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THE QUATERNARY RECORD OF *EUNEOMYS* (MAMMALIA, RODENTIA, CRICETIDAE) FROM NORTHWESTERN PATAGONIA: EVIDENCE FOR REGIONAL EXTINCTION

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Comparisons of fossil and modern locality records can reveal significant temporal changes in the geographic distribution of a species. Such contrasts, in turn, can be used to draw important inferences regarding patterns of environmental change (e.g., Rebane, 2002; Moritz et al., 2008; Pardiñas et al., 2012). Species that have a narrow fundamental niche (i.e., ecological specialists) provide particularly useful subjects for such analyses. Due to their generally close association with specific habitat conditions, changes in the distributions of these taxa are expected to reveal especially clear signals of changes to environmental conditions.

The subfamily Sigmodontinae is a phylogenetically and ecologically diverse clade of New World rodents, extant members of which are the subject of a growing body of research (Patton et al., 2015). This includes studies of multiple sigmodontine taxa that occur in the Patagonian region of Argentina and Chile (Pardiñas et al., 2011). Whereas some of these species occupy a wide range of habitats, others are much more specialized and are associated with a limited set of ecological conditions (e.g., Pearson and Pearson, 1982; Pardiñas et al., 2003). Among the latter is the chinchilla mouse, *Euneomys mordax* Thomas, 1912, which is a member of the recently erected tribe Euneomyini (see Pardiñas et al., 2015). Representatives of this clade occur in Andean and peri-Andean environments from central Perú to southernmost Chile (Musser and Carleton, 2005; Patton et al., 2015). Extant populations of *E. mordax* are known from isolated, high-elevation localities in the southern Andes of central Argentina and Chile (Reise and Gallardo, 1990; Pearson and Christie, 1991; Braun and Pardiñas, 2015; Ojeda et al., 2015; see Supplementary Data 1). The large-bodied (~125 g) *E. mordax* appears to be a habitat specialist that is associated with wet alpine meadows (Pearson and Christie, 1991).

The fossil record for Patagonian sigmodontines is sparse and is derived primarily from material deposited in owl roosts during the Late Pleistocene and, more typically, the Holocene (e.g., Pardiñas et al., 2011; Tammone et al., 2014). Although, the few

assemblages that have been studied suggest that the local compositions of small mammal communities were stable during much of the Holocene (e.g., Pearson, 1987; Pearson and Pearson, 1993; Pardiñas, 1999), shifts in patterns of abundance and geographic distribution become evident at larger spatial scales when Pleistocene records are compared with current assemblages (e.g., Simonetti, 1994; Rebane, 2002; Pardiñas et al., 2012; Pardiñas and Teta, 2013; Formoso et al., 2015). For this reason, northwestern Patagonia has been the focus of multiple studies regarding Late Pleistocene–Holocene climate change and associated impacts on both individual taxa and communities (Premoli et al., 2000; Sérsic et al., 2011; Gallardo et al., 2013; Tammone et al., 2014). Despite this effort, many assemblages are poorly characterized and their relationships to environmental conditions remain controversial (e.g., Lacey, 2001; Saavedra and Simonetti, 2003; Teta et al., 2014; Prevosti et al., 2015).

Here, we describe the first fossil record for *E. mordax* from northwestern Patagonia (Argentina) that dates to the Pleistocene–Holocene transition. Although previous research in this region has revealed subfossil material dating to ca. 2240 years before present (Pearson, 1987; Pearson and Christie, 1991), no older specimens of this species have been reported. After providing a description of the new fossil material, we use comparisons of modern and paleontological locality records for *E. mordax* to characterize apparent temporal changes in the distribution of this species. We discuss these analyses in the context of both documented changes in Patagonian habitats over the past 10,000 years and the results of current ecological niche models for *E. mordax*. In addition to contributing to our knowledge of the fossil record for sigmodontines in Patagonia, our findings generate new insights into temporal changes in environmental conditions in this dynamic Andean landscape.

Institutional Abbreviations—CMI, Colección de Mamíferos del Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; CNP-E, Colección de Material de Egagrópilas y Afines 'Elio Massoia' del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Mendoza, Argentina; MVZ, Museum of Vertebrate Zoology, Berkeley, California, U.S.A.

Anatomical Abbreviations—af, anteromedian flexid; am, anterior murid; Hp, height of the m1 at protoconid; LM/m,

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length of the upper/lower molar; **LTR**, length of the lower tooth row (alveolar); **M1**, **M2**, **M3**, **m1**, **m2**, **m3**, upper (M) and lower (m) first, second, and third molars, respectively; **mf**, mesopterygoid fossa; **mps**, maxillary-palatine suture; **plg**, palatal lateral groove; **ppp**, posterolateral palatal pits; **UTR**, length of the upper tooth-row (alveolar); **WM/m**, width of the upper/lower molar; **WZP**, width of the zygomatic plate.

MATERIALS AND METHODS

Two fossil specimens of *Euneomys mordax* were studied: a right maxillary with M1–M3 (CNP-E 739-1) and a right dentary with m1–m2 (CNP-E 738-1). Taxonomic identification of this material was achieved via comparison with the following modern reference specimens. *E. mordax*: Argentina, Mendoza Province, Valle Hermoso (CMI 6807), 6 km S Las Leñas (MHNSR 1231, 1238, 1281), Laguna de la Niña Encantada (CNP-E 55-7; seven specimens); Neuquén Province, 1.5 km S Copahue (MVZ 183288, 183289). *Euneomys petersoni*: Argentina, Chubut Province, Altiplanicie del Somuncurá, Laguna Blanca (CNP 2406, 2408, 2411–2413); Mendoza Province, Laguna de la Niña Encantada (CNP-E 55-6; five specimens). The ages of fossil materials were ascertained via radiocarbon dating of associated stratigraphic levels. Radiocarbon dates were calibrated using the ShCal13 calibration curve (Hogg et al., 2013) as implemented in

the OxCal4.2 calibration software package (Bronk Ramsey, 2009). Fossil specimens were treated with magnesium to enhance the visibility of key structures in photographs.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
 RODENTIA Bowdich, 1821
 CRICETIDAE Fischer, 1817
 SIGMODONTINAE Wagner, 1843
EUNEOMYS Coues, 1874
EUNEOMYS MORDAX Thomas, 1912
 (Figs. 2, 3A, D)

Referred Specimens—CNP-E 739-1: right maxillary with M1–M3 and zygomatic plate from an adult individual (Figs. 2A, 3A); CNP-E 738-1: right dentary with the incisor and m1–m2, angular and coronoid processes present, but partially broken, from a young individual (Figs. 2B, 3D).

Locality and Age—Cueva del Caballo paleontological site (40°45'36"S, 71°05'56"W, WGS 84, 830 m), Río Negro Province, Argentina (Fig. 1A). CNP-E 739-1 was collected in unit VI at a depth of 229 cm; CNP-E 738-1 was collected in unit VII at a depth of 343 cm (Fig. 1B). Unit VI was dated at 5510 ± 100 ¹⁴C years BP (LP-2669; 6453–5994 2σ cal years BP); unit VII was

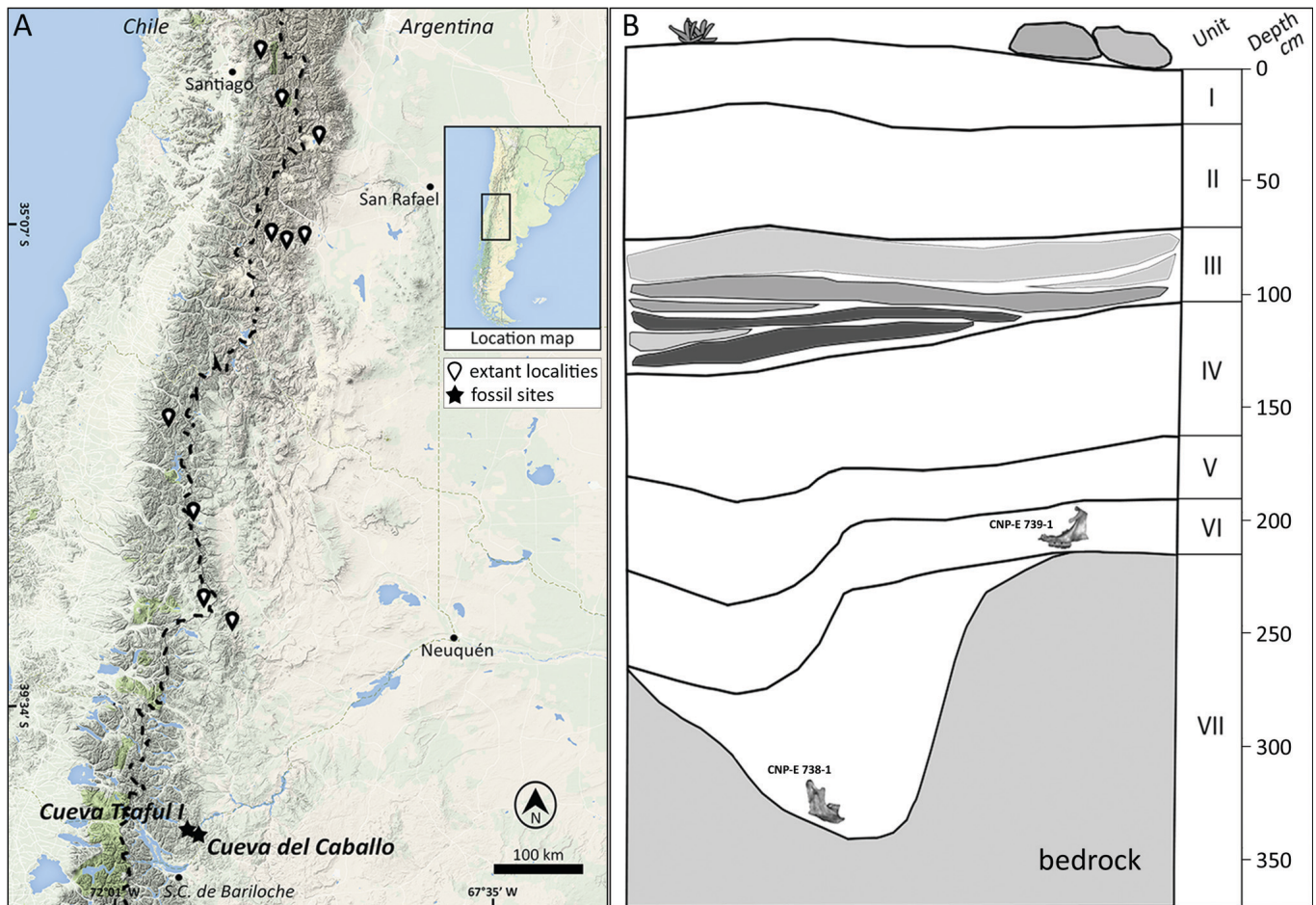


FIGURE 1. Map of the study area and stratigraphic profile of the study site. **A**, map of northwestern Patagonia showing the location of the paleontological sites Cueva del Caballo and Cueva Trafal I, as well as the known localities for extant populations of *Euneomys mordax* (see Supplementary Data 1). **B**, illustration of the stratigraphic profile for the excavation site at Cueva del Caballo; the strata in which the fossil materials described here were found are indicated.

dated at between 10620 ± 100 and 9720 ± 100 ^{14}C years BP (AA-100205 and AA-103026, respectively; 12713–12105 and 11247–10725 2σ cal years BP, respectively).

Stratigraphic Context—Cueva del Caballo is a cave located in an outcrop of pyroclastic rocks from the Ventana Formation. Its stratigraphic deposit is primarily volcanic in origin and is composed of layers of ash mixed with mud, sand, and gravel sediment. During the austral summer of 2008, a 1 m by 0.5 m pit was excavated using hand-held trowels and following natural stratigraphic levels. Sixteen stratigraphic levels were identified between the surface and the underlying bedrock (depth = 368 cm). For analysis, these stratigraphic levels were divided into seven subsets based on sedimentary characteristics and radiocarbon dates. Dental, cranial, and postcranial elements from small mammals were found throughout the deposit and represent the primary faunal component of the site. Evidence of human occupation was scarce and temporally restricted to the last 2000 years.

Description—Specimen CNP-E 739-1 consists of a complete right maxillary with M1–M3 and the zygomatic plate. This specimen was determined to be an adult based on the degree of molar wear. The zygomatic plate is high, narrower at the top, and robust. The plate is markedly concave for the insertion of the medial masseter. The labial edge of the incisive foramen is marked by a sharp ridge (Fig 2A); the posterior end of this foramen matches the procingulum of M1. The posterior palate is characterized by several large pits located in a transversely compressed fossa that, at its anterior end, leads to a palatal lateral groove that crosses the maxillary-palatine suture and runs parallel to the tooth row (Fig. 3A). The anterior border of the mesopterygoid fossa, of which only the outer anterior edge is present, is distinctively bullet-shaped. The molars are hypsodont and laminated, with thick enamel (Fig. 2A). The occlusal surfaces (*sensu* Hershkovitz, 1962) of the teeth are flat and characterized by deeply invaginated labial and lingual folds (Figs. 2A, 3A). Whereas M2 is markedly sigmoid in shape, M3 is well developed and retains a trace of the paraflexus that is preserved as an internal ring (Fig. 3A).

Specimen CNP-E 738-1 consists of a fragmentary right dentary with m1 and m2 as well as the portion of the incisor located within the alveolus (socket) for this tooth. The minimal wear evident on the occlusal surfaces of the molars suggests that the specimen was a juvenile. The body of the mandible is robust. The upper and lower branches of the masseteric crest come together to form a single sharp ridge that rises gradually toward the diastema. The mental foramen is visible from the labial side. The capsular projection, although broken at the apex, is conspicuous and is located between the mandibular condyle and the coronoid process. The base of the latter is broad, and the dental canal is large. The molars are hypsodont and slightly crested (*sensu* Hershkovitz, 1962; Fig. 2B); the procingulum of the m1 is connected to the rest of the tooth by an anterior murid composed of a thin bridge of enamel (Fig. 3D).

Comparisons—Taxonomic identification of the fossil specimens was based on comparisons of these materials with modern specimens of *E. petersoni* and *E. mordax*. All of the above features of the fossil samples are consistent with *E. mordax* but differ from *E. petersoni* as follows: (1) the fossa containing the posterolateral palatal pits is generally oval in shape in *E. petersoni* but is transversely compressed in *E. mordax* and CNP-E 739-1 (Fig. 3A–C); (2) this fossa does not extend anteriorly as a groove in *E. petersoni* but does so in *E. mordax* and CNP-E 739-1, with the maxillary-palatine suture entering the fossa only in the latter two examples (Fig. 3A–C); (3) the anterior border of the mesopterygoid fossa has a medial palatine process in *E. petersoni* but is more rounded in shape in *E. mordax* and CNP-E 739-1; (4) the molars are less hypsodont in *E. petersoni* and the M3 in this species lacks any remnant of paraflexus, although this

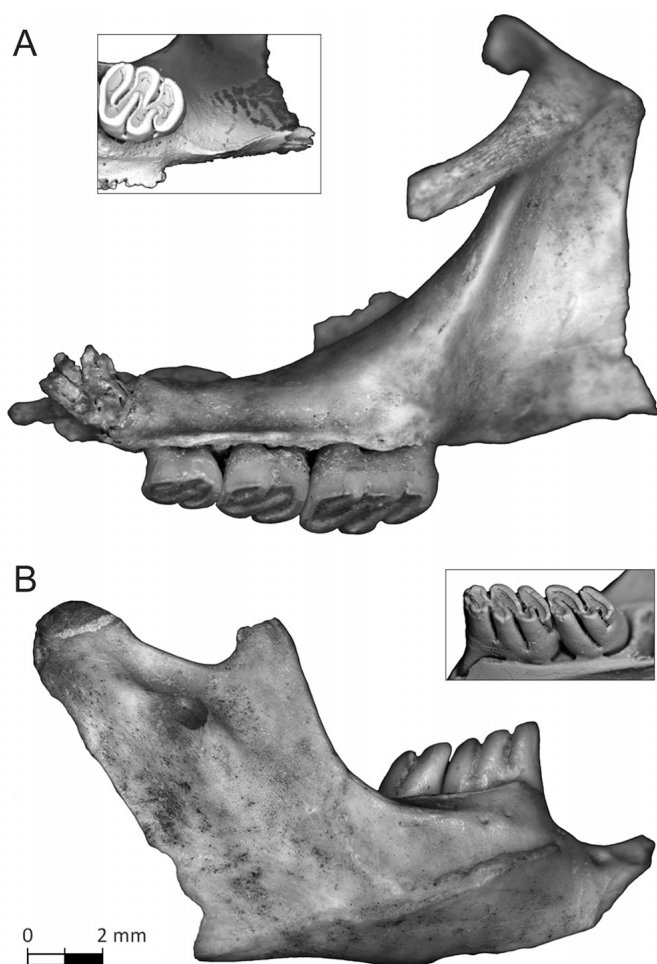


FIGURE 2. Lateral view of the two fossil specimens of *Euneomys mordax* from Cueva del Caballo, Río Negro, Argentina. **A**, right maxillary (CNP-E 739-1); inset, close-up of the incisive foramen in ventral view to show the sharp ridge along the labial side. **B**, right dentary (CNP-E 738-1); inset, close-up of m1–m2 in lingual view to show the degree of hypsodonty.

structure is evident in *E. mordax* and CNP-E 739-1; and (5) the procingulum of m1 is dissected by an anteromedian flexid and is isolated from the remaining portion of the molar in *E. petersoni* (Fig. 3F), whereas the procingulum lacks the anteromedian flexid and is connected to the rest of the tooth by an anterior murid in *E. mordax* and CNP-E 738-1 (Fig. 3D–E). Dental measurements from the two fossil specimens are consistent with those of *E. mordax* and indicate that the animals recovered from the Cueva del Caballo site were clearly larger than *E. petersoni* (Table 1).

DISCUSSION

Taxonomy

Both qualitative and quantitative characteristics of the fossil specimens recovered from Cueva del Caballo are consistent with those found in modern specimens of *Euneomys mordax*. In contrast, the only other species in this genus that currently occurs in northwestern Patagonia, *Euneomys petersoni*, is clearly smaller and differs morphologically from the fossil material in several important ways. As part of their characterization of subfossil mammalian remains from the nearby Cueva Trafal I (5 km north-northwest of Cueva del Caballo; Crivelli Montero et al.,

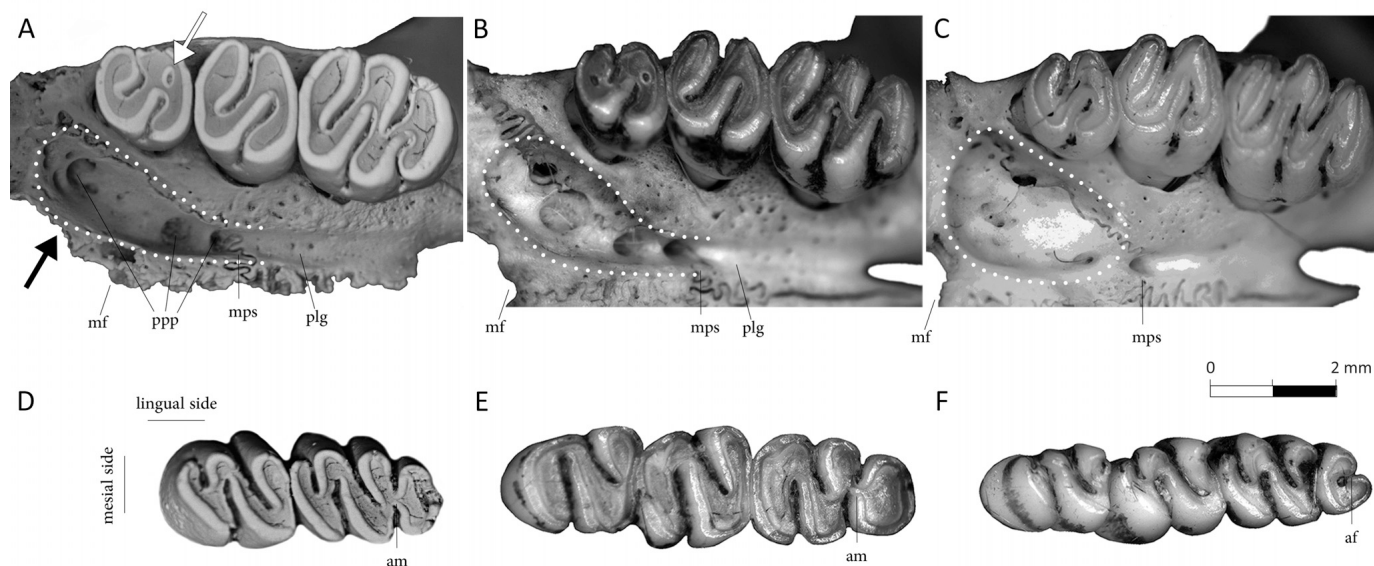


FIGURE 3. Comparisons of fossil and modern specimens of *Euneomys*. Upper panels: ventral views of the right maxillary (including M1–M3) are shown for **A**, fossil specimen CNP-E 739-1; **B**, modern specimen of *E. mordax* (MHNSR 1231); and **C**, modern specimen of *E. petersoni* (CNP-E 55-6). White arrow indicates the remnant of the paraflexus in M3; black arrow and dotted line highlight the shape and extension of the fossa containing the posterolateral palatal pits. Lower panels: occlusal views of the lower molars of **D**, fossil specimen CNP-E 738-1; **E**, modern specimen of *E. mordax* (MHNSR 1238); and **F**, modern specimen of *E. petersoni* (CNP-E 55-6).

1993), Pearson and Christie (1991) reported two forms of *Euneomys* in deposits dating back to 2400 years before present. They identified one of these forms as *E. petersoni* (cited in their publication as *E. chinchilloides*), which was characterized by an alveolar length of the lower molars <6.8 mm (mean = 6.0 mm, N = 179). The other form, identified as *E. mordax*, had an alveolar length of the lower molars >6.8 mm (mean = 7.1 mm, N = 9). The lower alveolar lengths of the fossil specimens from Cueva del Caballo were greater than 6.8 mm (Table 1), indicating that the sizes of these specimens are more consistent with the larger-bodied *E. mordax*.

Evidence for Regional Extinction

The specimens of *E. mordax* from Cueva Trafal I were recovered in a stratigraphic level dated at 2230 ± 40 years BP (Pearson and Christie, 1991). This record, coupled with the

dates assigned to the Cueva del Caballo specimens, indicates that *E. mordax* was present in this region of Patagonia from the Pleistocene-Holocene transition to at least the mid- to late Holocene. The nearest known extant population of *E. mordax*, however, is located approximately 200 km to the north of both Cueva del Caballo and Cueva Trafal I. Assuming that the gap between historical and modern locality records does not simply reflect incomplete sampling in this region, the absence of extant populations of *E. mordax* near the two cave sites suggests a recent shift in the geographic distribution of this species.

To determine if the fossil sampling localities at Cueva del Caballo and Cueva Trafal I occur in habitats consistent with those occupied by extant populations of *E. mordax*, we constructed a probability distribution model for this species using MaxEnt 3.3.3 k (Phillips and Dudík, 2008). Models were based upon all available modern locality records for

TABLE 1. Measurements (in mm) of *Euneomys* cf. *E. mordax* from the Holocene sequence of Cueva del Caballo (Neuquén, Argentina; CNP-E 739-1 and CNP-E 738-1) compared with recent specimens of *E. mordax* and *E. petersoni*.

Specimen/Sample	Species	WZP	UTR	LM1	WM1	LM2	WM2	LM3	WM3
CNP-E 739-1	<i>E. cf. mordax</i>	3.8	6.5	2.7	2.1	2.1	2.0	1.7	1.5
CM 6807	<i>E. mordax</i>	2.8	6.8	2.9	2.2	2.0	2.0	1.5	1.7
MVZ 183288	<i>E. mordax</i>	3.5	6.7	2.9	2.5	1.7	2.1	1.6	1.6
MVZ 183289	<i>E. mordax</i>	3.8	6.5	2.8	2.5	1.8	2.1	1.5	1.5
Mendoza (N = 8) ^a	<i>E. mordax</i>	3.5 ± 0.2	6.6 ± 0.4	2.9 ± 0.1	2.9 ± 0.1	1.8 ± 0.1	2.0 ± 0.1	1.6 ± 0.2	1.6 ± 0.2
Mendoza (N = 5) ^b	<i>E. petersoni</i>	2.4 ± 0.1	5.5 ± 0.2	2.5 ± 0.1	1.9 ± 0.1	1.7 ± 0.3	1.8 ± 0.1	1.3 ± 0.3	1.4 ± 0.1
		Hp	LTR	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
CNP-E 738-1	<i>E. cf. mordax</i>	1.7	7.0	3.0	1.8	2.1	2.0	—	—
CM 6807	<i>E. mordax</i>	1.5	7.1	3.0	2.0	2.0	2.2	—	—
MVZ 183288	<i>E. mordax</i>	1.2	7.6	3.0	2.0	2.0	2.1	—	—
MVZ 183289	<i>E. mordax</i>	0.9	7.6	3.2	2.0	2.1	2.0	—	—
Mendoza (N = 3) ^a	<i>E. mordax</i>	—	6.9 ± 0.3	2.7 ± 0.2	1.9 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	—	—
Mendoza (N = 5) ^b	<i>E. petersoni</i>	—	6.1 ± 0.1	2.4 ± 0.2	1.5 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	—	—

^aSpecimens from Las Leñas (MHNSR 1231, 1238, 1281) and Laguna de la Niña Encantada (CNP-E 55-7).

^bSpecimens from Laguna de la Niña Encantada (CNP-E 55-6).

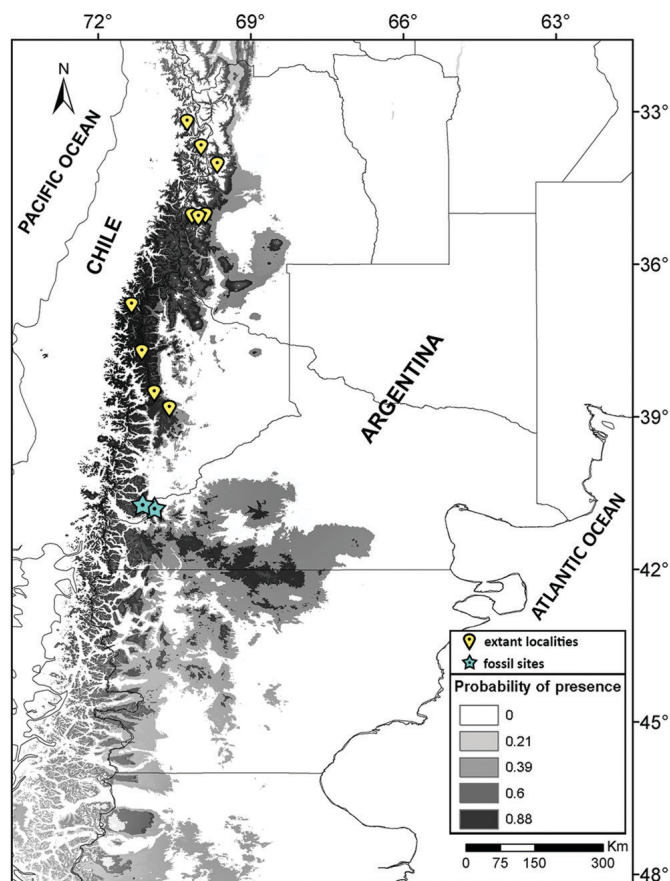


FIGURE 4. Predicted probability of occurrence of *E. mordax* in northwestern Patagonia based on a distributional niche model constructed using environmental parameters for known extant localities of this species (see Supplementary Data 1).

E. mordax (Braun and Pardiñas, 2015); the associated WorldClim variables plus 19 additional bioclimatic variables—including aspects of topography and climate—were included at a spatial resolution of 30 arc-seconds (Hijmans et al., 2005). The performance of the model was assessed using the area under the curve (AUC) test, values for which typically range from 0.5 to 1.0 (Swets, 1988), with outputs of 1.0 expected to have the highest predictive power. We ran 10 model replicates and retained the average model (Fig. 4), which had a high predictive power (AUC = 0.98 ± 0.038 [SD]). Seven variables contributed 90.3% to the model variation. These were October minimum temperature (27.9%), January precipitation (21.4%), May minimum temperature (15.9%), September minimum temperature (7.5%), precipitation during the driest month (6.8%), July minimum temperature (6.7%), and precipitation during the wettest quarter (4.1%).

The average distributional model revealed that there is a moderate (0.39) to high (0.88) probability that *E. mordax* should occur in the modern habitats surrounding Cueva del Caballo (Fig. 4). Neither trapping surveys nor examination of modern owl pellets, however, have revealed evidence of extant populations of this species in this region (e.g., Monjeau, 1989; Pearson, 1995; Pardiñas et al., 2003; Trejo and Lambertucci, 2007). Although Pearson (1995) noted the possible presence of *E. mordax* at a high-elevation location about 60 km southwest of our fossil site, this anecdotal report has not been substantiated. Thus, despite the presence of presumably suitable habitat in the region surrounding Cueva del Caballo, extant populations of *E. mordax* appear to be absent,

suggesting that this species has undergone a change in geographic distribution since the deposition of the fossil material described here.

Paleoenvironmental Implications

Extant populations of *E. mordax* occur in medium-high-elevation Andean environments in Mendoza and Neuquén provinces in Argentina as well as in adjacent parts of Chile (Greer, 1965; Reise and Gallardo, 1990; Pearson and Christie, 1991). Extant populations of *E. mordax* appear to be relatively ecologically specialized, typically occurring in wet alpine meadows characterized by deep, moist soils and nearly 100% ground cover, including grasses, sedges, brush, and patches of ñire (*Nothofagus antarctica*). Elevations at which extant populations have been reported range from 1600 to 3300 m, with most populations occurring above 1800 m (Braun and Pardiñas, 2015; Ojeda et al., 2015; M. Christie, unpubl. data).

Given this habitat specialization, the apparent range shift by *E. mordax* revealed by our comparisons of modern and fossil specimen localities can be used to explore potential patterns of environmental change in this region of Patagonia. For example, both Cueva del Caballo and Cueva Trafal I are located at elevations below 1000 m (see Supplementary Data 1); although material at both sites was deposited by owls that could have hunted at higher elevations, no areas above 1500 m occur in the vicinities of these caves. This suggests that ‘alpine’ habitats suitable for *E. mordax* must have been present at lower elevations during the Late Pleistocene and most of the Holocene. Increasing precipitation during the second half of the Holocene in combination with higher summer temperatures (Heusser and Streeter, 1980; Markgraf et al., 2002) may have contributed to the loss of ‘alpine’ meadow habitats at the altitudinal range of Cueva del Caballo and Cueva Trafal I. This change in available habitats may, in turn, have contributed to the apparent loss of *E. mordax* from the vicinity of these caves. Potential support for this hypothesis comes from the roughly concurrent loss from this region of two other species of caviomorph rodents specialized for mesic ‘alpine’ habitats: *Ctenomys sociabilis* and *Octodon bridgesii* (Pardiñas and Teta, 2013; Tammone et al., 2014; Teta et al., 2014).

In summary, our description of two new fossil specimens of *E. mordax* from Cueva del Caballo provides multiple insights into the faunal history of northwestern Patagonia. First, the identification of these specimens as *E. mordax* adds to our general knowledge of the poorly characterized history of the small mammal fauna of the region. Second, comparisons of historical and modern locality records for *E. mordax* suggest that this species has experienced a substantial recent range contraction in northwestern Patagonia. Third, given the apparent specialization of extant populations of *E. mordax* for mesic, high-elevation meadows, this change in distribution implies that the region surrounding our study site has undergone significant environmental modification during the Holocene. Collectively, these analyses underscore the importance of comparing modern and historical specimens to explore temporally dynamic interactions between environmental conditions and faunal diversity.

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