 7.9 in Sweden (Stubbe 1993). Length of the lower molar in *M. martes* from Poland (mm; mean \pm SE; 133 males and 103 females) was 9.9 ± 0.32 and 9.0 ± 0.34 (Reig 1989). Wolsan (1989) gave a classification of morphotypes according to shape and size of teeth for species of *Martes* that was later used to identify *M. zibellina*, *M. martes*, and *M. foina* (Kosintsev and Gimranov 2015).

Vertebral formula of *M. martes* is 7 C, 14 T, 6 L, 3 S, 16–19 Ca, total 46–49 (Stubbe 1993), but Heptner et al. (1967) reported the number of caudal vertebrae as 15–22. Partial spinal lengths (mean % of the total length of the spine and parenthetical range) were: cervical 20.2 (19.6–20.7), thoracic 43.7 (43.0–44.2), lumbar 29.3 (29.0–29.8), sacral 6.8 (6.5–7.1), and tail 73.5 (70.8–77.9—Stubbe 1993). Female *M. martes* have two (Görner and Hackethal 1988) or three pairs (Grakov 1981; Stubbe 1993) of teats. Lactation lasts about 2 months (Starkov 1940).

The heart of *M. martes* is reniform, located between the 6th and 10th rib, and its apex is directed caudolaterally. Heart index (heart-to-body mass ratio; % \pm SE) of 49 males and 38 females, respectively, was 9.3 ± 0.2 and 9.5 ± 0.2 (Tumanov 2003) and of 53 males and 38 females was 8.66 ± 0.22 and 8.91 ± 0.29 , respectively (Polezhaev 1998). Diameter of the aorta was 4.8 mm near the heart and 2.5 mm at the trifurcation; length of aorta was 36.5% of the body length (Tumanov 2003). The thoracic part of aorta was 52.3% of its total length. Diameter of the vena cava was 5.4 mm, external jugular 3.5 mm, internal jugular 2.0 mm, subclavian 3.3 mm, renal 3.5 mm, and portal 3.3 mm (Tumanov 2003). Kidney index (kidney-to-body mass ratio, % \pm SE) was 3.7 ± 0.17 and 4.25 ± 0.32 for 53 males and 38 females, respectively; lung index (lung-to-body mass ratio, % \pm SE) was 13.15 ± 0.79 and 14.51 ± 0.97 in 53 males and 38 females, respectively; spleen index (spleen-to-body mass ratio, % \pm SE) for 53 males and 33 females was 2.43 ± 0.13 and 2.19 ± 0.24 ; and adrenal gland index (adrenal-to-body mass ratio, % \pm SE) for 29 males and 27 females was 0.05 ± 0.023 and 0.06 ± 0.016 (Polezhaev 1998).

Intestinal lengths of 33 male and 19 female *M. martes* (% \pm SE) relative to body length was 436 ± 8.5 and 405 ± 8.2

for small intestines and 38 ± 1 and 39 ± 1.4 for large intestines; liver-to-body mass ratio (% \pm SE) in 48 males and 37 females was 3.4 ± 0.6 and 3.5 ± 0.7 (Tumanov 2003) and in another 53 males and 38 females 3.51 ± 0.18 and 3.78 ± 0.19 (Polezhaev 1998). The stomach of *M. martes* can contain up to 60–90 g of food, but most often it contains up to 50 g (Heptner et al. 1967), with a maximum of 115 g and an average mass of 35.5 g (Danilov and Tumanov 1976).

Function.—Body mass of *Martes martes* changes seasonally. In northwestern Russia, maximum female body mass of 1 kg occurred in September and near maximum mass of 0.95 kg occurred in May and October–November and 0.92 kg in April and December; minimum body mass of 0.85 kg occurred in June (Tumanov 2003). These changes were consistent with seasonal dynamics in daily food consumption (g) for five males (average body mass 1.22 kg) and five females (average body mass 0.89 kg), respectively: 243 g and 191 g in spring, 212 g and 182 g in summer, 295 g and 220 g in autumn, and 232 g and 208 g in winter, or an average of 26.6 and 29.7 kcal/100 g body mass. Daily caloric need in kcal for an individual weighing 0.93 kg was 268.1 in spring, 264.4 in summer, 335.3 in autumn, and 271.7 in winter, or an average of 30.6 kcal/100 g of body mass (Tumanov 2003). Seasonal dynamics of body mass and the need for food determine the physiological state of an individual and its reproductive condition. Seasonal dynamics of adrenal gland mass of 27 females in autumn–winter (mean \pm SE) and five females in spring–summer were 85.6 ± 4.1 mg and 96.3 ± 3.5 mg, and the thickness of the cortical layer was 0.90 ± 0.05 mm and 0.95 ± 0.06 mm, respectively (Tumanov 1993). *Martes martes* has a rather high cerebral index (brain-to-body mass ratio, % \pm SE; $n = 12$) of 18.4 ± 0.8 , higher than that of the Eurasian polecat (*Mustela putorius*), American mink (*Neovison vison*, currently *Neogale vison*), European mink (*Mustela lutreola*), Eurasian otter (*Lutra lutra*), wolverine (*Gulo gulo*), and European badger (*Meles meles*—Tumanov 2003).

Martes martes molts in spring and autumn; onset of molt is associated with photoperiod. Spring molting begins in March and lasts through early June, and autumn molt is from late August to early November. Timing of molting depends on condition and nutrition of the individual, its age, and weather; molt occurs faster in autumn (Ternovsky 1977). In northern parts of the distribution, spring molting begins 1–2 weeks later than southern parts (Danilov and Tumanov 1976). *Martes martes* has its complete winter fur for about 5 months and its summer fur for about 2 months. Adult females molt faster than males, and less well-fed individuals molt faster than fat or sick individuals (Starkov 1947).

Average monthly body temperatures of captive female *M. martes* were 37.6–39.5°C, being lowest in August and October and highest in March (Tumanov 2003). Respiration rate of 15 captive adult males was 59/min; pulse rate was 325 ± 8.0 for eight males and 345 ± 17.8 for three females (Tumanov 2003). Heart rate was 259 beats/min/kg of body mass for males and 312 for females; breathing frequency was 27 breaths/min for males and 31 for females (Ternovsky et al. 1981).

Water and energy metabolism of *M. martes* was compared with the steppe polecat (*Mustela eversmanii*) in 1995 and *M. zibellina* in 1998 at Chernogolovka Research Station of Moscow province (Meshcherskii et al. 2003). A high level of metabolism was noted in *M. martes* and *M. zibellina*, as expressed in a greater amount of digestible food (coefficient of dry food digestibility, $92.5 \pm 0.5 SE$), water (total water intake, 216 ± 34 g/kg of body mass/day), and correspondingly higher evaporative water loss (proportion of evaporative water losses in the total balance, $49.1 \pm 4.3\%$) and heat dissipation (proportion of energy taken in that was dissipated with evaporation, $28.0 \pm 2.4\%$), compared with the steppe polecat (Meshcherskii et al. 2003).

ONTOGENY AND REPRODUCTION

Ontogeny.—At birth, *Martes martes* weighs 20–27 g (Ternovsky and Ternovskaja 1994), its auditory canals are closed (open at 28–33 days), and it is blind (eyes open at 30–36 days). Young are covered with light gray juvenile down that becomes gray-brown fur in a few days. At 40–45 days of age, young develop canines and incisors. Juveniles feed on mother's milk for 1.5–2 months and then gradually switch to meat (AspISOV et al. 1967; Grakov 1981). Young leave the nest at 37–40 days old. By July at the age of 10 weeks, juveniles weigh about 0.4 kg. Rather rapid growth of juveniles continues until autumn when they reach 0.6–0.7 kg (80% of adult body mass), and they are hardly distinguishable from their parents in appearance. During this period, families break up, and juveniles transition to an independent life (Danilov and Tumanov 1976). Young *M. martes* molt in September (Heptner et al. 1967).

Based on CBL and mass of mandible Pavlinov (1977) showed that the skull of *M. martes* grows slowly during almost the animal's entire life, but a higher specific growth rate was recorded in the period from 10 months to 1+ years of age; a noticeable decrease in specific growth rate was recorded from 4 to 7 years of age. Skull sizes in four age groups of *M. martes* were mean CBL (mm, males and females, respectively) of 81.0 and 74.7 for juveniles, 82.2 and 75.7 for yearlings, 83.2 and 76.3 for 2+ years old, and 81.8 and 75.5 mm for 3+ years old and mean mastoid width (mm) of 35.6 and 34.3 for juveniles, 35.6 and 34.2 for yearlings, 35.0 and 32.6 for 2+ years old, and 34.8 and

32.9 mm for 3+ years old (Polezhaev 1998). The growth rate of the skull of *M. martes* on average begins to decrease after 2 years of age (Yazan 1972).

In the wild, *M. martes* rarely lives up to 10 years; the proportion of individuals reaching 6–7 years of age was 5.1%, 7–8 years was 3.6%, and 10+ years of age was 1.4% ($n = 646$ —Pavlinov 1977). A hunting sample of 1,245 individuals contained 1.5% 5-year-olds and only 2.5% 6-year-olds and above; maximum age of males was 11–16 years (Grakov 1981). Siivonen (1979) noted that life expectancy of *M. martes* was 8–10 years and rarely up to 15 years. In captivity, *M. martes* lives up to 18 years (Starkov 1940).

Reproduction.—Breeding season of *Martes martes* is from late June to mid-August (Stubbe 1993) and usually occurs in July–August (AspISOV et al. 1967). Danilov and Tumanov (1976) provided detailed data on the sexual cycle of male and female *M. martes* and indicated that estrus in females was rather short, from late June to late July, but active spermatogenesis in males was much longer, from late April to late August (Fig. 7). Ovulation was triggered by mating (Kler 1941).

Schmidt (1943) indicated a gestation period of 249–286 days ($n = 19$) with birth dates from 10 March to 5 May. Ternovsky and Ternovskaya (1994) reported gestation at 265–279 days ($n = 5$), and Tumanov (2003) reported 240–264 days ($n = 10$). At an experimental cage farm, birth of young was recorded only in the morning (Tumanov 2003). Births in central Germany occurred in March and April (Stier 2012). Mating dates on the experimental farm study by Ternovsky and Ternovskaya (1994) were from 6–12 July to 25 July, with coitus lasting up to 150 min (average 50 min—Schmidt 1943). In the wild, mating occurred 14 June–30 July (Germany—Stier 2012). During the second year of life, 10–45% of females become reproductive (Heptner et al. 1967; Danilov and Tumanov 1976; Stubbe 1993). Up to 10% of adult females 2+ years old do not reproduce (Grakov 1981). In captivity, females generally enter estrus at 3 years of age (Grakov 1981; Stubbe 1993), although a tame female at 456 days of age mated with a wild male and gave birth after 264–274 days (Austria—Krott 1973). The peculiarity of the structure of the female reproductive system, with the ovary inside the oviduct, excludes ectopic pregnancies in *M. martes* (Manteifel 1934).

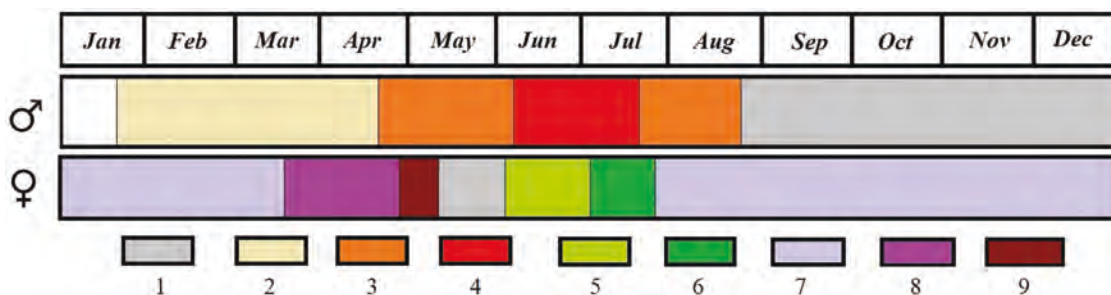


Fig. 7.—Sexual cycles, male (above) and female (below), of *Martes martes* (Danilov and Tumanov 1976, redrawn by VM): 1—quiescence, 2—passive spermatogenesis, 3—active spermatogenesis, 4—mating period, 5—proestrus, 6—estrus, 7—pregnancy before implantation, 8—pregnancy after implantation, and 9—parturition.

The first reported *M. martes* offspring born in captivity was at the Moscow Zoo (Manteifel 1934). Based on daily observations that began in 1927 at the zoo, dates of mating for *M. martes* were 28 and 29 July 1928, and the first litter (a single offspring) was born after 237 days on 22 March 1929. This female also mated on 18–22 July 1929 and 21–25 July 1930 and had two young on 24 March 1930 and four young on 26 March 1931, respectively (Manteifel 1934). These observations showed that the breeding biology of *M. martes* was very similar to *M. zibellina*, suggesting hybridization could potentially occur.

In the 1920s and 1930s, breeders in Europe and North America were unsure about the regular breeding patterns of four species of *Martes*: *americana*, *martes*, *pennanti* (currently considered *Pekania pennanti*), and *zibellina* (Ashbrook and Hanson 1927, 1930). A common mistake of breeders, taken from hunters, was that the mating season of *Martes* took place in February–March; however, in the 1920s, researchers began to doubt this. Numerov (1969) confirmed that summer breeding of captive males and females resulted in the first offspring the following spring: *M. martes* on 22 March 1929 at the biological station of the Moscow Zoo, *M. zibellina* (ibid.) on 3 April 1929, *M. foina* on 7 April 1929 at Hirschegg-Riezlern farm, Germany (Austria at present), and *M. americana* on 23 April 1929 on a farm in Saratoga Springs, New York, United States (Ashbrook and Hanson 1930).

Dimensions of the genitals of young and adult *M. martes* differ markedly. In juvenile males, mass of testes with appendages in winter was 120–260 mg (mean, 210), and in adults, 210–520 mg (mean, 350); in June–July, mass of the genitals of adult males reached 1,900–2,500 mg (northwestern Russia—Danilov and Tumanov 1976). Stier (2012) proposed that sperm in the testes of *M. martes* in Germany was present only when the genitals weighed more than 1,300 mg. Spermatozoa of *M. martes* and *M. zibellina* are the same in size and shape. Length of the sperm head is about 8 μm , width is about 6 μm , and length of the tail is about 55 μm (Starkov 1947).

Mean mass of the uterus of juvenile females was 82 mg in autumn and can be as large as 205 mg in winter, 375 mg in a pregnant female, and 865 mg in March. Mean mass of the uterus during a female's first pregnancy in winter is 308 mg compared to 402 mg in a female with repeated pregnancies (Gribova 1956). In January–February, genital mass was 280–430 mg (on average 330) in juvenile females and 680–1,280 mg (on average 940) in adult females (Danilov and Tumanov 1976). Size of the embryo blastocyst during the latent stage (6–7 months) does not change much and is 0.8–1.0 mm (Starkov 1947). At the end of winter (before implantation), sizes of the corpora lutea in ovaries are about 1,210–1,349 μm (Gribova 1956) but by March increase to 1,700–1,800 μm (Danilov and Tumanov 1976). Based on the analysis of the number of corpora lutea of pregnancy (CLP) in the ovaries, Grakov (1981) found that the proportion of pregnant females at 1 year of age was 82%, 2 years 90%, 3 years 100%, 4 years 92%, 5 years 100%, and 6 years 100%. Those same females had an average of 3.0, 3.42, 3.25, 3.46, 3.34, 4.0, and 3.28 CLP in the ovaries, respectively (Grakov 1981). Thus,

highest reproduction in the wild is characteristic of females 3–5 years old.

The most reliable data on the number of young in a litter come from captive *M. martes*; 1–4 young/litter, on average 3.0 (Schmidt 1943) but one litter of eight young was recorded on a farm in Pushkino, Moscow region (Portnova 1941). According to data from a survey of Russian hunters in 1959–1964, an average of 3.55 young/litter (range 1–8) in 1,184 nests, a maximum of 4.9 young in 34 litters in the Kaliningrad region, and a minimum 3.38 young in 314 litters in northern regions of Russia (Grakov 1981). After giving birth, females remain in the nest for the first 2 days, then leave their litters for 5–10% of the day during the rest of the first week, 30% of the day from the second week to 1 month, and 40% of the time after that (Stier 2012). Mortality of young while in the nest is estimated at 24–25% (Danilov and Tumanov 1976).

Number of young (mean \pm SE) in wild litters was 3.8 ± 0.35 in the Arkhangelsk region ($n = 49$ litters), 3.3 ± 0.09 in Vologda ($n = 186$), 3.2 ± 0.14 in Kirov ($n = 49$), 3.8 ± 0.15 in Sverdlovsk ($n = 48$), and 3.5 ± 0.13 in Perm ($n = 57$ —Grakov 1981). To estimate population growth, fecundity of females can also be assessed by counting the number of corpora lutea in ovaries of females caught by hunters. The number of CLP (mean \pm SE) in pregnant females was 4.13 ± 0.28 in the Arkhangelsk region ($n = 19$), 3.24 ± 0.19 in Vologda ($n = 33$), 3.60 ± 0.14 in Kirov ($n = 42$), 3.38 ± 0.14 in Sverdlovsk ($n = 36$), and 3.24 ± 0.19 in Perm ($n = 18$ —Grakov 1993).

For about 50 years, management of hunting of *M. martes* in Russia has used the phenomenon of delayed implantation (and analysis of the age–sex structure of hunting samples) to predict population growth (Grakov 1993). Female *M. martes* harvested in winter contained CLP in their ovaries, which were detected histologically and counted. Based on such calculations, it is possible to estimate number of offspring in the next spring and plan the hunting quota for the next hunting season. With systematic monitoring, embryonic mortality can be disregarded, and the number of CLP in a female's ovary is equated to the number of young in a litter (Grakov 1981, 1993).

Many researchers described the phenomenon of “spring excitement” or pseudomating in species of *Martes* (Kler 1941; Grakov 1964, 1973). Such arousal is characteristic of adults and juveniles that have not yet reproduced. It is not directly related to implantation of embryos at the end of winter and not recorded in every spring. Tumanov (2003) believed that pseudomating was an ancestral feature in the behavior of *M. martes*, acquired by species of *Martes* because of glacial changes in the climate, but Grakov (1964) considered this to occur in the beginning of the formation of pair bonds between males and females.

ECOLOGY

Population characteristics.—Demographic parameters in populations of *Martes martes* are quite variable. The most stable characteristic is sex composition. Sex ratio in litters

is close to 1:1, and in young and adult *M. martes*, it is also often close to equality. Nevertheless, method-dependent deviations from equilibrium, especially if samples are small, have been noted (Stubbe 1993), similar to those noted for certain age groups (Ansoerge 1992; Helldin 1997; Stier 2012). In wild populations of *M. martes*, males almost always slightly outnumber females [% females \pm SE (*n*): Poland 43.6 \pm 3.2 (236—Reig and Ruprecht 1989), Sweden 43.5 \pm 2.3 (469—Helldin 1999), Switzerland 27.5 \pm 8.9 (80—Marchesi 1989), Finland 49.8 \pm 8.9 (462—Lampio 1951), Germany 39.5 \pm 3.7 (177—Ansoerge 1992), Arkhangelsk region 49.5 \pm 3.2 (238), Tatarstan 39.0 \pm 2.9 (286), Pechora River basin 46.0 \pm 2.4 (432), Kirov region 49.1 \pm 4.5 (126—Grakov 1981), Karelia 46.2 \pm 1.5 (1286), and Leningrad region 47.7 \pm 3.7 (220—Danilov and Tumanov 1976).

Age compositions of populations of *M. martes* are highly variable both geographically and temporally [% juvenile \pm SE (*n*): southeastern Germany 82.5 \pm 2.8 (177—Ansoerge 1992), northeastern Germany 43.6 \pm 4.3 (133—Stier 2012), Sweden 49.9 \pm 2.3 (469—Helldin 1999), Poland 32.6 \pm 3.1 (236—Reig and Ruprecht 1989), Pechora River basin 31.1 \pm 1.8 (646—Rossolimo and Pavlinov 1974), Arkhangelsk region 68.8 \pm 2.5 (330), Vologda region 59.2 \pm 3.9 (154), Kirov region 60.4 \pm 3.1 (257), Sverdlovsk region 72.4 \pm 3.5 (167—Grakov 1981), and Karelia 46.2 \pm 1.5 (195—Danilov and Tumanov 1976). In the Russian part of the distribution of *M. martes*, age structure as determined from the annual layers in the canine cementum (Klevezal and Kleinenberg 1967) was 64.3% juveniles, 11.5% yearlings, 11.2% 2+ years, 6.2% 3+ years, 2.9% 4+ years, 1.5% 5+ years, and 2.5% 6+ years (*n* = 1,245—Grakov 1981). In Karelia, age distribution of a sample of 195 *M. martes* was 35.9% juveniles, 27.7% yearlings, 19.5% 2+ years, and 16.9% for 3+ years and older (Danilov and Tumanov 1976). In nature, *M. martes* rarely lives up to 10 years; for example, the proportion of 10-year-old and older individuals among 646 *M. martes* was only 1.4% (Rossolimo and Pavlinov 1974).

Proportions of juveniles in populations of *M. martes* are often very large, inconsistent with the observed litter size and natural population growth. Juvenile individuals are predominantly removed by hunting (i.e., selective capture and shooting—Grakov 1973, 1981; 1993). The main methods of harvesting of *M. martes* are active (shooting with or without a dog) and passive (trapped with a bait). For example, in northwestern Russia, 73.4% are harvested by shooting with the help of a tracking dog, 7.4% by shooting without aid of a dog, and 13.8% by trapping (Danilov and Tumanov 1976). But in the Urals, the main method of harvesting is trapping. Hunting occurs usually in October–December (for exceptions in different European countries, see “Conservation”), and it can be limited by deep snow that complicates both pursuing *M. martes* and working a dog.

Population densities of *M. martes* (individuals/10 km²) vary considerably: for example, Poland 5.4 (range 3.6–7.5—Zalewski and Jedrzejewski 2006); Rivne region 0.53 and Sumy region 4.0 (Ukraine—Abeletsev 1968); eastern Germany 1.6 (Ansoerge 1988) and 5–10 (Stubbe 1993); Bulgaria 4.0, Czechoslovakia

6.1, Lithuania 0.1–9.4, Scotland 3–30 (Nesvadbova and Zejda 1984; Stubbe 1993); south of Tataria 2.6 (Aspsov 1973); south of the Sverdlovsk region 5.4–8.3, Perm region 0.5–1.3, northern Urals 1.5, Pechora River basin 2.8 (Polezhaev 1998); Kurgan region 2–2.5 (Bakeev and Bakeev 1973); and Caucasus in the Krasnodar region 6.3 (Bakeev 1973). Densities can vary significantly, both seasonally and annually. Settlement of certain habitats by *M. martes* depends on many factors such as abundance and availability of food, weather, and human influences.

Space use.—It is thought that *Martes martes* preferentially occupies forested areas (Storch et al. 1990; Brainerd and Rolstad 2002; Proulx et al. 2004; Stier 2012); and, as shown by Zalewski and Jedrzejewski (2006), forest fragments of only about 2 km² are sufficient for *M. martes* to populate a new area. It inhabits closed lowland and mountainous southern and northern forests from the Atlantic to western Siberia and from Fennoscandia to Iran (Proulx et al. 2004). In the south and north, the distribution coincides with the boundaries of the forest zone.

Martes martes inhabits coniferous, deciduous, and mixed forests, as well as their fragments. Optimal habitats are forests with incomplete canopy and dense understory vegetation (Herrero et al. 2016). In the last 50 years, sparse forests, transformed by logging and a fragmented landscape, have ceased to be factors limiting distribution of *M. martes* in Eurasia (Bakeev and Bakeev 1973; Grakov 1981, 1993; Proulx et al. 2004; Balestrieri et al. 2010; Herrero et al. 2016). Expansion to agricultural and forest-steppe habitats has been observed in Europe (Marinis and Massetti 1993; Pittiglio 1996; Mergey et al. 2011; Manzo et al. 2018). The distribution of *M. martes* has also expanded in its southeastern part, western Siberia, and the Altai region (Grakov 1981, 1993; Inozemtsev and Rizhkov 2007; Kassal and Sidorov 2013; Herrero et al. 2016; Monakhov et al. 2020). In the last decades, *M. martes*, as in the Kurgan forest-steppe (Trenichev 1990), has spread in the Kulundinskaya steppe and the Altai belt pine forests (and its Kazakhstan part too) and continues to approach the distribution of *M. zibellina* in the Altai Mountains; formation of a new region of interspecific hybridization is possible. These factors highlight the significant ecological plasticity of *M. martes* (Manzo et al. 2018).

In ordinary habitats, *M. martes* has a permanent individual home range but also uses several temporary adjacent home ranges. Size of a home range is quite variable both within and among populations. For example, recorded sizes of home ranges (ha; males and females, respectively) were 1,126 and 257 in northwestern Germany (Schröpfer et al. 1997), 2,160 and 1,337 in northeastern Germany (Stier 2012), 2,860 and 975 in northern Finland (Pulliainen 1984), 600 and 930 in Scandinavia (Brainerd 1997), 628 and 357 in Scotland (Balharry 1993), and 335 and 215 for Switzerland (Marchesi 1989). In the eastern part of its distribution, home ranges of individual *M. martes* were determined to be 600 ha in the Urals, 440 ha in the Tambov region, 32–72 ha in the Caucasus (Heptner et al. 1967), 400–5,000 ha (mean 1,500) in Karelia, 300–3,000 ha (mean 900) in the Pskov region, 3,000–5,000 ha in the Murmansk region (Danilov and Tumanov 1976),

600 ha in the Pechora River basin (Yazan 1972), 400–600 ha in the Kirov region, and 600–2,200 ha in the Tver region (Grakov 1981). Sizes of individual home ranges and physical activity depend on abundance and availability of food, climate, age, sex, and population density. Adult *M. martes* occupy areas 2–3 times larger than juveniles. Using radio-tracking in Germany, male home ranges were 1.1–1.6 times larger than those of females. Males were most active in summer and females in autumn; males were least active in winter and females in spring (Stier 2012).

Sizes of home ranges of *M. martes* are related to distance traveled during daily movement: up to 21 km (Nyholm 1970) and on average 4.7 km for males and 2.9 km for females (Pulliainen 1981) in Finland, 1.6–13.4 km in the Pechora River basin (Yazan 1972), 8 km in Arkhangelsk Oblast (Grakov 1981), 1.2–15 km in northwestern Russia (Danilov and Tumanov 1976), 0.6–5.5 km in the Tver region, and 0.6–3.2 km in the Caucasus (Heptner et al. 1967). As a rule, the lengths of daily movements of males are longer than those of females, and at the end of winter, they are longer than in the first one-half of winter. Long-distance migrations are not typical for *M. martes* but a few special cases have been documented. Marchesi (1989) recorded marked *M. martes* moving 5–7 km and up to a maximum of 14 km, and Nyholm (1970) documented migrating individuals moving up to 54 km. Two ear-tagged *M. martes* in the Kirov region were recaptured 15 km away and 3 km away from their release sites (Grakov 1981). If food resources and availability are low, *M. martes* moves greater distances, making long diurnal routes of up to 28.2 km (Stubbe 1993). Heptner et al. (1967) reported that movements of *M. martes* are more frequent in autumn and associated this with the dispersal of juveniles searching for places of residence.

Martes martes typically avoids human settlements, as evidenced by the data on tracks and visual fixation, and capture distances. Stier (2012) noted its preference for woodland. Waechter (1975) reported that captures of *M. martes* were most often (55%) recorded 500–1,000 m from the boundaries of human settlements and 38.7% at >1 km. No *M. martes* were caught in the city, but 29.7% were caught in fields and gardens and 70.3% in the forest (Waechter 1975).

Camera traps showed that *M. martes* preferred forests (Stubbe 1993; Lang and Simon 2010; Stier 2012), but it did occur in treeless areas (meadows, fields, roads, clearings, and even housing areas), sometimes at significant population densities and a near-constant presence. Such fragmented landscapes in Switzerland were 67–92% populated (average 88%) with *M. martes* (Weber et al. 2018).

Diet.—*Martes martes* is an omnivorous predator (Heptner et al. 1967; Danilov and Tumanov 1976; Grakov 1981; Clevenger 1994; Zalewski 2004; Balestrieri 2016), and almost everyone considers it an opportunist and a generalist. Food resources of *M. martes* have been studied relative to geographical characteristics of diets in populations from different countries, seasonal and sexual differences in diet, overlap of food items with other species of small and large predators, dietary habits in urbanized environments, proportions of animal and plant food in diets, and feeding habits on islands and mainland territories.

Diets of *M. martes* vary geographically; in southern latitudes, it prefers plant food (up to 75% of encounters) and invertebrates (about 10%), but it prefers small- and medium-sized mammals (50–65%) and birds (15–20%) in northern latitudes (Zalewski 2004).

Nineteen plant species, 34 invertebrate species, and 22 vertebrates, nine of which are mammals have been recorded in the diet of *M. martes* (Mikheev 2002). Abelentsev (1968) reported 22 species of mammals in the diet of *M. martes*; however, the mammalian prey species listed for the western versus eastern parts of the geographic range of *M. martes*, varied according to the geographical distribution of the species. In eastern Europe and western Siberia, the mountain hare (*Lepus timidus*), Siberian flying squirrel (*Pteromys volans*), muskrat (*Ondatra zibethicus*), and grouse species (*Tetrao*, *Tetrastes*, *Lyrurus*, and *Lagopus*) are added prey of *M. martes*, and proportions of small mammals, hedgehog (*Erinaceus*), and mole (*Talpa*) decrease, whereas the house mouse (*Mus musculus*) disappears (Grakov 1981).

Small mammals (mainly bank voles, *Clethrionomys glareolus*) dominate the diet of *M. martes* (47% of all prey in winter and 42% in summer); plant food (berries) represents 16% in winter and 21% in summer, birds 15% and 13%, medium mammals 10% and 4%, and invertebrates 5% and 15%, respectively (Zalewski 2004). Insects and plant foods in winter diets are more abundant in the south than in the north (Zalewski 2004). Small mammals and juicy fruits predominated in the diets of the mainland *M. martes* of Cantabria, whereas on the island of Menorca, in addition to the previous items, birds and insects also made up about equal proportions (Clevenger 1993). Clevenger (1995) and Ruiz-Olmo and Nadal (1991) identified the main role of plant food in the Balearic and on Menorca in winter, 56.2% and 70.6%, respectively. Other continental studies of *M. martes* of western Europe showed the importance of small mammals in winter diets in Germany (35.9%—Ansoorge 1989), Poland (60.3%—Jedzejewski et al. 1993), Lithuania (51–52%—Maldziunaite 1959; Baltrunaite 2001), Belarus (36.5%—Sidorovich et al. 2010), Sweden (39.8%—Helldin 2000), northwestern Italy (31.2%—Balestrieri et al. 2011), and Hungary (39.8%—Lanszki et al. 2007). In Eastern Europe, similar data were obtained: 37.4% in Karelia and 54.6% in the Murmansk region (Danilov and Tumanov 1976), 43.0% in the Onega River region, 45.6% of the Northern Dvina River region, 53% of the Caucasus, 76.4% in the Trans-Urals, 86.5% in the Vologda region, 61.4% in the Kirov region, and 67.2% in the Perm region (Grakov 1981).

Plant food, mainly berries, in winter diets of *M. martes* was 44.5% in Switzerland (Marchesi 1989), 33.1% in Scotland (Caryl et al. 2012), 26.7% in Norway (Selas 1992), and 38.9% in Belarus (Sidorovich et al. 2010). In the eastern part of Europe, a predominance of plant food in the winter diets of *M. martes* was extremely rare and mainly associated with abundant fruiting of rowan (*Sorbus aucuparia*) that occurred every 2–4 years (Grakov 1981). Other food groups such as birds, large- and medium-sized mammals, invertebrates, amphibians, and reptiles

were sometimes primary dietary items, but they were more often secondary and auxiliary foods.

Some comparisons of diets of *M. martes* and sympatric carnivores (other species of *Martes*, mustelids, and canids) have been made. Baltrunaite (2001) found that a red fox (*Vulpes vulpes*) feeding niche overlapped 60–70% with *M. martes*, which was confirmed by Lanszki et al. (2007). Most often, comparisons have been made between *M. martes* and *M. foina*: their diets in western Europe overlapped 93–95% (Marchesi et al. 1989; Clevenger 1994; Posluszny et al. 2007). In Ukraine, overlap was considerably less at 41.2% due to *M. foina* eating synanthropic species of animals, poultry, and cultivated fruits (Mikheev 2002; one of the common names of *M. foina* is “domestic marten”). Foraging areas of the two species spatially overlapped little (Mikheev 2002).

Diets of sympatric *M. martes* with *M. zibellina* have been assessed in the Urals, although direct comparisons of the two are rare in the literature. Yazan (1972) found that diets of *M. martes* in the Pechora River basin contained 55.4% small mammals, and 32.3% plant food (mainly cedar nuts of *Pinus sibirica* and rowan), and those of *M. zibellina* had 33.3% and 38.1%, respectively; dietary overlap was 85–91%. In the same area > 25 years later, Polezhaev (1998) found similar diets: *M. martes*, 59.2% small mammals and 24.5% plant food, and *M. zibellina*, 70.3% and 23.3%, respectively; overlap was 95–98%. Monakhov (2016) analyzed long-term data (frequency, %) of winter feeding of *M. martes* and *M. zibellina* in the Ural region. Main food items of *M. martes* were mouse-like rodents (43.1), birds (26.7), other rodents (16.4), insectivores (14.5), and cedar nuts (14.2). Those of *M. zibellina* were mouse-like rodents (70.9), cedar nuts (34.0), birds (17.2), berries (12.9), and insectivores (6.4). *Martes martes* in the Ural region was characterized by a higher degree of predation than *M. zibellina* (Monakhov 2016).

Intraguild predation was noted by Brzeziński (2014) when red fox young were caught in a den by *M. martes* in Poland. *Martes martes* also catches larger prey such as hare (*Lepus*), hedgehog (*Erinaceus*), beaver (*Castor*), muskrat (*O. zibethicus*), nutria (*Myocastor coypus*), hazel grouse (*Bonasia bonasia*), black grouse (*Lyrurus tetrix*), capercaillie (*Tetrao urogallus*), and ducks (Anatidae) and eats the remains of ungulates (e.g., Suidae, Cervidae, and Moschidae). *Martes martes* will store prey when not completely consumed (Danilov and Tumanov 1976; Grakov 1981). Yazan (1972) proposed that females select smaller prey (voles, small birds, and hazel grouses) and males select larger prey (hares, wood grouse, partridge, and black grouse). Cannibalism by *M. martes* was documented in Sweden (Helldin 2000).

Diseases and parasites.—*Martes martes* and other species of *Martes* are considered disease-resistant in the wild and captivity (Starkov 1947; Schmidt 1951). According to Grakov (1981), bacteriologists examining the carcasses of *M. martes* did not find any unusual pathogens. There have been no massive epizootics in *M. martes* populations, and cases of rabies infection were rare (Stubbe 1993).

Novel coronavirus 2019 (SARS-CoV-2) has not been observed in *M. martes*. Nevertheless, it is impossible to completely deny susceptibility to the virus because cases of infection have been reported in caged American mink (<https://www.who.int/emergencies/disease-outbreak-news/item/2020-DON301>) and wild American mink in the United States (<https://promedmail.org/promed-post/?id=8015608>; https://www.oie.int/fileadmin/Home/eng/Our_scientific_expertise/docs/pdf/COV-19/A_Factsheet_SARS-CoV-2.pdf).

There are many studies on external and internal parasites of *M. martes* but fewer than for *M. foina* (Schmidt 1943). Various mites and ticks found on *M. martes* include *Sarkoptes scabiei* (scabies—Schmidt 1943), *Ixodes ricinus*, *Hyalomma asiatica*, *Ornithodoros tartakovskyi*, and *Euriparasites emarginatus* (Abelentsev 1968). A new mite, *Rhipicephalus pusillus*, was recorded in *M. martes* on the Balearic islands (Moneris et al. 2011). Quite often, fleas have been recorded directly on prey or in nests but they are not specific to *M. martes* and found on several species of *Martes*. Fleas common to the Eurasian red squirrel (*Sciurus vulgaris*) such as *Tarsopsylla octodecimdentatus* (= *T. uralensis*) are found only on *M. martes*, but *Monopsyllus sciurorum* is found on *M. martes* and *M. foina*. Many flea species commonly found on small mammals were also found on *M. martes*: *Amphipsylla*, *Ctenophthalmus*, *Ctenopsyllus*, *Hystrichopsylla*, *Palaepsylla*, *Rectofrontia*, and *Spilopsyllus* (Schmidt 1943) and *Ctenocephalides*, *Chaetopsylla*, *Ceratopsyllus*, and *Leptopsylla* (Abelentsev 1968).

There is evidence that *M. martes* serves as a host for helminths. For example, the frequency of infection of various helminths was 89.1% in Karelia, 62.5% in the Novgorod region, 63.6% in the Pskov region, and 85.3% in Leningradskaya (Danilov and Tumanov 1976). The following helminths have been recorded in *M. martes*: Trematoda—*Paragonimus kellicoti* and *Euparyphium melis*; Cestoda—*Taenia intermedia*, *T. hydatigena*, and *T. mustelae*; and Nematoda—*Filaria martis*, *Filaroides mustelarum*, *Diocetophyme renale*, and *Trichinella spiralis* (Schmidt 1943) and *Trichinella nativa* (Yushkov 1999). Abelentsev (1968) also noted: Cestoda—*Spirometra erinacei-europaei*, *Taenia tenuicollis*, and *Hydatigera taeniaeformis*; Nematoda—*Capillaria mustelorum*, *C. plica*, *C. putorii*, *Skrjabingylus nasicola*, *Agamospirura* sp., *Crenosoma vulpis*, *Aelurostrongylus falciformis*, *Spiroptera hamulosa*, *Thominx perforans*, and *Angiostrongylus ten.* Berestov (1985) found: Trematoda—*Alaria alata*; Cestoda—*Taenia martis*, *Dipylidium caninum*, and *Mesocestoides lineatus*; and Nematoda—*Ascaris columnaris*, *Strongyloides martis*, *Molineus patens*, *Crenosoma petrovi*, *Filaroides martis*, *Skrjabingylus petrowi*, *Capillaria mucronata*, *Thominx aerophilus*, and *Soboliphyme baturini*.

For *M. martes* in western Europe (mainland and insular parts of Spain), new helminths were described by Segovia et al. (2007): *Euryhalmis squamula* (Trematoda, frequency of 1%); *Pearsonema plica*, *Eucoleus aerophilus*, *Aonchotheca putorii*, *Uncinaria criniformis*, *Sobolevingylus petrowi*, *Baylisascaris columnaris*, *Spirocerca lupi*, *Mastophorus muris*, *Spirura ritypleurites seurati*, and *Physaloptera sibirica* (Nematoda,

1–51%); and *Centrorhynchus aluconis* (Acanthocephala, 3%). *Martes martes* in the Komi Republic had two species of Cestoda and 10 species of Nematoda, of which *Ascaris devosi* was new (Yushkov 1995, 1999).

In 1953–1955, 97–100% of 199 examined *M. martes* had nematode infections (Grakov 1978). Relative occurrence of nematodes in *M. martes* in northwestern Russia was 87.7%, cestodes 9.6%, and trematodes 6.1% (Danilov and Tumanov 1976); Yushkov (1995) found cestodes at 10.8% and nematodes at 42.9% in animals from Udmurtia. Grakov (1981) concluded that predominance of *Filaroides* and *Skrjabinogylus* decreased to the east, and Yushkov (1995) and Tumanov (2003) observed that it decreased to the north. Tumanov (2003) reported higher infections of *Filaroides* in males than females, and in juveniles compared to adults, and an inverse relationship between body condition and intensity of invasion similar to that identified by Monakhov (1999) for *M. zibellina*. Grakov (1981) stated that helminth infestations were not fatal in wild *M. martes*; however, they significantly weakened the body and increased the possibility of secondary diseases, and under severe conditions in the northern taiga, *M. martes* could not maintain energy balance and died from hypothermia. In contrast, Danilov and Tumanov (1976) concluded that helminthiasis did not have noticeable effects on populations of *M. martes*.

Recent studies showed new records on helminthiasis throughout the distribution of *M. martes*. These included *Skrjabinogylus* in Sweden (Hansson 1968), Germany (Heddergott 2009; Heddergott et al. 2015), and Ireland (Stuart et al. 2010); *Filaroides* in Georgia (Kankava et al. 1983), Estonia (Kastein 2016), Spain (Segovia et al. 2007), and central Russia (Tsvetkov and Korablev 2019); *Trichinella* in Italy (Pozio 2000), Poland (Cybulska et al. 2020), Latvia (Kirjušina et al. 2016), Spain (Segovia et al. 2007), and the Pechora River basin (Yushkov 1995); and *Uncinaria* in Bulgaria (Yanchev 1986) and Ukraine (Varodi et al. 2017). New species of nematodes found in *M. martes* are *Uncinaria stenocephala* (Yanchev 1986), *Troglostrongylus acutum* (Heddergott and Müller 2020), *Taenia polyacantha* and *Istmiophora melis* (Kastein 2016; Varodi et al. 2017), and *Pearsonema martron* (Varodi et al. 2017), along with the causative agent of infectious hepatitis *Hepatozoon* sp. (Simpson et al. 2005).

Interspecific interactions.—Potentially dangerous predators of *Martes martes* that could impact population size are rare (Heptner et al. 1967), although Proulx et al. (2004) indicate predation by the red fox as a factor in the decline in the *M. martes* population in Sweden. Potential enemies are large- and medium-sized predators, which sometimes attack *M. martes*, mainly young animals. These include wolverine (*Gulo gulo*), Eurasian lynx (*Lynx lynx*), red fox, gray wolf (*Canis lupus*), feral dogs (*Canis lupus familiaris*—Grakov 1981), and European wildcat (*Felis silvestris*—Abelentsev 1968; Stubbe 1993). Birds attacking *M. martes* are Eurasian eagle owl (*Bubo bubo*), northern goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*), Eurasian sparrowhawk (*Accipiter nisus*),

white-tailed eagle (*Haliaeetus albicilla*—Heptner et al. 1967), great gray owl (*Strix nebulosa*), Ural owl (*Strix uralensis*), northern hawk owl (*Surnia ulula*—Abelentsev 1968; Görner and Hackethal 1988). Also, according to hunters, *M. martes* is preyed on by brown bear (*Ursus arctos*), Chinese raccoon dog (*Nyctereutes procyonoides*), and common raven (*Corvus corax*).

Competitors of *M. martes* for food are red fox, Chinese raccoon dog, *M. foina*, *M. zibellina*, European polecat, Siberian weasel (*M. sibirica*), other mustelids, viverrids, and frugivorous birds (Schmidt 1943, Abelentsev 1973, Bakeev 1973, Grakov 1981, Proulx et al. 2004). However, Aspisov (1973) believes that *M. martes* has no serious enemies and competitors.

HUSBANDRY

Attempts to breed *Martes martes* on cage farms in western Europe began in the early 20th century (Streuli 1932; Schmidt 1943, 1951) following the development of breeding protocols for the silver fox, a melanistic form the red fox, and later *M. americana* and the fisher in North America (Ashbrook and Hanson 1927, 1930). Initially, it was impossible to breed captive *M. martes* because it was thought to mate in late winter (Cocks 1900); by the end of the 1920s, the natural mating time was identified as July (Starkov 1940; Grakov 1981; Stubbe 1993; see “Reproducton”). Small breeding farms of *M. martes* occurred during those years in Germany (Schmidt 1943) and Poland (Stubbe 1993). Subsequently, captive breeding of *M. martes* was gradually stopped because sufficient fur was available in the wild, and it was not particularly valuable compared with that of *M. zibellina* (Schmidt 1951; Grakov 1981).

A significant obstacle to captive breeding of *M. martes* is low fecundity compared with, for example, American mink and silver fox. Currently, *M. martes* is bred only in zoos and research facilities (e.g., Warsaw Zoological Garden—Landowski 1962; Hankensbüttel Otter Center, Germany; Alpenzoo Innsbruck, Austria, and experimental scientific stations Kirov and Novosibirsk, Russia). Also in captivity, self-gnawing (automutilation), a stress-related behavior, was noted, as well as Aujeszky’s disease or pseudorabies (Manteifel 1934; Grakov 1981; Slugin and Rodyukov 1985).

BEHAVIOR

Reproductive behavior.—As a sedentary species, *Martes martes* regularly marks and examines its territory, especially on boundaries of neighboring territories and during the breeding season. *Martes martes* marks its territory with urine (sometimes feces) and secretions from abdominal glands while abdominal rubbing or sliding; these marking behaviors are more often used by males than females (Goethe 1964; de Monte and Roeder 1990; Ludwig 1998; Rozhnov 2011). According

to Rozhnov (2011), marking with plantar and anal gland secretions is doubtful.

In the wild, one male mates with one female. Females have 1–4 periods of estrus in one mating season, repeated after an average of 7–12 days (Starkov 1947). According to Manteifel (1934), a female *M. martes* on a farm in the Moscow Zoo was bred by a male three times on 21, 22, and 25 July 1930 and delivered young on 26 March 1931. Krott (1973) noted that male *M. martes* actively bite the female during coitus, leaving a wound on the back of her head.

The mating season of *M. martes* typically occurs from the end of June to mid-August (Stubbe 1993), and implantation is delayed about 7 months. Once the young are born, the female cannot leave the nest for long periods of time in May and June. At this time, females are caring for young that require protection and feeding. In July–August, females were absent from young 20–50% of the time (Krott 1973; Stier 2012). The male probably shares equally in the raising of young and it has been noted that the young were hidden in trees, rocky crevasses, and caves, always in a safe out of the way place that the male selected (Krott 1973). *Martes martes* lived in pairs from the beginning of winter until late summer at the end of the mating season and then alone until winter began (Krott 1973).

In general, sexual behavior of *M. martes* is very similar to that of *M. zibellina* (Manteifel 1934; Portnova 1941; Starkov 1947; Danilov and Tumanov 1976; Grakov 1981; Stubbe 1993). Hybridization in *M. martes* in the wild and captivity has only been recorded with *M. zibellina* (Manteifel 1934; Portnova 1941; Grakov 1969, 1994). This hybrid, called “kidus,” has been known for a long time (e.g., Pallas 1831; Sabaneev 1875; Belousov 1915). It is believed that the kidus is partially fertile; however, successful crosses were recorded only between female kidus and male *M. martes* (Portnova 1941; Grakov 1981). Successful hybridization between *M. martes* and *M. foina* is considered impossible (Schmidt 1951; Heptner et al. 1967; Grakov 1969; Stubbe 1993). There has been only one statement (Streuli 1932), not scientifically confirmed, about a hybrid litter on a farm in Alsace, but the litter died soon after birth.

Communication.—*Martes martes* is a solitary species, and individuals rarely come into contact except to breed. Contact is often accompanied by aggression, which is probably why they try to avoid each other. Territorial disunity creates problems in communication and finding partners during mating season. To overcome such problems, *M. martes*, like other Mustelids, communicate with a system of indirect contacts, leaving traces, and recognition of scent marks (Pulliainen 1982; Rozhnov 2011).

Miscellaneous behavior.—*Martes martes* leads a solitary lifestyle, except for the breeding period with the formation of unstable pairs. Activity peaks occur in evening and morning hours, although some authors consider *M. martes* to be predominantly a nocturnal predator (Aspisov et al. 1967; Görner and Hackethal 1988; Lang and Simon 2010). It typically searches for food at dusk when its prey (mice and voles) is active (Stubbe 1993). However, activity and foraging depend on

weather conditions and abundance of food. *Martes martes* has been known to forage midday only before inclement weather events (blizzard, snowstorm). Radio-tracking data from a 1988–1989 study in Spain (Sierra Cabrera Mountains) showed that *M. martes* was active 23–47% of a 24-h period (Rozhnov 2011); and after snow fall, *M. martes* can remain in a nest for 2–3 days (Danilov and Tumanov 1976).

Some consider *M. martes* an opportunist in terms of eating behavior. Whereas small mammals and birds dominate diets in winter, diets in summer and autumn are fruit-dominated (Jedrzejewski et al. 1993; Stubbe 1993; Helldin 1999; Baltrunaite 2001). Most of the day, *M. martes* rests in a shelter.

The mode of movement of *M. martes* displays the features of a typical land animal, but it often uses trees to find prey and escape danger (Görner and Hackethal 1988). *Martes martes* moves mainly in small leaps of 65–70 cm in length (Grimmberger 2014), but when escaping, it can leap up to 3–4 m across the ground and in trees (Stubbe 1993). Adults can easily smell a hunting dog at a distance and hide from it. Young *M. martes* escape in trees or hide in shelters. It is an agile, tireless, strong predator with excellent hearing and well-developed hunting skills, which allow it to successfully find prey by sound and smell (Grakov 1981).

GENETICS

Genetic studies of mustelids started in the 1960s when researchers began to examine their chromosomes (Wurster and Benirschke 1968; Orlov and Malygen 1969) and later, allozyme proteins (Kilpatrick et al. 1986; Lidicker and McCollum 1997; Lodé 1998, 1999), and specifically in *Martes martes* (Simonsen 1982; Mitton and Raphael 1990; Williams et al. 1999).

The karyotype of *M. martes* is characterized by a diploid number (2n) of 38 chromosomes (Fredga 1967); fundamental number of autosomal arms (FNa) is 64. There are nine pairs of submetacentric, five pairs of metacentric, and four pairs of acrocentric chromosomes (Dzuev et al. 2013). Heterochromosomes are represented by the submetacentric X chromosome, which is a medium-sized submetacentric, and the Y chromosome, which is the smallest metacentric of the set but largest among mustelids. Among the acrocentric autosomes, one of them is especially large with a pronounced secondary constriction. The rest of the acrocentric chromosomes are among the smallest in the karyotype (Grafodatsky et al. 1982).

In the new millennium, research used mainly two markers: short tandem repeats (STR) in nuclear DNA, or the so-called microsatellite loci, and the sequence of some mtDNA regions. Several studies have examined genetic variability of microsatellite loci in mustelid nuclear DNA (Davis and Strobeck 1998; Kyle et al. 2000, 2001; Stone and Cook 2002; Small et al. 2003). These markers are inherited from both parents and are noncoding regions and therefore selectively neutral, reflecting the current population genetics (up to several generations). Determination of nucleotide sequences (haplotypes) in regions of mtDNA allowed comparisons of mtDNA sequences in

different species or subspecies (e.g., Masuda and Yoshida 1994; Hosoda et al. 1999, 2000; McGowan et al. 1999; Stone and Cook 2002; Marmi et al. 2003). This made it possible to construct evolutionary trees and identify transformations that led to the separation of lineages, caused by mutations in genes that code for proteins.

Davison et al. (2001) studied mtDNA from *M. martes* from 14 European countries and classified them into three clusters. Cluster I contained haplotypes common in *M. martes* throughout Europe, cluster II contained four haplotypes typical for Finland and Sweden, and cluster III contained two haplotypes from Great Britain. Hosoda et al. (2000) obtained data on cytochrome-*b* for seven species of *Martes*. For comparison, Davison et al. (2001) also sequenced the cytochrome-*b* fragment for 19 *M. martes* from among those for which haplotypes were previously obtained based on the control region. As a result, for cluster I (identified by the d-loop) by cytochrome-*b*, haplotypes were identical to *M. martes* from Germany and northeastern Russia, in group II to *M. zibellina* from Khabarovsk (Hosoda et al. 2000), and in group III the same as *M. americana*. Presence of cluster II haplotypes in Finland and Sweden was interpreted by Davison et al. (2001) as hybridization of *M. zibellina* among *M. martes* of Fennoscandia, which took place in the 15th and 17th centuries when *M. zibellina* reached northern Finland and Sweden (Brink 1957; Kirikov 1960). The finding of *M. americana* haplotypes in animals within the United Kingdom is consistent with data on *M. americana* escapees from fur farms reported by Kyle et al. (2003).

Using mtDNA, Pertoldi et al. (2008) revealed the commonality of Danish and Swedish *M. martes*, explaining this by the postglacial expansion of the species throughout Europe. Their results were consistent with those of Davison et al. (2001) but did not confirm introgression with *M. zibellina*. Ruiz-Gonzalez et al. (2013) described the *M. martes* cluster as a compact group based on mtDNA variability; however, among the group, there was still noticeable division into three main subgroups of haplotypes based on geographic characteristics: Ural, Central European, and South European. The history of the formation of the divisions is associated with glacial refugia (Ruiz-Gonzalez et al. 2013).

A more detailed analysis of the genetic and phenotypic relationships between *M. martes* and *M. zibellina* was carried out by Pishchulina (2013). She generally confirmed findings of Ruiz-Gonzalez et al. (2013), with the allocation of a special group of *M. martes* in the Caucasus. She also revealed decreased haplotype diversity within *M. martes* in Europe and especially low diversity in the Urals. Pishchulina (2013) agreed with Ruiz-Gonzalez et al. (2013) that *M. martes* survived the Ice Age in two refugia, and then, in the postglacial period, populated Europe from two regions: Mediterranean refugium where the South European and Central European subgroups remained and from a northeastern refugium where the Fennoscandia-Russia group persisted (Ural). Pishchulina (2013) also revealed isolation of populations of *M. martes* in the South Ural glacial refugium. Pertoldi et al. (2014) found a predominant contribution to the

postglacial recolonization of central and western European populations were *M. martes* that survived the Last Glacial Maxima in unknown northern refugia.

Genetic analysis of the occurrence of hybrid individuals between *M. martes* and *M. zibellina* (kidus) was conducted by Rozhnov et al. (2010). A predominance of mitogroups “Sobol” and “Marten” was revealed in both allopatric and sympatric populations of the two species, but 20% of *Martes* in the Urals were F1–F2 backcross hybrids, and most of the remaining individuals carried an insignificant proportion of genes of another species. Nevertheless, populations of *M. martes* and *M. zibellina* in general retain their genetic isolation, but hybridization in the sympatric zone occurs constantly (Pishchulina 2013).

For the purposes of taxonomy and identifying the structure of populations, it is quite important to identify which species of *Martes* occur in hunting samples, especially those obtained in the sympatric zone. Based on identification of microsatellite loci for the species of *Martes*, genetic methods have been developed to separate *M. martes* from *M. foina* (Domingo-Roura 2002; Pilot et al. 2007; Basto et al. 2010; Ruiz-Gonzalez et al. 2013), *M. americana* (Davis and Strobeck 1998; Kyle et al. 2003), and *M. zibellina* (Pishchulina 2013; Zhu et al. 2017; Modorov et al. 2020; Ranyuk et al. 2021).

Complete mitochondrial genomes have been described for *M. flavigula* (Xu et al. 2012), *M. zibellina* (Xu et al. 2013), and *M. martes* (Li et al. 2014). However, the aspirations of geneticists are aimed at decoding the complete genome. This work would significantly expand knowledge about the origin of the species and subspecies and would provide a basic dataset for revealing the factors of intraspecific variability in the phylogeny. For species of *Martes*, only the complete genome draft of a single *M. zibellina* from the Changbai Mountains in China now has been described (Liu et al. 2020).

CONSERVATION

Martes martes is classified as “Least Concern” (LC) on the International Union for Conservation of Nature’s Red List of Threatened Species (Herrero et al. 2016); it is relatively abundant in the main part of its geographic distribution and is hunted and trapped for its fur. In most countries, hunting is seasonal and follows hunting quotas (Herrero et al. 2016). Usually, hunting seasons coincide with the cold season of the year when skins of *M. martes* have the best properties of winter fur. *Martes martes* is the most valuable fur animal in European countries and second after *M. zibellina* in Russia (Grakov 1981). In the 1960s, auction sales of *M. martes* skins reached 20,000–30,000 pelts from Europe (mainly from Germany, Norway, and Sweden) and 60,000–100,000 from the Soviet Union (Grakov 1981). Average annual offers at the fur “Sojuzpushnina” auction in St. Petersburg in 2016–2020 were 11,000 skins (range 4,628–18,222) of wild *M. martes* with an average price of skin of \$50.00–70.00. Most harvested skins remain with the hunters and are used for making clothes. Some populations have been overharvested, and

numbers have declined in Britain and Denmark (Proulx et al. 2004; Herrero et al. 2016).

In the early 2000s, the status of *M. martes* was assessed by a group of experts (Proulx et al. 2004) for countries in which it is a hunting species, including Austria, Croatia, Czech Republic, Finland, France, Latvia, Lithuania, Norway, Poland, Romania, Russian Federation, Serbia, Croatia, Slovenia, Macedonia, Bosnia and Herzegovina, Sweden, Switzerland, and Turkey. In Austria and France, *M. martes* is hunted year-round (Proulx et al. 2004). In some countries, it is protected under various classifications. For example, “Vulnerable” in Albania, United Kingdom, Italy, Bulgaria, and the Netherlands; “Threatened” in Denmark, Portugal, and Spain; and “Endangered” in Hungary (Proulx et al. 2004) and Kazakstan (Herrero et al. 2016). In the United Kingdom, *M. martes* is classified as “Critical” in England and Wales (Mathews et al. 2018). In many countries, it is protected in national and local reserves and national parks (Herrero et al. 2016).

Translocations were rarely used for *M. martes*. After examining two subfossil specimens from the island of Mallorca, Valenzuela and Alcover (2015) concluded that the first translocations of *M. martes* took place in the 2nd and 3rd centuries in the southeastern Spain. Pavlov et al. (1973) noted the only translocation in Russia was five males and five females from the Arkhangelsk region in the former USSR to the Sary-Chelek Nature Reserve in Kyrgyzstan in February 1962. The release was intended to increase the species composition of predators to reduce the number of small rodents; however, the small number of *M. martes* did not result in a viable population, and after 2 years, no trace of them was observed there (Pavlov et al. 1973). More recently, a translocation was carried out in Wales because numbers of *M. martes* in England had fallen catastrophically low due to overhunting (Langley and Yalden 1977). In 2015–2017, 51 *M. martes* were transported to Wales from Scotland to enhance the local population (Sainsbury et al. 2019), and these translocations were considered successful (Mathews et al. 2018). Unintended introductions of the related *M. americana* occurred in England when some individuals escaped from breeding farms (Kyle et al. 2003).

The primary factors affecting the conservation of *M. martes* are uncontrolled hunting and logging of closed coniferous forests, leading to fragmentation of habitats and loss of connectivity among affected populations (Mathews et al. 2018). Development of human transportation networks creates new barriers and causes deaths of mostly juveniles and yearlings on roadways (Seiler et al. 2004; Langevelde et al. 2009; Balestrieri et al. 2010; Stier 2012). Such networks also increase the risk of predation from larger carnivores and avian predators (Sidorovich et al. 2010). Nevertheless, the wide distribution and overall abundance of *M. martes* suggest that its conservation status is currently secure.

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