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Microtus cabrerae (Rodentia: Cricetidae)

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Abstract: *Microtus cabrerae* Thomas, 1906, or Cabrera's vole, is a medium-sized arvicoline, and one of the largest *Microtus* species. *M. cabrerae* is an Iberoccitane endemic, which is currently restricted to the Iberian Peninsula, where it presents a highly fragmented distribution. The species is the sole extant representative of the anagenetic *Iberomys* lineage with origin in the early Pleistocene. *M. cabrerae* is primarily restricted to wet habitats dominated by tall grasses, sedges, and rushes. The species has experienced strong population declines mainly during the past 10 years, particularly due to agricultural intensification. *M. cabrerae* is currently classified by the International Union for Conservation of Nature and Natural Resources as "Near Threatened," and is listed in the Habitats Directive and Bern Convention, thus requiring appropriate conservation measures.

Key words: arvicoline, Cabrera vole, Cabrera's vole, Iberian Peninsula, Iberoccitane endemic, *Iberomys*, Near Threatened species

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Microtus cabrerae Thomas, 1906
Cabrera's Vole

Microtus cabrerae Thomas, 1906:576. Type locality "Sierra Guadarrama, near Rascafria, N. of Madrid, Altitude about 1000–1300 m."

Microtus asturianus Miller, 1908:198. Type locality "Pajares, Léon, Spain" (see "Nomenclatural Notes").

Microtus dentatus Miller, 1910:459. Type locality "Molinicos, Sierra da Segura, Abacete, Spain."

Microtus cabrerai Trouessart, 1910:181. Incorrect subsequent spelling of *Microtus cabrerae* Thomas, 1906 (see "Nomenclatural Notes").

Iberomys cabrerae: Cuenca-Bescós and Laplana, 1995:69. Name combination (see "Nomenclatural Notes").

Iberomys dentatus: Cuenca-Bescós and Laplana, 1995:69. Name combination (see "Nomenclatural Notes").

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Arvicolinae, tribe Arvicolini, subgenus *Iberomys*. The subgenus is monotypic, containing a single extant species and *M. cabrerae* is currently considered monotypic (see "Nomenclatural Notes").

NOMENCLATURAL NOTES. The species name *cabrerae* honors Angel Cabrera Latorre (1879–1960), a well-respected mammalogist of the Museu Nacional de Ciencias Naturales in Madrid, who was mentored by Oldfield Thomas from the Natural History Museum in London (Tellado and Molina 2010). Thomas (1906) described the species from a single specimen collected in the same year by Manuel Martínez de la Escalera in Sierra Guadarrama, Spain. In addition to this type specimen, an additional specimen purchased from Émile Parzudaki, who was a natural history dealer, traveller,

Fig. 1.—Wild-ranging adult *Microtus cabrerae* (sex not determined) near Bicos, Odemira, southwestern Portugal (37°48′N, 8°30′W), May 2004. Photograph by Joaquim Pedro Ferreira used with permission.

and collector in Paris, has been in the British Museum since 1853 (Thomas 1906). However, because the collection locality of this specimen was overly general (vaguely described as "Spain") and may be unreliable, no description was made at that time (Niethammer et al. 1964).

There has been frequent reconsideration of the alignment of *M. cabrerae* under various subgenera. The species was 1st included in the subgenus *Microtus* by Pavlinov and Rossolimo in 1987 (Musser and Carleton 2005). Based on archaic morphological characters, Chaline (1972a) used the subgenus *Iberomys* for *M. cabrerae*. However, the same author later included the species in the subgenus *Arvalomys* together with *M. arvalis*, *M. agrestis*, and other American voles (Chaline 1974). *M. cabrerae* was then included in the subgenus *Agricola* by Zagorodnuyuk in 1990 (Musser and Carleton 2005), although recent phylogenetic data (Jaarola et al. 2004) supported its reclassification under the subgenus *Iberomys*, as earlier proposed by Chaline (1972a). *M. cabrerae* is the type and sole extant representative of species from the *Iberomys* subgenus. Other species included in this subgenus are *M. huescarensis* (Mazo et al. 1985) and *M. brecciensis* (Giebel 1847), ancestors of *M. cabrerae* (e.g., Cabrera-Millet et al. 1983). The subgenus *Iberomys* has been considered a separate genus from *Microtus* based on morphology of m1 (Cuenca-Bescós and Laplana 1995; Laplana and Cuenca-Bescós 1998; see "Diagnosis" and "Form"), and *I. cabrerae* is used by some authors (e.g., López-García 2008). The proposal of elevating the subgenus *Iberomys* to the genus level has been recently strengthened (Cuenca-Bescós et al., in press), based on morphological distinctiveness from other *Microtus* (see "Diagnosis"), paleogeographic history (see "Fossil Record"), and certain cytogenetic (see "Genetics) and ecological features (see "Ecology").

According to Niethammer et al. (1964), *M. cabrerae* could have been confounded with the species *M. asturianus* described by Miller (1908), especially because both may occur sympatrically in some localities, such as near Rascafria, where the type specimen of *M. cabrerae* was collected. However, *M. asturianus* has long been identified as a subspecies of *M. arvalis* (e.g., Ellerman and Morrison-Scott 1951). *M. dentatus* was 1st considered a distinct species (Miller 1910; Cabrera 1914), and later, tentatively recognized as a subspecies of *M. cabrerae* (Ellerman and Morrison-Scott 1951; Gromov and Polyakov 1992), with *M. c. cabrerae* occurring mostly in northern and central Iberia, and *M. c. dentatus* in southeastern Iberia. However, based on morphological (Niethammer et al. 1964; Ayarzagüena and López-Martínez 1976), electrophoretic (Cabrera-Millet et al. 1982), and biometric (Ventura et al. 1998) studies, no valid subspecific variation is currently accepted, and at present *M. dentatus* is considered a synonym of *M. cabrerae*. The species was referred to as *cabrerai* by Trouessart (1910), although the correct spelling of the species name is Thomas' original latinization of Cabrera to *cabrerae*. An association with *M. guentheri* was proposed in 1956 by Van den Brink (Niethammer et al. 1964), because this species resembles *M. cabrerae* in size, and similarly replaces *M. arvalis* in the southern corner of the *Microtus* distribution in a disjointed habitat across the southeastern Balkans, Turkey, Syria, Lebanon, Israel, and northern Libya (Musser and Carleton 2005; Grimmberger et al. 2009). However, *M. guentheri* differs morphologically from *M. cabrerae* more so than from *M. arvalis* (Niethammer et al. 1964).

Common names of *M. cabrerae* vary according to the language and region of origin, including topillo de Cabrera and topillo ibérico (Castilian); talpó de Cabrera (Catalan); Cabrera lursagua (Basque); rato de Cabrera (Portuguese); campagnol de Cabrera, campagnol denté, campagnol méditerranéen, and campagnol Ibérique (French); arvicola di Cabrera (Italian); Cabrera vole, Cabrera's vole, Iberian vole, and Mediterranean vole (English); and Cabreramaus (German). Recently, the Spanish common name Iberón (from *Iberomys*) has been proposed as an alternative to topillo de Cabrera, mainly for conservation purposes (Cuenca-Bescós et al., in press; see "Conservation").

DIAGNOSIS

Extant Iberian *Microtus* species include the semifossorial pine voles *Microtus lusitanicus* (Lusitanian pine vole, northern Iberia), *M. duodecimcostatus* (Mediterranean pine vole, southern Iberia), and *M. gerbei* (Pyrenean pine vole, Pyrenees and eastern Cantabria mountains); the field vole (*M. agrestis*, northern Iberia); and the common vole (*M. arvalis asturianus*, northern and central Iberia), which is larger than the nominal subspecies occurring across central and northern Europe (Niethammer et al. 1964; Palomo et al. 2007). Similarly to these species, the length of the tail of *M. cabrerae* is about one-third the snout–vent length (Niethammer et al. 1964; Madureira and Ramalhinho 1981). However, *M. cabrerae* (Fig. 1) can be easily distinguished from all these species by its much larger size. The range of physical dimensions of Iberian *Microtus* provided by Palomo et al. (2007) indicates that body mass of *M. cabrerae* is about 1.3–4.9 times larger than that of Iberian pine voles, and about 1.0–3.8 larger than that of *M. agrestis* and *M. a. asturianus*. The length of the body and tail are, respectively, about 1.1–1.7 and 0.9–2.7 times longer than those of Iberian pine voles, and about 0.8–1.9 and 0.7–1.8 times longer than those of *M. agrestis* and *M. a. asturianus*. Ears are relatively long, with length about 1.3–2.5 times longer than that of Iberian pine voles, and about 0.9–1.6 times longer than that of *M. a. asturianus* and *M. agrestis*. Also, hind-foot length is larger for *M. cabrerae*, and provides a particularly useful discriminant feature (usually > 20 mm for *M. cabrerae* and < 20 mm for all other Iberian *Microtus* species). As in *M. a.*

asturianus, *M. cabrerae* has 6 plantar pads, whereas all other Iberian *Microtus* species have 5.

Microtus cabrerae also displays distinct cranial features (Fig. 2). Its larger size, the smaller incisive capsule on the lower jaw, and the often complex 3rd molar (both M3 and m3), which usually cannot be found in any other *Microtus* species from the Palearctic (Niethammer et al. 1964; Engels 1972), help distinguish it from other Iberian *Microtus* species. However, the main characteristic distinguishing *M. cabrerae* and the *Iberomys* lineage from other extant rootless-toothed Arvicolinae is the marked transverse asymmetry of the molars, in particular the m1, with wider lingual triangles than labial triangles. In addition, the salient angles are more acute, contrasting with those of other *Microtus*, *Chionomys*, and *Arvicola* species, with rounded salient angles (e.g., Cuenca-Bescós and Laplana 1995; see "Form" for details).

Microtus cabrerae is thus easily distinguishable from all other Iberian *Microtus* species based solely on morphological criteria. However, according to Niethammer et al. (1964), the comparison with *M. a. asturianus* is particularly relevant because this species may be almost equal in size to *M. cabrerae*, and both may have been potentially misidentified in the past. Indeed, *M. cabrerae* resembles *M. a. asturianus* when it comes to proportions, number of sole pads (6), and number of teats (2 pectoral pairs and 2 inguinal pairs, total = 8). However, the zygomatic arch in *M. cabrerae* is about 1.3 times wider than in *M. a. asturianus*, and the nasal bones (nasalia) get less narrow caudally. The incisive foramina are also wider (1.7–2.1 mm compared to 0.9–1.4 mm in *M. a. asturianus*). Apparently, in contrast to *M. a. asturianus*, the species has no connected supraorbital cristae, but 2 supraorbital ridges separated by a broad hollow (Niethammer et al. 1964). The mandibular foramen lies further caudally on the top of the ridge of the bone encapsulating the posterior portion of the incisors (as in *M. agrestis*), which is another characteristic differentiating *M. cabrerae* from the similar *M. a. asturianus* (Engels 1972). However, the most probable characteristic distinguishing these species is the much smaller incisive capsule on the lingual side of the processus articularis of the mandible of *M. cabrerae*. Unlike in *M. a. asturianus*, the capsule of the lower incisor (i1) in *M. cabrerae* only continues until the branching point between the processus articularis and the processus angularis. However, like in other *Microtus* species with a shortened i1, the incisor capsule doesn't completely disappear over the processus articularis, but continues very narrowly (Niethammer et al. 1964). The upper molar rows of *M. cabrerae* are longer than those of *M. a. asturianus* (maximum lengths of about 8.0 and 6.8 mm, respectively—Niethammer et al. 1964). Other than the differences in the 3rd molar structure (in particular m3), the species also differ in the pattern of the chewing surface of the M1, which has generally longer and narrower loops in *M. cabrerae* (Niethammer et al. 1964; see "Form").

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of the right mandible of an adult female *Microtus cabrerae* (Museu Bocage—National Museum of Natural History, Lisbon, Portugal, specimen MB01-001208) collected in Grandola, Portugal (38°8′N, 8°33′W) by Inês Rosário on 17 June 2004, donated by Maria da Luz Mathias. Greatest length of skull is 29.8 mm.

Distinctive features of the fur are the exceptionally long guard hairs in adults, which are more numerous than those of *M. agrestis* (Niethammer et al. 1964). Guard hairs on the dorsum of *M. cabrerae* often extend out of the coat about 1 cm, and may have black ends on the distal side, and a subterminal yellow part, giving to the species a more dark yellowish color than in *M. agrestis* (Niethammer et al. 1964; Engels 1972). Similar but less-prominent guard hair is only known in the Eurasian water vole (*Arvicola amphibius*—Niethammer et al. 1964). For *M. cabrerae*, the mean length of the guard hair is almost one-half as high as the down-hair mean length, whereas for *M. a. asturianus* the guard hair only sticks up one-third of its length out of the down hair (Niethammer et al. 1964). In addition, hair density of adult *M. cabrerae* is greater than that of *M. a. asturianus*, and particularly so in relation to *M. agrestis* (Niethammer et al. 1964). The relatively longer whiskers (vibrissae) also are characteristic of adult *M. cabrerae* ($\bar{X} \pm SE$ of 26.7 ± 0.48 mm), compared to *M. a. asturianus* (21.9 ± 0.71 mm) and *M. agrestis* (22.9 ± 0.60 mm—Niethammer et al. 1964).

GENERAL CHARACTERS

Microtus cabrerae is a medium-sized Arvicolinae species, although among the members of the genus it has one of the largest body masses, with a mean mass of about 52 g, ranging between 30 and 78 g (Ventura et al. 1998; Fig. 1). The general characteristics of the long and thick fur give the coat a rough, brownish olive color on the dorsal side and yellowish tinge on the ventral side (Thomas 1906; Niethammer et al. 1964; Engels 1972). Like other Arvicolinae, juveniles of *M. cabrerae* are darker in color than subadults and adults. Ears are small and almost completely covered with hair, and the tail is short and slightly bicolored (brownish white above, white below). The long and weighty feet are grayish, and the number of hind-foot sole pads is 6 (Thomas 1906; Engels 1972). No main physical differences are seen between males and females. However, sexual dimorphism in *M. cabrerae* can be found regarding pelvis dimensions in adult individuals (Ayarzagüena and Cabrera 1976; see "Form").

Morphometric variability was described in detail by Ventura et al. (1998) from 148 specimens collected between 1977 and 1981 in several localities from different geographic regions across Spain (provinces of Albacete, Cáceres, Cuenca, Madrid, Jaén, Zaragoza, and Huesca), showing no differences in any of the morphological and cranial measurements taken between sexes and among localities. Ventura et al. (1998) provided the following body measurements (mm; mean and range; provinces of Albacete, Cáceres, Cuenca, Madrid, and Jaén): body length, 118.27 (100.00–135.00, $n = 51$); tail length, 40.48 (30.00–52.00, $n = 52$); ear length, 13.96 (9.80–16.60, $n = 60$); hind-foot length, 20.38 (18.20–22.00, $n = 63$); and the following cranial measurements (mm; mean and range; provinces of Albacete, Cáceres, Cuenca, Madrid, Jaén, Zaragoza, and Huesca): condylobasal length, 28.2 (24.97–30.58, $n = 55$); condyloincisive length, 28.34 (25.35–30.48, $n = 49$); nasal length, 9.45 (7.87–10.21, $n = 56$); incisive foramen length, 5.65 (4.83–8.18, $n = 80$); upper diastema length, 8.67 (7.21–9.37, $n = 77$); length of upper molar row (taken from the molar crowns), 6.63 (5.56–7.37, $n = 77$); braincase height, 8.61 (8.00–9.40, $n = 48$); braincase height (taken from the tympanic bullae), 11.18 (10.37–11.66, $n = 37$); interparietal foramen magnum height, 3.64 (3.12–4.54, $n = 47$); greatest incisive foramen width, 1.85 (1.54–2.22, $n = 75$); interorbital width, 3.56 (2.98–3.92, $n = 69$); nasal width, 3.76 (3.04–4.31, $n = 76$); occipital (or mastoid) width, 12.35 (10.90–13.35, $n = 49$); zygomatic width, 17.12 (14.66–18.77, $n = 55$); mandibular length, 18.31 (15.78–19.93, $n = 81$); length of lower molar row (taken from the molar crowns), 6.55 (5.42–7.38, $n = 70$); articular height, 9.98 (8.08–10.99, $n = 81$); and (from Albacete, Cáceres, Madrid, Jaén, Zaragoza, and Huesca): occipitonasal length, 19.02 (17.76–20.37, $n = 27$); braincase width, 10.51 (9.56–11.41, $n = 30$); and rostral width, 4.59 (3.88–5.07, $n = 74$).

DISTRIBUTION

Microtus cabrerae is considered an Iberoccitane endemic, originally occupying the Iberian Peninsula and southern France (e.g., Ayarzagüena and López-Martínez 1976; Cabrera-Millet et al. 1983; Sesé et al. 2011a). The geographical area of the species has globally decreased from the late Pleistocene (about 0.13–0.01 million years ago) to recent times (see "Fossil Record"), and at present, its distribution range is restricted to the Iberian Peninsula (e.g., Ayarzagüena and López-Martínez 1976; Cabrera-Millet et al. 1982; Fernández-Salvador 1998, 2007b; Fernandes et al. 2008; Fig. 3). The 1st episode of range contraction of *M. cabrerae* took place during the Last Glacial Maximum (late Pleistocene, about 24 thousand years ago), and was followed by an expansion phase during the Holocene Climatic Optimum (Neolithic period, about 8 thousand years ago—Laplana and Sevilla 2013). Climatic warming and aridification during the Bronze Age (Middle Sub-Boreal period, about 5.0–2.5 thousand years ago) are possible reasons to explain the subsequent range contraction of *M. cabrerae* (Cabrera-Millet et al. 1982; Fernández-Salvador 1998). However, population retraction may have been particularly pronounced from the Iron Age (Sub-Atlantic period, about 2.5 thousand years ago) to present, suggesting that the reduction and fragmentation of the distribution of *M. cabrerae* may be largely attributed to agricultural expansion since that period (Garrido-García and Soriguer-Escofet 2012; Laplana and Sevilla 2013), which has resulted in the destruction of suitable habitats for the species (see "Conservation").

Currently, *M. cabrerae* is reported to occur in the southern and western slopes of the major mountain systems of Iberian Mediterranean areas (e.g., Fernández-Salvador 1998, 2007b; Fernandes et al. 2008; Sesé et al. 2011a; Fig. 3).

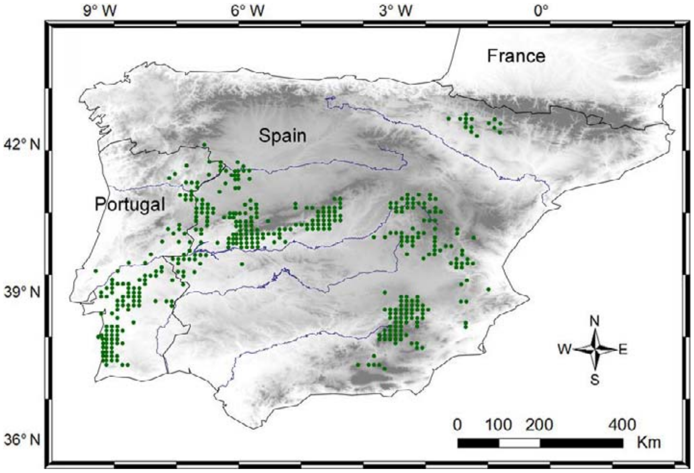

Fig. 3.—Current known distribution of *Microtus cabrerae* in Portugal and Spain (each green dot represents occurrence records of the species mapped at a 10- by 10-km resolution), following Fernández-Salvador (2007b) and Mira et al. (2008), updated with records from local studies (e.g., Rosário and Mathias 2007; Garrido-García et al. 2008, 2013; Ortuño 2009; Pita et al. 2010; and the database from the Conservation Biology Unit, University of Évora). Major rivers (blue lines) and mountain ranges (gray scale) across the Iberian Peninsula also are represented.

In Spain it occurs in the Pre-Pyrenees (several localities in Huesca, Zaragoza, and Navarra); Central System (Salamanca, Cáceres, Madrid, and several localities in Ávila and Toledo); Southern Iberian System (Albacete, Cuenca, and a few areas in Murcia and Valencia); Subbetic Sierras (Jaén, and some localities in Málaga and Granada); as well as several areas in Zamora (Vericad 1970, 1971; Ayarzagüena et al. 1975, 1976; Soriguer and Amat 1988; Ayanz 1992; Fernández-Salvador 1998, 2007b; Ventura et al. 1998, and references therein; Garrido-García 1999; Garrido-García et al. 2008; Ortuño 2009). In Portugal the species occurs over the most central region of the country (Estremadura, Ribatejo, Alto Alentejo, and Beira Interior), extending its range to the northeastern side (Trás-os-Montes, Douro Internacional), and to the southwest (western Alentejo and the northwesternmost tip of Algarve—e.g., Queiroz et al. 2005; Mira et al. 2008). Four main, apparently disconnected, areas were recognized: Luso-Carpetano (the largest area), Montibérico, Bético, and Prepirenaico (the smaller and most isolated area—Garrido-García et al. 2013).

The distribution range of *M. cabrerae* is included in the thermo-, meso-, and supra-Mediterranean bioclimatic zones of Rivas-Martínez (1981), with the species clearly avoiding the Euro-Siberian zone, and regions with particularly high summer temperatures (Mitchell-Jones et al. 1999; Mira et al. 2008). Typically, *M. cabrerae* occurs in geographical regions characterized by medium rainfall values (between 600 and 1,200 mm), low to medium humidity values (< 85%), and acid to neutral siliceous soils (pH between 3 and 7—Mira et al. 2008) at elevations up to 1,500 m, or limestone substrates up to 800 m (Ayanz 1992; Fernández-Salvador 1998, 2007b).

FOSSIL RECORD

Microtus cabrerae evolved from the radiation of the 1st rootless-toothed voles within the *Allophaiomys* complex group (Chaline 1970), which were widespread in southern Europe during the early Pleistocene, 2.59–0.78 million years ago (Agusti 1991), and whose presumed ancestor is the Pliocene (5.33–2.59 million years ago) water vole, *Mimomys* (Ruiz Bustos and Sesé 1985; Chaline and Graf 1988). *M. huescarensis* (Ruiz Bustos 1988) is the 1st representative of the anagenetic *Iberomys* lineage, appearing in the Iberian Peninsula by the end of the early Pleistocene, about 0.78 million years ago. The *Iberomys* lineage is distinguished from other rootless-toothed Arvicolinae by markedly asymmetric, triangle-shaped molars, in particular the m1 (e.g., Cabrera-Millet et al. 1983; Cuenca-Bescós and Laplana 1995; see "Form"). During the middle Pleistocene, about 0.78–0.13 million years ago, *M. huescarensis* was replaced by *M. brecciensis* (Giebel 1847), which became the most abundant and widespread vole in the Iberoccitane province (Iberian Peninsula and the Mediterranean region of southern France). *M. brecciensis* (*Hipudaeus brecciensis*—Giebel 1847; Forsyth Major 1905) is the direct ancestor of the extant *M. cabrerae* (Cabrera-Millet et al. 1983), which gradually reduced its distribution range from the late Pleistocene to the present (López-Martínez 2009). Differences in mandible and dental morphologies between *M. brecciensis* and *M. cabrerae* were described by Ayarzagüena and López-Martínez (1976) and Sesé et al. (2011b); examination of data suggests that *M. cabrerae* is larger in size than *M. brecciensis*.

Archaeological and paleontological sites with fossils of *Iberomys* (*heuscarensis–brecciensis–cabrerae*) were thoroughly inventoried by Garrido-García and Soriguer-Escofet (2012) and Laplana and Sevilla (2013). Fossils of *M. huescarensis* were found at 4 sites in Spain: near Atapuerca (Burgos—Laplana and Cuenca-Bescós 1998; Cuenca-Bescós et al. 1999), Vallparadis, Terrassa (Barcelona—Martínez et al. 2010), Almenara-Casablanca (Castellón—Agustí et al. 2011), and Caravaca de la Cruz (Murcia—Walker et al. 2013).

Fossils of *M. brecciensis* were found at more than 50 sites from the Iberian Peninsula (including Portugal, Spain, and Britain-Gibraltar), France, and Italy (Garrido-García and Soriguer-Escofet 2012). In addition, fossils described as *H. brecciensis* were apparently found in the Balkan Peninsula (Marjan, Croatia—Vuletic 1953), although no information on cranial measurements or molar size and structure is available for confirmation. Fossils of *M. brecciensis* were 1st documented by George Cuvier in 1823 from Sète (Hérault, France—Ayarzagüena and López-

Martínez 1976). Fossils of *M. brecciensis* also were found in other localities in southern France, including Montoussé (Hautes-Pyrénées—Clot 1975), Tautavel (Pyrénées-Orientales—Desclaux 1992), Caniac-du-Causse (Lot—Séronie-Vivien and Tillier 2002), Cénac and Saint Julien (Dordogne—Jeannet and Vital 2009), La Colombière (Hérault—Chaline 1972a), Cèdres Plan d'Aups (Var—Defleur et al. 1990), and Lazaret (Nice, Alpes-Maritimes—Valensi and Abbassi 1998). The most representative records in France are from several localities along the Rhône Valley, such as Soyons (Ardèche—Defleur et al. 2001). The fossils from Saint-Estève-Janson (Bouches-du-Rhône—Chaline 1972a) and Orgnac (Ardèche—Desclaux and Defleur 1997; Jeannet 2000) were particularly important in identifying distinct morphotypes, classified by Chaline (1972a) as *M. b. mediterraneus* and *M. b. orgnasensis*, respectively. *M. b. mediterraneus* was previously described by Chaline (1967) as *M. mediterraneus*, which was recently synonymized with *M. brecciensis* (Cuenca-Bescós et al., in press). Late Pleistocene fossils also were found at Plan d'Aups (Var—Defleur et al. 1990), described as *M. b. defleuri*, and in l'Hortus Cave (Valflaunès, Hérault—Chaline 1972b), described as *M.* cf. *brecciensis mediterraneus-dentatus* with characteristics of both *M. b. mediterranicus* and *M. b. organsensis* (Chaline 1972b; Ayarzagüena and López-Martínez 1976).

In Spain, middle Pleistocene fossils of *M. brecciensis* were found at Cúllar de Baza (Granada) by Ruiz Bustos, who 1st assigned the populations to *M. b. mediterraneus* of St. Esteve Janson (1976) and later (1988) to *M. b. brecciensis* (Sesé 1989; Ruiz Bustos 1988, 1999; Agustí et al. 2000). Fossils also were found at other localities from Granada, such as Huéscar, Cueva del Agua, and Piñar (Mazo et al. 1985; Sesé 1989; Agustí et al. 2000; López-García 2008), and in several caves in the Atapuerca Mountains (Burgos—e.g., Gil and Sesé 1991; Gil 1997; Cuenca-Bescós et al. 1998, 2001, 2010b; Galindo-Pellicena et al. 2011; López-García et al. 2011c). The relatively wide distribution of *M. brecciensis* during the middle and late Pleistocene is evidenced by its presence in many localities across Spain, including Torrelaguna, Aranda, and Jarama (Madrid—López-García 2008; Sesé et al. 2011a, 2011b); Buenavista and Salchicha (Toledo—Sesé et al. 2000); Villacastín (Segovia—Arribas 1994); Ambrona (Soria—Sesé 1986); Aguilón (Zaragoza—Cuenca-Bescós et al. 2010a); Gabasa (Huesca—López-García 2008); Bagur (Girona—Martí and Villalta 1974); Baix Penedès and Terrassa (Barcelona—Rabadà 1990; López-García 2007, 2008; Minwer-Barakat et al. 2011); Penedès (Tarragona—Rabadà 1990); Vilafamés (Castellón—Olària et al. 2004–2005); Vilamarxant, Ribera Baixa, and La Valldigna (Valencia—Montañana 1984, 2008, 2010; Peris 2003); Caravaca de la Cruz (Murcia—Walker et al. 2006, 2013); Véles Rubio and Tabernas (Almeria—Delgado-Castilla et al. 1993; Gonzáles-Ramón et al. 2012); El Higuerón (Malaga—López Martínez 1972);). Valleja (Cádiz—Jennings et al. 2009); and, in Britain, the Devil's Tower (Gibraltar—Garrod et al. 1928).

Middle Pleistocene fossils of *M. brecciensis* have been found throughout Italy (B. Sala and E. Locateli, in litt.), at localities such as Rifreddo, Sant'Arcangelo Basin (Potenza, Basilicata—Masini et al. 2005); Paglicci Cave near Rignano Garganico (Foggia, Apulia—Colamussi 2002 [not seen, cited in Sala and Locateli 2009]); La Pineta site (Isema, Molise—Sala 1996; Coltorti et al. 2005); Montagnola Senese (Florence, Tuscany—Colamussi 2002 [not seen, cited in Sala and Locateli 2009]); Valdemino Cave near Borgio (Savona, Liguria—Sala and Masini 2007); and Mount Zoppega (Verona, Veneto—Bartolomei 1980 [not seen, cited in Sala and Locateli 2009]). In Portugal, fossils of *M. brecciensis* were found in Goldra (Loulé, Faro—Antunes et al. 1986), in Caldeirão Cave (Tomar, Santarém—Povoas et al. 1992), and in Aroeira Cave (Torres Novas, Santarém—Marks et al. 2002).

Subfossils of *M. cabrerae* are relatively common in many late Pleistocene–Holocene deposits in the Iberian Peninsula and southern France. Unlike its ancestor *M. brecciensis*, *M. cabrerae* is absent from Italy and the Cantabria region of Spain (Sesé et al. 2011a). In Spain, subfossils of *M. cabrerae* are known from Maltravieso Cave (Cáceres—Bañuls and López-García 2010; Cardona et al. 2012); Cueva de la Zarzamora (Segovia—Sala et al. 2011); Getafe, Pinilla del Valle, Terralaguna, and Jarama (Madrid—Sesé et al. 2000, 2011a, 2011b; López-García 2008); and Baños de Mula (Murcia—Agusti et al. 1990). Fossils of *M. cabrerae* also were found in many areas where *M. cabrerae* is no longer present, including Sant Esteve de la Sarga (Lleida—Oms et al. 2006); Alta Garrotxa and Vilanova de Sau (Girona—López-García 2008); Capellades, Stiges, and Alorda (Barcelona—López-García et al. 2007; López-García and Cuenca-Bescós 2008); Capellades and Vallès Occidental (Barcelona—López-García 2008); Alorda Park (Tarragona—Valenzuela et al. 2009); Albocàsser (Castellon—Sesé 2011); Cabezo Redondo near Villena, Marina Alta, and Moraira-Teulada (Alicante—López-García 2008; Cuñat 2010); Guadix, Baza, and Dorro (Granada—Garrido-García 2008); Alcaucín and Maro (Malaga—López-García 2008); Atapuerca Mountain caves (Burgos—Cuenca-Bescós et al. 2010a; López-García et al. 2010); Becerreá (Lugo—López-García et al. 2011a); and in Britain, Gorham's Cave (Gibraltar—López-García et al. 2011b).

Late Pleistocene and Holocene remains of *M. cabrerae* found in southern France support the overall contraction of the eastern part of its range up to present (see "Distribution"). Known localities in France with fossil *M. cabrerae* include Montpellier (Hérault—Heim de Balsac 1939; Ayarzagüena and López-Martínez 1976; Gromov and Polyakov 1992); Montagne Noire (Tarn—Deliry 2009); Bagnères-de-Bigorre (Hautes-Pyrénées—Clot and Evin 1986); Donzère (Drôme—Jeannet and Vital 2009); Bérigoule (Vaucluse—

Slimak et al. 2002); and Ardèche (Deliry 2009). In Portugal, remains of *M. cabrerae* were found in Caldeirão Cave (Tomar, Santarém—Povoas et al. 1992), as well as at Caldas da Rainha (Leiria—Niethammer 1970) and Castro Zambujal (Lisboa—Storch and Uerpmann 1976), from where the species is currently absent.

FORM AND FUNCTION

Form.—*Microtus cabrerae* has robust body and skull shape. In dorsal view the lateral margins of the skull are markedly and uniformly convex, with nasals protruding forward more than the incisive (Niethammer et al. 1964; Gromov and Polyakov 1992). The skull has no connected supraorbital ridge, and 2 parallel interorbital ridges (Niethammer et al. 1964; Madureira and Ramalhinho 1981). The cranial upper profile is likewise markedly convex in lateral view, with nasals longer than the diastema. *M. cabrerae* has large incisive and tympanic foramens, robust mandible with well-developed digastric apophysis, mandiblular foramen displaced toward the posterior edge, and clear labiolingual asymmetry in the molars, which is characteristic of the subgenus *Iberomys* (Niethammer et al. 1964; Ayarzagüena and López-Martínez 1976; Cabrera-Millet et al. 1983; Cuenca-Bescós and Laplana 1995).

Relationships of skull and cranial measurements (see "General Characteristics") with body mass revealed isometric scaling for body length, positive allometry for tail length, and negative allometry for condylobasal, upper diastema, and mandible lengths (Ventura et al. 1998). Several cranial measurements were shown to be isometrically scaled with upper diastema length, such as the interparietal–foramen magnum and articular heights; the rostral and zygomatic widths; and the condylobasal, nasal, incisive foramen, and condyloincisive lengths (Ventura et al. 1998). A negative allometry relative to upper diastema length is apparent for maxillary and mandibular toothrow; skull-case height; occipitonasal and mandible lengths; and braincase, nasal, and occipital widths (Ventura et al. 1998). The relationship between the zygomatic width and diastema length indicates that the broadening of the zygomatic arches runs parallel to the elongation of the viscerocranium (Ventura et al. 1998). The relatively important growth of the zygomatic arch complex is probably associated with the strong development of the lateral masseter during postnatal life. Similarly to other rodent species, the pronounced mass development of masseter and lateral pterygoid muscles is related to the predominant development of the articular process over the growth of the mandible (Ventura et al. 1998).

Dentition of *M. cabrerae* is characteristic of the subgenus *Iberomys*. Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. Dental measurements and ratios follow the terminology of van der Meulen (1973): superior incisives are equally thick (norma frontalis and lateralis), and inferior incisives are robust and more rounded (Niethammer et al. 1964; Ayarzagüena and López-Martínez 1976). First inferior molars (m1) are large (1.20–1.43 mm), have acute salient angles, and have a characteristic oblique and asymmetric anteroconid complex, sometimes with slight buccal reentrant angles 4 and 5, and variable development in the lingual reentrant 5 angle (Niethammer et al. 1964; Ayarzagüena and López-Martínez 1976; Cuenca-Bescós and Laplana 1995; Cuenca-Bescós et al., in press). The 3rd molars have, respectively, 3 and 4 prisms below (m3) and above (M3). The m3 is characterized by its peculiar mesial edge, which often lacks dental enamel. In addition, there is great variability in m3 triangles T1 and T2, which may either be confluent, semiconfluent, or isolated, resulting in distinct morphotypes (Ayarzagüena and López-Martínez 1976). Usually, individuals with confluent triangles constitute the least-represented morphotype across geographical populations (e.g., 16.67%, 12.19%, and 17.39% for Albacete-Jaén, Zaragoza-Huesca, and Madrid, respectively). Geographical variation in the proportion of individuals with completely isolated triangles (e.g., 61.11%, 56.52%, and 29.27% for Albacete-Jaén, Zaragoza-Huesca, and Madrid, respectively) is likewise unrelated to distinct geographical populations (Ventura et al. 1998).

Postcranial skeletal features relative to other Iberian *Microtus* include the longer and more-robust humerus, with smaller and less-protruding articular head; the longer and more-robust olecranon process of the ulna; and the more-robust pelvis, with a longer and wider ilium (Cuenca-Bescós et al., in press). Standard morphometric indexes relating the length of the pelvis and other pelvic measurements (e.g., distance from the posterior angle of the ischium to the nearest edge of the acetabulum; distance from the ventral apex of the pubis or pubic symphysis to the nearest edge of the acetabulum; and the thinnest width of the pubis), suggest sex-related differences in pelvis shape of *M. cabrerae*, which are most noticeable in adults (Ayarzagüena and Cabrera 1976). Males show relatively small testis, with testis length–head and body length index around 0.06 (Ventura et al. 1998; see "Reproduction") and the processus urethralis of the baculum has 3 almost equal ends (Niethammer et al. 1964).

The lengths of posterior sections of the gastrointestinal track measured in 2 individuals (1 male and 1 female) from Alandroal (Évora, Portugal) revealed that the relative lengths of the small intestine, the colon, and the cecum with respect to the total length of the intestine (about 64 cm) were about 39%, 35%, and 26%, respectively (Costa 2003). This suggests that in proportional terms the cecum of *M. cabrerae* is relatively long when compared to other voles (about 18% among 8 *Microtus* species—Vorontsov 1979), which is presumably related to its particularly great specialization in terms of habitat and food consumption (see "Ecology").

Function.—Bioenergetics of *Microtus cabrerae* reveal its physiological ability to cope with Mediterranean environments characterized by high ambient temperatures and drought during the summer (Mathias et al. 2003; Santos et al. 2004). Controlled experiments carried out on nonreproductive adults, fed ad libitum a low-fiber diet, and exposed to ambient temperatures ranging from 10°C to 33.5°C, revealed that mean values of oxygen consumption varied between 1.13 ml O_2 g^{-1} h^{-1} at 33.5°C (the lower limit of the thermoneutral zone) and 3.69 ml O_2 g^{-1} h^{-1} at 10°C (Mathias et al. 2003). The lower limit of the thermoneutral zone assigned for *M. cabrerae* is considerably higher than corresponding values in other *Microtus* species from temperate regions (Mathias et al. 2003 and references therein). Conversely, resting metabolic rate of *M. cabrerae* at its lower limit of the thermoneutral zone (taken as approximately the basal metabolic rate) is much lower than that of other congeneric voles (Mathias et al. 2003 and references therein). Metabolic economy by *M. cabrerae* also is evidenced by its ability to increase thermal conductance near the thermoneutral zone (mean values at 10–25°C: 0.144–0.160 ml O_2 g^{-1} $°C^{-1}$; and at 33.5°C: 0.301 ml O_2 g^{-1} $°C^{-1}$—Mathias et al. 2003). The species is thus able to approximate its body temperature to the temperature of the environment during hot, stressful periods, thus exhibiting temporal heterothermy at high ambient temperatures (Mathias et al. 2003). Energy assimilation associated with the conductance value at an ambient temperature of 24°C (0.16 ml O_2 g^{-1} $°C^{-1}$) averaged around 3 times the resting metabolic rate at the lower limit of the thermoneutral zone, which falls within the range expected for rodent species (Santos et al. 2004 and references therein). At 24°C ambient temperature, low-fiber food digestibility is high (about 92.5% and 91.15% for dry matter and energy, respectively) and voles consume about 11.7% of their body mass to maintain constant mass (Santos et al. 2004). However, as for other *Microtus* species (e.g., Gross et al. 1985; Derting and Bogue 1993), food intake should increase under natural conditions, because it should mostly include cellulose-rich grasses, particularly for *M. cabrerae* during the summer, when the quality of available food is presumably lower (Soriguer and Amat 1998; Santos et al. 2004; Rosário et al. 2008; Pita et al. 2010; see "Diet").

In the wild, *M. cabrerae* is predominantly diurnal, with activity peaking around noon during the wet season (between October and April) and at dawn and dusk during the dry season (between May and September—Pita et al. 2011b). Reduction of activity during hottest hours of the day in summer is thought to represent a behavioral mechanism for physiological optimization of metabolism and thermoregulation. The overall circadian activity during summer is globally lower than during the wet season (Ventura et al. 1998; Pita et al. 2011b). In addition, there may be shifts in activity patterns in the presence of other competitor voles (Pita et al. 2011b; see "Interspecific interactions")

ONTOGENY AND REPRODUCTION

Ontogeny.—After birth, pups of *Microtus cabrerae* have larger body mass relative to other *Microtus* species, averaging (± *SE*, range) 3.47 ± 0.39 g (2.9–4.2 g—Fernández-Salvador et al. 2001). This is probably related to the positive relation between neonate and adult body masses in *Microtus* species, because *M. cabrerae* is 1 of the largest species within this genus (Innes and Millar 1994; Fernández-Salvador et al. 2001; see "General Characteristics"). Neonates are hairless, with dark-gray dorsal areas on the head, body, and tail, and unpigmented ventral parts of these regions. Eyes are closed, ear pinnae are folded down, incisors are not erupted, toes are fused, and vibrissae are about 2 mm long (Fernández-Salvador et al. 2001). Mean body-size measurements (mm; ± *SE*, parenthetical ranges—Fernández-Salvador et al. 2001) were: head and body length = 39.80 ± 1.39 (38.00–42.00); tail length = 7.21 ± 0.78 (6.00–9.00); hind-foot length = 7.13 ± 0.47 (6.50–8.00); and ear length = 3.00 ± 0.26 (2.50–3.50).

Main early physical developmental events include (Fernández-Salvador et al. 2001) unfolding of the ear pinnae at day 2, eruption of incisors at day 3, and complete growth of dorsal hair at day 5. Efficient walking is acquired between the 7th and 8th days. At day 9 the ventral hair is fully grown and pups respond to auditory stimuli. At day 11 of life the eyes are totally open and toes are separated. Pups start exploring the area around the nest at 12 days old, and begin eating solid food at day 13 of life. Weaning takes place at 15 days after birth, when pups have a body mass between 10 and 14 g, measure 68–78 cm long (head and body), and have hind-foot lengths of 16–17 mm, tails lengths of 16–18 mm, and ears about 10 mm long. Body mass growth curves during early postnatal development (Fernández-Salvador et al. 2001) reflect significant lower growth rates (g/day; $\bar{X}$ ± *SE*) during lactation (0.53 ± 0.09) than during the postweaning period (0.85 ± 0.16, between 16 and 21 days). Conversely, most body-size–related variables show higher growth rates (mm/day) during lactation than during postweaning, with respective mean ± *SE* values of 2.50 ± 0.19 and 1.70 ± 0.25 for head and body length; 0.71 ± 0.05 and 0.28 ± 0.08 for hind-foot length; and 0.63 ± 0.05 and 0.28 ± 0.09 for ear length. Growth rate of tail length is similar during lactation and postweaning (0.74 ± 0.10 and 0.74 ± 0.19, respectively). The increase in hind-foot and ear lengths starts to stabilize noticeably earlier (around day 21) than the increase in body mass, head and body length, and tail length (around day 40—Fernández-Salvador et al. 2001). The allometric analysis of Ventura et al. (1998; see

"Form") suggests that in common with other mammal species, the braincase completes most of its growth during prenatal and early postnatal life, although the facial region grows at a greater rate than the braincase during postnatal development. At 80 days old, *M. cabrerae* has a body mass of 25–40 g, measures 105–120 mm long (head and body), and has hind-foot lengths of 21–22 mm, tail lengths of 30–37 mm, and ear lengths of about 15 mm (Fernández-Salvador et al. 2001).

Reproduction.—Although *Microtus cabrerae* may reproduce throughout the year (Ventura et al. 1998; Fernández-Salvador et al. 2005a, 2005b; Pita et al. 2010), breeding activity is reportedly higher during the winter, and in very dry years reproduction may even cease completely at the end of the spring and probably into the summer (Ventura et al. 1998; Fernández-Salvador et al. 2005b; Rosário 2012). Reduction or cessation of reproduction during the months with lowest rainfall and highest temperatures has been associated with major declines in food quantity and quality (Ventura et al. 1998; Fernández-Salvador et al. 2005a, 2005b; see "Diet"). *M. cabrerae* may have thus evolved an opportunistic reproductive pattern enabling initiation and termination of reproduction according to the availability of green grass (Fernández-Salvador et al. 2005b).

Global analysis of monthly variation in body mass and testis size, together with the relative position of testis and skull morphology, suggested that sexually mature males have in general a body mass greater than 32 g. Testis have maximum and minimum diameters varying between 5 and 8 mm, and between 4 and 6 mm, respectively; and testis volume varies between 39 and 166 mm^2 (Ventura et al. 1998). Pregnant females have a mean number (± *SD*, range) of 4.91 ± 1.51 (3–7) embryos, which tends to decline from winter to summer (Ventura et al. 1998). Examination of data from captive animals suggests that some prenatal mortality may occur, because mean (number of neonates ± *SE*) litter size was 4.0 ± 0.89, ranging from 3 to 5 individuals (Fernández-Salvador et al. 2001). Gestation length is about 23–24 days, and females build nests 5 or 6 days before parturition (Fernández-Salvador et al. 2001). Captive-born litters weigh between 11.3 and 17.3 g at birth, which is about 21–30% of maternal body mass. Female body mass seems to be correlated with overall litter mass, but not as much with mean body mass of neonates (about 6.6% of adult mean body mass), and with litter size. The sex ratio of captive neonates does not differ from 1:1 (Fernández-Salvador et al. 2001).

Microtus cabrerae displays a predominantly monogamous mating system and a *k*-strategy of reproduction when compared with other *Microtus* species (Fernández-Salvador et al. 2001, 2005a). Monogamy was 1st inferred for the species by Ventura et al. (1998) based on the lack of differences in body size between males and females (see "General Characteristics"), and on the relatively small testis size of adult males (see "Form"). A monogamous mating system in *M. cabrerae* also is supported by the equally sized and highly overlapping home ranges and core areas among male–female pairs (Pita et al. 2010; Rosário 2012; see "Space use"); the reduced scent-marking behavior in pair-bonded animals, relative to nonpaired ones (Gomes et al. 2013c); the trend toward even sex ratios of populations (Fernández-Salvador et al. 2005a, 2005b); and the fact that after parturition, males spent most of their time with the females and their pups in the nest (Fernández-Salvador et al. 2001). However, deviations from this basic monogamous mating system toward polygyny strategies have been suggested in some wild populations of *M. cabrerae*, based on the increased activity of males relative to females during the wet season, which might suggest that males may have access to more than 1 female at high densities and high-quality resources (Pita et al. 2011b). Eventual shifts from single-partner mating and breeding to a facultative resource-defense polygynous strategy with cooperative breeding is supported as well by the high spatial overlap among females at both the home-range and core-area scales (Pita et al. 2010; see "Ecology"), and by a few cases of male home ranges containing several female home ranges (e.g., Pita et al. 2010; Rosário 2012). In addition, the sex ratio in some populations tends to favor females over males (e.g.,Pita et al. 2010; Rosário 2012), which also increases the potential for facultative polygyny (Emlen and Oring 1977).

ECOLOGY

Population characteristics.—Populations of *Microtus cabrerae* are mostly found in agro–silvo–pastoral systems dominated by cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*—e.g., Ayanz 1992; Santos et al. 2005, 2006), as well as in open farmlands with relatively spaced woodlots (e.g., Pita et al. 2006, 2007). Locally, populations are patchily distributed, with individuals being typically grouped in more-or-less distinct population units or subpopulations (often referred to as colonies—e.g., Fernández-Salvador 1998; Pita et al. 2006; Rosário and Mathias 2007), occupying wet habitat patches often smaller than 2,000 m^2 and usually smaller than about 500 m^2 (Ayanz 1992; Fernández-Salvador 1998; Pita et al. 2006, 2007; Santos et al. 2006, 2007; see "Space use"). Populations of *M. cabrerae* thus appear to be spatially structured, and a metapopulation-like dynamic has been suggested for the species in highly fragmented agricultural landscapes, with annual extinction and colonization rates reaching values up to 33% and 17%, respectively (Pita et al. 2007).

Microtus cabrerae is infrequently trapped in wildlife surveys (e.g., Landete-Castillejos et al. 2000), and has been considered as trap-shy (Fernández-Salvador et al. 2001), which makes it particularly difficult to census accurately and to estimate local population sizes and dynamics based on trapping data. For this reason, most studies regarding the population ecology of *M. cabrerae* have been largely based on raptor (e.g., barn owl [*Tyto alba*]) pellet analysis (e.g., Silva 1998; Rodríguez and Peris 2007; Mira et al. 2008) and surveys of species-specific presence signs (e.g., Santos et al. 2005; Pita et al. 2007), which sometimes have been used to derive abundance indexes based on their conspicuity and freshness (e.g., Ayanz 1992; Santos et al. 2006). Typical presence signs include surface runways, grass clippings, and the distinctive dark-green feces about 4–8 mm long, which are usually found in piles (latrines).

Some studies based on capture–mark–recapture techniques have provided important insights on local abundances and population dynamics of *M. cabrerae* (e.g., Landete-Castillejos et al. 2000; Fernández-Salvador et al. 2005b; Rosário 2012). In a population from Riópar (Albacete, Spain) sampled during 6 months (October 1998–April 1999), density estimates varied between 66 individuals/ha in winter and 255 individuals/ha in March (Landete-Castillejos et al. 2000), which falls within the range usually found for other rodent species in open-grass habitats (e.g., farmlands and steppes—Jędrzejewski and Jędrzejewska 1996; Landete-Castillejos et al. 2000). These estimates were much higher than those reported by Fernández-Salvador et al. (2005a) in a population from Cuenca (Spain) sampled monthly between April 1997 and April 1999, which varied between 17 and 115 individuals/ha, reaching maximum values in August–September 1997, followed by 2 peaks in March–April 1998 and April 1999 (Fernández-Salvador et al. 2005b). Density estimates in 4 habitats near Grandola (Portugal) sampled between January and December of 2004 also were much lower, ranging between 12.44 individuals/ha (in May, August, and September) and 49.75 individuals/ha (in December—Rosário 2012). It is possible, however, that population densities reported in these studies may be overestimated, because they were roughly derived as the number of animals present divided by the area of the trapping grids. Because suitable patches are usually very small in relation to overall available habitat, the actual densities of *M. cabrerae* in natural populations should thus in general be much lower than those often recorded for other Iberian *Microtus* species (e.g., *M. duodecimcostatus* and *M. lusitanicus*—Mira 1999; Palomo et al. 2007), which may result from its strict environmental requirements, high habitat specialization (see "Space use"), and monogamous mating system (see "Reproduction"). Indeed, the mean number of individuals in habitat patches smaller than 300 m^2 is usually less than 1 (Fernández-Salvador et al. 2005b), and it has been suggested that habitat patches of about 500 m^2 may be required for the persistence of 1 breeding pair and its offspring (Pita et al. 2010; see "Space use"). Nevertheless, despite potentially inflated density estimates reported in Landete-Castillejos et al. (2000), Fernández-Salvador et al. (2005a) and Rosário (2012) suggest that, apart from the summer maximum during the 1st year in the study of Fernández-Salvador et al. (2005a), population abundances of *M. cabrerae* should in general increase from the winter to the end of the spring, and are very likely to decrease thereafter, particularly in years with extremely hot and dry prolonged summers, when there are marked declines in both habitat quality and quantity (Fernández-Salvador et al. 2005b; Pita et al. 2006, 2010). These results are in agreement with breeding and reproduction timings reported for the species (see "Reproduction"), as well as with the monthly fluctuations in recruitment rates (new born and immigrants), which are globally lower than those recorded in other *Microtus* species (e.g., Fernández-Salvador et al. 2005b and references therein). In addition, several studies based on searching for presence signs across ecological contexts and geographical ranges also suggest a general decrease in surface activity of *M. cabrerae* during the summer (e.g., Ayanz 1992; Ventura et al. 1998; Pita et al. 2006), which in turn suggests that the development of a standardized protocol for presence-sign sampling for *M. cabrerae* may indeed be used to infer population abundance across space and time.

Other than the intrinsic demographic and reproduction parameters found at the local (patch) scale, populations of *M. cabrerae* also seem to depend on extrinsic environmental factors operating at larger (multipatch) scales, which are likely to affect the degree at which habitat patches are occupied by the species (Pita et al. 2007). Indeed, in addition to being highly responsive to the size and isolation paradigms of classical metapopulation theory, (meta)population dynamics of *M. cabrerae* in Mediterranean farmland also seem to depend on habitat-patch dynamics, resulting from the appearance–disappearance of habitat patches, either due to natural events, such as seasonal droughts and overfloodings, or resulting from land management operations, including plowing, burning, and overgrazing (Pita et al. 2006, 2007). Furthermore, spatial population structure of *M. cabrerae* seems to be particularly influenced by the characteristics of the matrix surrounding habitat patches, presumably because these characteristics may affect dispersal ability or motivation to disperse (Pita et al. 2007). In this context, it has been suggested that habitat patches surrounded by extensively grazed seminatural grasslands should be particularly effective in lowering the costs of dispersal in Mediterranean farmland (Pita et al. 2007).

Although dispersal abilities and rates of *M. cabrerae* have not been properly investigated to date, patch-occupancy modeling approaches have suggested that, at least within relatively short time intervals (about 3 months), the species may be unlikely to colonize empty habitat patches distanced by more than a few hundred meters from a potential source (mean distance about 400 m—see Pita et al. 2007). These predictions are in accordance with the only dispersal movement successfully detected during a telemetry study in open farmland, which reported a single unidirectional movement of about 448 m made by 1 adult male during a single night across a grassland field extensively pastured by sheep (Pita et al. 2010). However, in agro–silvo–pastoral systems dominated by cork oak, distances of up to about 1,000 m were recorded within a week (H. Sabino-Marques, in litt.). In addition, in a study regarding postfire recolonization by *M. cabrerae*, it was reported that the species was able to recolonize empty habitat patches distanced by at least 1,364 m from the edge of a burned area in about 8 months (Rosário and Mathias 2007). It is therefore plausible that longer distances could be traveled during the life span of an individual, particularly in animals eventually displaying more than 1 single dispersal event, or using certain low-quality patches as stepping stones to more suitable, although distant patches.

Space use.—*Microtus cabrerae* has semifossorial habits and is restricted to habitats dominated by wet perennial mixed grasses with abundant sedge–rush communities, near small streams, ponds, and agricultural field margins with high soil moisture conditions, which in most cases are fed by the water table, or by irrigation systems (e.g., Fernández-Salvador 1998; Pita et al. 2006, 2007, 2011a; Santos et al. 2006, 2007; Luque-Larena and López 2007). Habitat patches are usually delimited by crops or rather xerophytic vegetation, which are seldom if ever used by voles (Ayanz 1992; Pita et al. 2011a). Within habitat patches, *M. cabrerae* selects microhabitats with tall (usually > 30 cm) and dense (near 100%) herbaceous cover, which has been hypothesized to offer protection from both extreme temperatures and predators (Pita et al. 2006, 2011a). High-quality habitats for *M. cabrerae* are often dominated by perennial grasses such as *Agrostis castellana*, *Briza maxima*, *Festuca ampla*, *Brachypodium phoenicoides*, *Holcus lanatus*, and *Phalaris coerulescen* (e.g., Santos et al. 2006). Representative annual grasses include *Vulpia myuros*, *Gaudinia fragilis*, *Avena barbata*, *Bromus hordeaceus*, *B. madritensis*, and *Agrostis pourretii* (e.g., Ayanz 1992; Santos et al. 2006). Among the sedge–rush vegetation, the most frequent species are *Juncus*, *Carex*, and *Scirpus* (e.g., Ayanz 1992; Santos et al. 2006). Common forb species often found in habitats of *M. cabrerae* include *Leontodon*, *Hypericum humifusum*, and *Tolpis barbata*. Reed species such as *Phragmintes* and *Typha*, and shrubs such as *Rubus*, *Cistus*, *Ulex*, *Genista*, *Dittrichia viscosa*, and *Lavandula luisieri* also may be common in the wet, grassy habitat patches used by *M. cabrerae* (e.g., Ayanz 1992; Santos et al. 2006; Pita et al. 2011a), and together with sedges and rushes are mostly used as refuge and nesting cover (e.g., Fernández-Salvador 1998; Santos et al. 2006; Luque-Larena and López 2007; Pita et al. 2011a).

In fragmented landscapes, wet grassland vegetation along road verges also has been reported to provide alternative breeding habitats for *M. cabrerae* (e.g., Ayanz 1992; Pita et al. 2006; Santos et al. 2006, 2007), reaching up to 30% of the habitats available for the species (Pita et al. 2006). However, road-verge habitats are typically dominated by annual grasses, as well as ruderal and nitrophilous species, thus presumably providing relatively poor-nutrition habitats for *M. cabrerae*, particularly during the summer (Santos et al. 2007; see "Diet"). In addition, road-verge habitats are often associated with higher management interference (e.g., mowing), and are presumably associated with increased mortality rates due to road kills. In fact, regardless of its small size, road-killed *M. cabrerae* have been sometimes recorded in wildlife road mortality monitoring studies (e.g., Carvalho and Mira 2011; A. Mira, in litt.).

Despite its general habitat specialization, *M. cabrerae* seems to select vegetation types differently across seasons and scale of analysis, with the selections of wet, rushlike vegetation being much stronger during hot and dry summer months and at fine spatial scales (e.g., Santos et al. 2005; Luque-Larena and López 2007; Pita et al. 2011a). Such apparent seasonal shifts in habitat-selection profiles are thought to be a consequence of the seasonal changes in habitat quality for the species, with the sites dominated by wet vegetation presenting, in general, higher risk of flooding during the wet season, while conversely retaining the required soil humidity and protection for nesting during the summer (Pita et al. 2011a).

Residency times *M. cabrerae* within habitat patches usually do not exceed 4 months, and are apparently longer in larger patches, where individuals may persist for up to 12 months (Fernández-Salvador et al. 2005b). Radiotelemetry studies conducted in southwestern Portugal's Mediterranean farmlands indicated strong fine-scale site fidelity of individual *M. cabrerae*, with home-range size within a month averaging around 300–400 m^2 (depending on estimation methods), and ranging between about 40 and 1,000 m^2 (Pita et al. 2010). The core areas, areas where individuals spent 50% of their time, were as small as about 2 m^2 to about 182.4 m^2 (Pita et al. 2010). Variation in both home-range size and core-area size seemed unrelated to season and sex, and the spatial overlap between males and females (as well as among females) reached more than 87% for home-range size and 100% for core-area size, whereas space sharing among males seems rather unlikely (Pita et al. 2010). Similar patterns of space use have been inferred from capture–recapture data collected in a population near Valdemorillo de la Sierra (Spain), although estimated home ranges were based on individual locations recorded within 4 days, thus resulting in much smaller areas, ranging between 18.4 and 356 m^2 ($\bar{X} \pm SD = 112.3 \pm 85$ m^2—Fernández-Salvador 2007a). Conversely, home-range sizes based on capture–recapture studies covering longer sampling periods (up to 7 months) in cork-oak landscapes from southwestern Portugal yielded much larger areas (up to 2,581 m^2), which tended to be smaller during the dry season, when surveyed habitats also were smaller (Rosário 2012). Despite the differences in home-range size estimates according to the time interval considered, and the sampling techniques and estimation methods used, in general, studies carried out so far have consistently highlighted the reduced overlap among home ranges of adjacent bonded pairs (Fernández-Salvador 2007a; Pita et al. 2010; Rosário 2012). Such spatial organization of *M. cabrerae* may be related, in part, to olfactory signaling between males and females through urine scent-marking, which is thought to be mostly related to the increased likelihood of finding mates (Gomes et al. 2013a). In addition, the patterns of space sharing among *M. cabrerae* within habitat patches reinforce the monogamous mating system usually attributed to the species, while also retaining the possibility for eventual cooperative breeding (Pita et al. 2010), or other social groups including adults from the same sex (Fernández-Salvador 2007a; see "Reproduction"). Experimental studies have shown that space use and activity of *M. cabrerae* may be affected by predators (see "Interspecific interactions"), with voles avoiding areas with higher perceived predation risk, which are signaled by alarm pheromones released in their urine (Gomes et al. 2013b).

***Diet*.**—Studies regarding the diet composition of *Microtus cabrerae* have been mostly based on noninvasive techniques demonstrating that, like other *Microtus*, the species is mainly herbivorous (e.g., Soriguer and Amat 1988; Costa 2003), feeding on animal matter (e.g., insects) at very low percentages (Soriguer and Amat 1988). Microhistological fecal analyses conducted in west-central Spain (Salamanca and Caceres—Soriguer and Amat 1988) and southwestern Portugal (Odemira—Costa 2003) indicated that *M. cabrerae* feeds mostly on leaves, stems, and seeds of monocotyledon plants, in particular from the families Gramineae and Cyperaceae (both studies), Juncaceae (Soriguer and Amat 1988), and Liliaceae (Costa 2003). Although grasses typically have low concentrations of digestible energy and proteins, their high consumption by *M. cabrerae* is in general agreement with requirements reported for other voles (e.g., *M. agrestis* [Stenseth et al. 1977], the meadow vole [*M. pennsylvanicus*], the California vole [*M. californicus*], and the prairie vole [*M. ochrogaster*—Batzli 1985]). In particular, the study of Soriguer and Amat (1988) reported that more than 58% of the diet of *M. cabrerae* was composed of grasses including the genera *Bromus*, *Poa*, *Vulpia*, *Briza*, and *Avena*, and more than 7% comprised sedges and rushes, including the genera *Holoschoenus* and *Juncus*. Plant fragments most frequently identified (> 90% of the diet) included the genera *Holcus*, *Bromus*, *Avena*, *Agrostis*, *Corynephorus*, *Carex*, *Phalaris*, *Cynosurus*, and *Poa*. Among the dicotyledons (< 3% of the diet), the families Cistaceae (e.g., *Cistus*), Compositae (e.g., *Hypochaeris glabra*), and Linaceae (e.g., *Linum bienne*) were the most commonly found in fecal pallets (Costa 2003). Despite the general agreement among studies in terms of the plant species most often consumed (grasses), there were small differences in diet, probably related to variation in plant availability across study areas; for instance, the area surveyed in Costa (2003) had no rush cover. Likewise, seasonal changes found in the composition of the diet of *M. cabrerae* probably reflect the variation in plant availability throughout the year, with increased consumption of grasses during late spring, together with a general decrease in the intake of sedges and rushes compared to other seasons (Soriguer and Amat 1988). Despite this, *M. cabrerae* may show considerable diet selectivity when considering plant availability within habitat patches, because some items may be positively selected (e.g., plants from the generus *Bromus*), whereas others are apparently avoided (e.g., *Dittrichia viscosa*—Costa 2003). Therefore, although fecal microhistological analysis may produce biases in diet assessment by overestimating monocotyledons and underestimating dicotyledons due to their different physical characteristics and digestibility (e.g., Batzli 1985), it seems likely that monocotyledons tend to be consumed by *M. cabrerae* much more than dicotyledons. Support for a preference of *M. cabrerae* for monocotyledons over dicotyledons also was provided from a gastrointestinal analysis of 2 individuals from Alandroal (Évora, Portugal—Costa 2003).

Preference of *M. cabrerae* for monocotyledons also has been inferred from field observations, based on the identification of plant species with nibbling signals (e.g., *Scirpus*) and remains of herb clippings found in runways used by the species (e.g., *Holcus*, *Agrostis*, *Bracchipodium*, *Bromus*, *Carex*, *Vulpia*, and *Avena*), with animals apparently avoiding leguminous plants (Ayanz 1992). Such patterns of diet selectivity of *M. cabrerae* are probably related to plant palatability and protein content, as well as to individual energy requirements and environmental conditions (Soriguer and Amat 1988; Costa 2003; Rosário et al. 2008). In particular, experimental feeding trials carried out in captivity suggested that palatability may be of great importance for *M. cabrerae*, with perennial monocotyledons such as *Festuca ampla*, *Agrostis castellana*, and *Brachypodium phoenicoides* being among the most palatable plant species (Rosário et al. 2008). Indeed, despite its general preference for annual plants, such as those included in the genera *Bromus*, *M. cabrerae* seems to be much more dependent on perennial grasses able to provide food throughout the year (Santos et al. 2006, 2007; Rosário et al. 2008). Conversely, perennial dicotyledons seem to be the least palatable plant species, presumably because of their higher levels of secondary compounds such as terpenes and alkaloids known as potentially prejudicial for mammals (e.g., Rosário et al. 2008 and references therein).

Diseases and parasites.—No infectious diseases or disease agents have been reported to cause population declines of *Microtus cabrerae*. In addition, the difficulty in capturing *M. cabrerae* has hampered the detection of which species parasitize *M. cabrerae* (Gómez et al. 2003). The small, ribbonlike tapeworm *Paranoplocephala mascomai* was the 1st helminth species determined as an endoparasite of free-ranging *M. cabrerae* (Murai et al. 1980). This tapeworm was found in the 1st portion of the duodenum (between 1 and 8 specimens per host) in 9 of 70 individuals taken from 2 Spanish populations located in Madrid and Cuenca (overall infestation prevalence of 12.9%—Murai et al. 1980). Other wormlike helminths infesting *M. cabrerae* were later described from another 70 individuals coming from 8 populations located in Cáceres, Cuenca, and Madrid (Feliu et al. 1991). A total of 6 helminth species were found in this study: 1 fluke (the trematode *Notocotylus neyrai* with infestation prevalence of 2.8%), 4 tapeworms (the cestode *Taenia taenuicollis*, *Anoplocephaloides dentata*, *Paranoplocephala omphalodes*, and *Paranoplocephala mascomai*, with infestation prevalences of 2.8%, 25.7%, 4.2%, and 12.8%, respectively), and 1 roundworm (the nematode *Syphacia nigeriana* with infestation prevalence of 34.2%—Feliu et al. 1991). The diversity of gastrointestinal helminths infesting *M. cabrerae* is thus one of the most reduced among the Arvicolinae species, with *S. nigeriana* (a monoxenous ageohelminth infesting species of *Arvicola* and *Microtus*) being the most well-adapted species to *M. cabrerae* (Feliu et al. 1991 and references therein). The reduced number of endoparasitic species is particularly manifested by the lack of oligoxenous or eurixenous roundworm (nematode) species, which often infest the majority of species of Iberian Arvicolinae. This fact may result from the reduced probability of *M. cabrerae* picking up roundworm species typical of myomorph rodents, as a result of its restricted geographical range, patchy distribution, limited capacity of gaining new territories, and relatively reduced cohability with the most extended Arvicolinae throughout the Iberian Peninsula (Feliu et al. 1991; see "Interspecific interactions"). On the other hand, the nature of the habitats occupied by *M. cabrerae* may explain the appearance, although occasional, of *N. neyrai*, whose usual hosts are other Arvicolinae less dispersed through the Peninsula territory and with more-specialized habitats, such as seems to be the case of the southwestern water vole (*Arvicola sapidus*—Feliu et al. 1991).

Concerning ectoparasites of *M. cabrerae*, 4 flea species (order Siphonaptera) have been reported in individuals from 3 different areas in Cuenca (Spain): *Rhadinopsylla* (*Actenophthalmus*) *pentacantha*, *Ctenophthalmus* (*Ctenophthalmus*) *apertus personatus*, *Peromyscopsylla spectabillis spectabilis*, and *Nosopsyllus fasciatus* (Gómez et al. 2003). All 4 species have been reported in other voles (e.g., *Microtus*, *Arvicola*, and *Clethrionomys*) as well, and because none is considered host specific, their presence in *M. cabrerae* is not surprising (Goméz at al. 2003). The most abundant flea was *C.* (*C.*) *apertus personatus*, which also is known to parasitize *M. duodecimcostatus*, *M. arvalis*, the southwestern water vole, the long-tailed field mouse (*Apodemus sylvaticus*), and the greater white-toothed shrew (*Crocidura russula*—Goméz at al. 2003 and references therein)

Interspecific interactions.—According to its geographical range, *Microtus cabrerae* may be sympatric with other Iberian voles able to use habitat types that may share similarities with those typically selected by the species. These include *M. lusitanicus*, *M. a. asturianus*, and *M. agrestis* in the northern parts of its range (e.g., Trás-os-Montes and Douro Internacional in Portugal, and Castilla y Léon in Spain), *M. duodecimcostatus* in the southern parts of its range (e.g., southwestern Alentejo and Algarve in Portugal, and Castilla la Mancha and Andalucia in Spain), and the southwestern water vole across several parts of its range (e.g., southwestern Portugal and several localities from north to south of Spain, including Castilla y Léon, Castilla la Mancha, and Andalucia—e.g., Madureira and Ramalhinho 1981; Palomo et al. 2007).

Microtus cabrerae and *M. a. asturianus* have been referred to as having almost mutually exclusive ranges in Spain, because *M. a. asturianus* inhabits the northern one-half of the Peninsula, and if *M. cabrerae* would still exist in the south of France today, it is most likely that its expected habitat would be *arvalis*-free (Niethammer et al. 1964). Interaction with the southwestern water vole in sympatric areas has been reported to be particularly influential to *M. cabrerae*, because the species may show considerable niche overlap in terms of foraging habitat in space and time, and the southwestern water vole (which is more than 2 times larger) is expectedly a more efficient competitor (e.g., Ayanz 1992; Fernández-Salvador 1998; Landete-Castillejos et al. 2000; Pita et al. 2006, 2010, 2011a, 2011b). Indeed, although the southwestern water vole is considered a much more strictly riparian species usually indicating the presence of a constant watercourse with abundant vegetation (e.g., Mate et al. 2013), it also may persist in areas where water is relatively scarce (e.g., Fedriani et al. 2002; Román 2007; Pita et al. 2010, 2011a), thereby increasing its affinities with the habitats typically used by *M. cabrerae*, which in turn increases the potential for interspecific competition in sympatric areas, particularly during the dry season (e.g., Pita et al. 2011a). In southwestern Portugal, for instance, the 2 species may be found in the same habitat patches, within which they may coexist through spatial and temporal segregation at fine scales (Pita et al. 2011a, 2011b). In particular, the southwestern water vole tends to use the wettest parts of humidity gradients found within patches (Pita et al. 2011a), whereas *M. cabrerae* may adjust its circadian rhythm to avoid eventual antagonistic encounters with the southwestern water vole, by increasing (dry season) or decreasing (wet season) its daytime activity, when the southwestern water vole is respectively less and more active (Pita et al. 2011b). In addition, some overlap in dietary niches also may occur between the species, because the southwestern water vole also feeds primarily on monocotyledons of the families Graminae, Cyperaceae, Juncaceae, and, when available, Typhaceae (e.g., Ventura et al. 1989; Garde and Escala 2000; Román 2007). Other small mammals often observed in association with *M. cabrerae* at the local scale include the Algerian mouse (*Mus spretus*), the black rat (*Rattus rattus*), the long-tailed field mouse, and the greater white-toothed shrew (e.g., Landete-Castillejos et al. 2000; Pita et al. 2010). European rabbits (*Oryctolagus cuniculus*) and Iberian moles (*Talpa occidentalis*) also are frequently seen near areas populated by *M. cabrerae*.

Interaction of *M. cabrerae* with high densities of grazing livestock (cattle, sheep, and goats) is often hypothesized to result in population declines due to habitat degradation (overgrazing, over trampling, and soil compaction) increasing the probability of local extinction (e.g., Pita et al. 2007). However, extensive livestock herbivory (preferably sheep and goats) may be important to avoid the development of otherwise suitable habitats to more advanced successional stages, generally shrublands, taken as unsuitable for *M. cabrerae* (e.g., Pita et al. 2006, 2007; see "Conservation").

Microtus cabrerae may be predated by virtually any small or medium-sized predator with which it is sympatric, including snakes, raptors, and mammalian carnivores (either wild or domestic). Known predators of *M. cabrerae* include the barn owl (e.g., Mira et al. 2008), the common buzzard (*Buteo buteo*—Ayarzagüena et al. 1976), the ladder snake (*Elaphe scalaris*—Pita et al. 2011b), the red fox (*Vulpes vulpes*—Ayarzagüena et al. 1975, 1976), and the domestic cat (*Felis silvestris catus*—Ayarzagüena et al. 1976). One of us (RP) has observed the Egyptian mongoose (*Herpestes ichneumon*) and the cattle egret (*Bubulcus ibis*) predating *M. cabrerae*. The least weasel (*Mustela nivalis*) is sometimes captured within runway areas of *M. cabrerae* (e.g., Pita et al. 2010), and may be a particularly important predator on the species, as reported for other voles (e.g., Brandt and Lambin 2007).

HUSBANDRY

Microtus cabrerae may adapt to laboratory conditions set up to perform short-term studies designed to assess individual-level responses to different experimental treatments (e.g., Mathias et al. 2003; Santos et al. 2004; Rosário et al. 2008; Gomes et al. 2013a, 2013b, 2013c). However, long-standing captive breeding colonies designed to assess reproduction patterns are challenging to maintain (e.g., Fernández-Salvador et al. 2001; Gisbert et al. 2007). In the laboratory, captive *M. cabrerae* may be housed individually in wire-mesh or glass cages ranging from 40 by 25 by 15 cm up to 70 by 40 by 40 cm (see Mathias et al. 2003; Santos et al. 2004; Rosário et al. 2008; Gomes et al. 2013a), or as breeding pairs in cages of about 120 by 40 by 40 cm (Fernández-Salvador et al. 2001). Captive *M. cabrerae* may be kept under natural light conditions (Mathias et al. 2003; Santos et al. 2004) or particular photoperiod treatments (e.g., 12L:12D cycles [Fernández-Salvador et al. 2001] or 14L:10D cycles [Gomes et al. 2013a, 2013b, 2013c]), at ambient temperatures ranging between 18°C (Gomes et al. 2013a, 2013b, 2013c) and 26°C (Mathias et al. 2003). Captive *M. cabrerae* are usually fed a composite diet of apples, carrots, corn, and sunflower seeds, sometimes supplemented with diverse grass species collected at original habitats (Mathias et al. 2003; Santos et al. 2004; Rosário et al. 2008; Gomes et al. 2013a, 2013b, 2013c). Water is provided ad libitum, and cotton and dry grass are often provided as bedding and nesting material (e.g., Fernández-Salvador et al. 2001; Rosário et al. 2008). Cages may be prepared with soil and vegetation from original habitats to allow animals to exhibit their natural behavior, such as burrowing and path building (e.g., Fernández-Salvador et al. 2001; Gomes et al. 2013a, 2013b, 2013c). However, successful captive breeding of *M. cabrerae* may require that cages are maintained in the field, to more effectively mimic natural conditions (Fernández-Salvador et al. 2001).

GENETICS

Cytogenetic analysis revealed that *Microtus cabrerae* has a diploid number (2n) of 54 and a fundamental number (FN) of 64 (Díaz de la Guardia et al. 1979; Palacios and Cabrera 1979; Burgos et al. 1988a). Among the contemporary Iberian *Microtus* species only *M. gerbei* has the same diploid number (e.g., Musser and Carleton 2005). Other *Microtus* species occurring in different geographic ranges with a diploid number of $2n = 54$ are *M. californicus* (North America), the Persian vole (*M. irani*, Iran), and Guenther's vole (*M. guentheri*, southeastern Balkans, Turkey, Syria, Lebanon, and Israel—Díaz de la Guardia et al. 1979 and references therein). A main feature of the karyotype of *M. cabrerae* is the presence of enlarged sex chromosomes with large sections of constitutive heterochromatin (known as "giant sex chromosomes"—Díaz de la Guardia et al. 1979; Burgos et al. 1988a; Marchal et al. 2004), a characteristic found in *M. agrestis* ($2n = 50$—Burgos et al. 1988a; Jiménez et al. 1991; Marchal et al. 2004; Giménez et al. 2012) and 3 other *Microtus* species from other geographic areas: the rock vole (*M. chrotorrhinus*, $2n = 60$) from North America, the East European vole (*M. levis* = *epiroticus*, $2n = 54$) from eastern Europe, and the Transcaspian vole (*M. transcaspicus*, $2n = 52$) from Turkmenistan (Meylan 1967; Marchal et al. 2003, 2004 and references therein). The presence of small to intermediate amounts of heterochromatin in X and Y chromosomes also is known in other *Microtus* species showing normal- to medium-sized sex chromosomes (e.g., Modi 1987).

The karyotype of *M. cabrerae* was 1st described by Díaz de la Guardia et al. (1979) as consisting of 3 pairs of large submetacentric chromosomes (pairs 1, 2, and 3), 1 pair of small metacentric chromosomes (pair 4), and 22 pairs (pairs 5–26) of acrocentrics showing gradual differences in size. Variability in chromosome morphology was subsequently shown by Palacios and Cabrera (1979), who classified autosomes of *M. cabrerae* as follows: 2 pairs of metacentric chromosomes (pairs 1 and 2), 1 pair of submetacentric chromosomes (pair 3), 1 pair of subtelocentrics (pair 4), and 22 pairs of acrocentric–telocentric chromosomes (pairs 5–26), with uniformly distributed sizes. According to Díaz de la Guardia et al. (1979), the 3 biarmed chromosomes pairs 1, 2, and 3 are thought to result from 3 centric fusions (Robertsonian translocation) in an ancestor similar to *M. chrotorrhinus*, that is, with 2n = 60 and FN = 64. Chromosome banding techniques have additionally shown that autosomes of *M. cabrerae* have centromeric C-bands larger than those of other Iberian Arvicolinae species (Burgos et al. 1988a; Fernández et al. 2001).

As in *M. agrestis* and *M. chrotorrhinus*, the X chromosome in *M. cabrerae* is a submetacentric giant chromosome (Meylan 1967; Díaz de la Guardia et al. 1979). However, although *M. agrestis* and *M. chrotorrhinus* have a giant acrocentric Y chromosome, this chromosome is a giant subtelocentric in *M. cabrerae* (Marchal et al. 2004). These morphological differences concerning the Y chromosome of *M. cabrerae* might be the consequence of a pericentric inversion (Díaz de la Guardia et al. 1979), which is the most frequent type of chromosomal rearrangement found in the species (Burgos et al. 1988a). The X chromosome in *M. cabrerae* constitutes up to 15% of the haploid genome (about 20% in *M. agrestis*—Marchal et al. 2003, 2004), whereas the relative length of the Y is about 6.5% of the male haploid genome (Díaz de la Guardia et al. 1979). In addition to a euchromatic segment composing the distal three-fourths of the long arm, the X presents a large block of heterochromatin occupying the entire short arm, the centromere, and a one-fourth of the long arm (Burgos et al. 1988a, 1988b; Marchal et al. 2004; Fernández et al. 2001, 2002), whereas in *M. agrestis* C-band–positive material is distributed over the entire long arm, the centromere, and the proximal part of the short arm (Marchal et al. 2004). In addition, in *M. cabrerae* a telomeric C-band in the long arm also may be visible in the X chromosomes (Burgos et al. 1988a). As for the Y, similar to *M. agrestis*, this chromosome has a very long arm composed of constitutive heterochromatin and a very small euchromatic short arm in the pericentromeric region, although respective compositions differ between the species (Burgos et al. 1988c; Fernández et al. 2001, 2002; Marchal et al. 2004).

Similarly to *M. agrestis* and other *Microtus* species, the heterochromatin structure in sex chromosomes of *M. cabrerae* is highly heterogeneous, most likely the result of rapid amplification of blocks of repetitive sequences within the various sections, each with a different origin and composition (Burgos et al. 1988c; Bullejos et al. 1996; Fernández et al. 2001; Marchal et al. 2004). However, there are sequences present in the heterochromatin of the X of *M. cabrerae* that are absent in the heterochromatin of both sex chromosomes of *M. agrestis*, as well as in the Y chromosome of *M. cabrerae* (Fernández et al. 2001, 2002; Marchal et al. 2004). Based on results of G-banding, C-banding, and fluorochrome staining, 6 different subtypes of heterochromatin in the sex chromosomes of *M. cabrerae* have been described, 4 on the X chromosome and 2 on the Y chromosome (Burgos et al. 1988c; Fernández et al. 2001; Marchal et al. 2004). The X contains large (161-base pair [bp] unit length), late-replicating heterochromatic segments rich in AT base pairs (about 65.84%—Fernández et al. 2001), compared to analogous segments in other rodents (e.g., Bullejos et al. 1996). In *M. cabrerae*, this tandemly repetitive heterochromatic satellite DNA also is present on 3 interstitial bands in the heterochromatic block of the Y, and in the centromeric region of autosomes (Fernández et al. 2001). In addition, the heterochromatic regions of sex chromosomes of *M. cabrerae* are frequently involved in chromosomal rearrangements.

A length polymorphism was found in sex chromosomes of *M. cabrerae* and shown to result from deletion mutations affecting the heterochromatic block of both X and Y (Burgos et al. 1988b), particularly in the repetitive DNA sequences (Fernández et al. 2001). Based on this polymorphism, 3 different X chromosomes (the standard and 2 deleted X chromosomes) and 5 distinct Y chromosomes of different sizes have been described (Burgos et al. 1988b). Some sequences on the X euchromatin of *M. cabrerae* share homology with the Y euchromatin. Although this region of homology could correspond to pseudoautosomal regions, which are involved in pairing and segregation of chromosomes during meiosis in most mammals, this seems somehow unlikely, because sex chromosomes of *M. cabrerae* are asynaptic (Marchal et al. 2004).

Another feature of the molecular cytogenetics of *M. cabrerae* is the presence of multiple copies of the sex-determining region Y (*SRY*) gene, rather than the single copy observed in most mammal species (Bullejos et al. 1997; Fernández et al. 2002). Although multiple copies of the *SRY* gene also are found in other *Microtus* species (Bullejos et al. 1999), in *M. cabrerae* the *SRY* gene may be present in both males and females (Fernández et al. 2002), rather than solely in the nonrecombining region of the Y (e.g., Acosta et al. 2010). Fluorescent in situ hybridization determined that copies of *SRY* (specifically HMG-box copies) occur in the short arm, euchromatic region of the Y, and along the entire heterochromatic region of the X, including the entire short arm, the centromeric region, and the pericentromeric region of the long arm (Fernández et al. 2002). A detailed characterization of the sequence, structure, and organization of the complete *SRY* copies and their flanking regions, distributed on the X and Y chromosomes, revealed that all sequences are nonfunctional pseudogenes, because they have several premature stop codons resulting from base substitutions and deletions (Marchal et al. 2008). The most likely explanation is that these *SRY* copies are inactivated by heterochromatinization after their insertion into the constitutive heterochromatin (Fernández et al. 2002). In addition, the presence of different fragments of L1 and LTR retrotransposons in flanking regions may suggest their possible implication in the amplification of the *SRY* in the Y chromosome, and transportation to the X chromosome heterochromatin (Marchal et al. 2006, 2008). Because the Y chromosome is normally present in males and absent in females, and some cases of sex-reversal XY females have been described in this species (Burgos et al. 1988c), it is possible that 1 functional copy of the *SRY* gene located on the Y chromosome should act as the testis-determining gene in this species (Fernández et al. 2002). On the other hand, the X chromosome *SRY* copies must have always been inactive, because the presence of functional copies of this gene in females would give rise to sterile XX males, and consequently X chromosomes containing *SRY* copies would have been lost from the population (Fernández et al. 2002).

Phylogenetic analysis based on cytochrome-*b* gene (*Cytb*) sequences suggests that among the Arvicolinae, the *Iberomys* lineage seems to be either very old or has undergone accelerated evolution (Jaarola et al. 2004). Support for the basal position of *M. cabrerae* within the genus *Microtus* has been recently provided based on amplified fragment length polymorphisms, indicating that similar to *M. agrestis*, the species does not cluster with the main clade including other European species (Fink et al. 2010). Although its phylogenetic position is still not fully clarified, *M. cabrerae* can be easily distinguished from other *Microtus* based on mitochondrial DNA (mtDNA; *Cytb* and control region) and nuclear sequence (*SRY* and interphotoreceptor retinoid-binding protein genes) analysis (Alasaad et al. 2010, 2011; Barbosa et al. 2013). The recent development of species-specific primers (e.g., Mika1 and Mika2 for control mtDNA, and *SRY*-X1, *SRY*- F, and *SRY*-inv3 for the *SRY* gene), as well as the recent advances in DNA extraction protocols based on noninvasive genetic sampling (e.g., feces), have been particularly promising in broadening the repertoire of possible research approaches for studying and monitoring populations of *M. cabrerae* (e.g., Alasaad et al. 2010, 2011, 2012; Barbosa et al. 2013). However, to date, few studies have used molecular tools to evaluate the levels of genetic diversity and structure in *M. cabrerae*. Cross-species microsatellite amplification tested in a population from Jaén in Spain has shown high genetic variation (3–10 alleles per locus, varying between 90 and 298 bp) and no deviations from Hardy–Weinberg equilibrium for loci Chni19, Chni09, and Chni18 (European snow vole [*Chionomys nivalis*]); Moe1, Moe2 (tundra vole [*M. oeconomus*]); and Mar016, Mar049, Mar079, Mar105, and Mar113 (*M. arvalis*), thus providing a potential tool for further population genetic studies (Molecular Ecology Resources Primer Development Consortium et al. 2011). In addition, a recent study based on a random amplified polymorphic DNA–polymerase chain reaction technique has shown relatively high genetic diversity and no strong bottleneck events among 3 populations in Spain (Siles, Paterna de Madera, and Valdemorillo de la Sierra) and 1 in Portugal (Bicos), with both the southwest and the east of the Iberia suggested as possible last glacial refugia for the species (Alasaad et al. 2013). Nonetheless, studies including samples collected from more locations, and possibly involving the development of species-specific polymorphic microsatellite markers are still needed to properly reveal the phylogeographic patterns of *M. cabrerae*, and the extent of population structuring and distinctiveness, as expected from the species' spatial distribution patterns (see "Distribution" and "Population characteristics").

CONSERVATION

The conservation status of *Microtus cabrerae* was changed by the International Union for Conservation of Nature and Natural Resources from "Lower Risk/Near Threatened" (Baillie and Groombridge 1996) to "Near Threatened" in 2008, based on its restricted geographic range and reduced estimated area of occupancy (criterion B2), resulting from the severe fragmentation of suitable habitats and related population declines across many areas where the species was present in the past (Fernandes et al. 2008). Indeed, other than the several recent findings of *M. cabrerae* in some new localities where it was not previously known (e.g., Garrido-García et al. 2008; Ortuño 2009), empirical observations suggest an overall regressive trend of the species at both the regional and local scales (Fernández-Salvador 2007b). For instance, in Spain it is estimated that over the past 10 years, about one-third of populations of *M. cabrerae* from Cuenca, Toledo, Albacete, and Madrid have disappeared or endured strong modifications. Likewise, populations from Andalucia, Huesca, Zaragoza, Navarra, and Zamora also have undergone strong reductions and high rates of local extinction (Fernández-Salvador 2007b). Population trends in Portugal are not known, but recent steep declines also are suspected across most of its distribution within the country (Queiroz et al. 2005). At the national level the species is thus currently classified as "Vulnerable" in both Spain (criterion B2ab (iii)—Fernández-Salvador 2007b) and Portugal (criterion B2ab (ii, iii, iv, v)—Queiroz et al. 2005), although past national conservation status was "Rare" in both countries (Serviço Nacional de Parques, Reservas e Conservação da Natureza 1990; Blanco and González 1992). *M. cabrerae* is protected under legislation of the European Union, being included in the Annexes II and IV of the Habitats Directive (Council Directive 92/43/EEC), which imply the designation of special areas of conservation, and the need for strict protection of the species, respectively. The species also is listed as a strictly protected species in Annex II of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern, Switzerland, 1979).

The main threats recurrently associated with populations of *M. cabrerae* are related to the intensification of human activities reducing the availability of suitable habitats, including agriculture intensification, cattle overgrazing, road construction, and urbanization (e.g., Fernández-Salvador 2007a, 2007b; Pita et al. 2007). In particular, habitat destruction and fragmentation due to farming intensification (land and water management) have been referenced as the most prominent threats for *M. cabrerae* (e.g., Fernández-Salvador 2007a, 2007b). The nature of habitats of *M. cabrerae* make them areas highly sought for agriculture conversion, and thus over the past years large amounts of suitable habitat across the species' distribution range have been replaced by intensively managed fields mostly devoted to crop and livestock production (e.g., Landete-Castillejos et al. 2000; Pita et al. 2006, 2007; Fernández-Salvador 2007b). The effects of habitat loss and fragmentation could be particularly pervasive for *M. cabrerae* because, as a *k*-strategist (Fernández-Salvador et al. 2001) with low rates of population renewal (Fernández-Salvador et al. 2005b), the species should be particularly vulnerable to the severe environmental change imposed by agricultural intensification (Fernández-Salvador 2007a, 2007b). In addition, the species also may be subjected to strong natural interseasonal and interannual environmental fluctuations (e.g., in local climate conditions) affecting its reproduction success and abundance (e.g., Fernández-Salvador et al. 2001, 2005a; Rosário 2012). For instance, populations from the southwestern limit of the species' distribution range, which is presumably a potentially contracting range margin, have been shown to be particularly responsive not only to habitat fragmentation due to human activities (Pita et al. 2007), but also to the particularly severe and exceptional droughts affecting the region (e.g., in 2005 and 2012), which result in considerable reductions in populations of *M. cabrerae*, and extremely low recovery abilities (observed by RP). This may indicate that the species may be particularly sensitive to global warming and altering precipitation regimes, which in turn suggests that historic climate changes together with human activities are the main factors causing population declines of *M. cabrerae* (e.g., Garrido-García and Soriguer-Escofet 2012; Laplana and Sevilla 2013).

Effective conservation of *M. cabrerae* primarily involves the protection of its habitats at both the local and landscape scale (e.g., Queiroz et al. 2005; Pita et al. 2006, 2007, 2010, 2011b; Fernández-Salvador 2007a; Rosário 2012), eventually requiring some kind of agri-environmental or cross-compliance scheme, whereby farmers could be compensated for maintaining patches of wet grasslands containing the tall vegetation preferred by the species (Pita et al. 2006). Habitat management at the local scale should promote the retention of large habitats (up to 2,000 m^2) likely to include several breeding pairs and their maturing offspring (Pita et al. 2010). Efforts should be made to ban waste disposal, and limit operations such as mowing, burning, plowing, or herbicide spraying within habitat patches. Intensive cattle grazing should be avoided, whereas occasional extensive grazing may be considered to prevent eventual habitat degradation due to shrub encroachment (e.g., Fernández-Salvador 1998, 2007a, 2007b; Pita et al. 2006, 2007; Santos et al. 2006). Where local habitats cannot be protected, the translocation of animals from patches that will be affected by human activities (e.g., building of infrastructures such as roads) to other suitable areas could be an option, although its success is still to be evaluated (Gisbert et al. 2007). At the landscape scale attention should be given to the spatial arrangement of habitat patches to prevent isolation of local populations (or clusters of local populations), increasing the chances of both inbreeding and extinction events, while decreasing the likelihood of colonization due to dispersal failure (Pita et al. 2007). Particular importance also should be given to the matrix quality surrounding habitat patches, because it may strongly influence the dispersal abilities of *M. cabrerae*. In this context, improvement of landscape connectivity toward the long-term persistence of populations of *M. cabrerae* should consider not only the protection of appropriate habitat-patch networks, but also the maintenance of permeable matrix types, such as seems to be the case of extensively grazed seminatural grasslands (Pita et al. 2007; see "Population characteristics"). Overall, improving the conservation status of *M. cabrerae* would require the commitment of the central, regional, and local government administrations from both Portugal and Spain, with the need to deepen our understanding on how *M. cabrerae* responds to environmental changes across multiple spatial and temporal scales.

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