2023

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Diego A. Caraballo
Instituto de Ecología, Genética y Evolución de Buenos Aires, dcaraballo@ege.fcen.uba.ar

Sabrina Laura Lopez
Instituto de Cálculo, UBA-CONICET, Ciudad Universitaria - Cero + Infinito, Ciudad Autónoma de Buenos Aires

Sebastian Botero-Cañola
University of Nebraska - Lincoln, Sebastian.botero@ufl.edu

Scott Lyell Gardner
University of Nebraska - Lincoln, slg@unl.edu

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Diego A. Caraballo,[1] Sabrina Laura Lopez,[2]
Sebastian Botero-Canola,[3,4] and Scott Lyell Gardner[3]

1 Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA), UBA-CONICET, Ciudad Universitaria-Pabellón II, Ciudad Autónoma de Buenos Aires C1428EHA, Argentina
2 Instituto de Cálculo, UBA-CONICET, Ciudad Universitaria - Cero + Infinito, Ciudad Autónoma de Buenos Aires C1428EHA, Argentina
3 Manter Laboratory of Parasitology, University of Nebraska State Museum, and School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, Nebraska 68588-0514, USA
4 Fundación Laboratorios de Conservación Colombia, Medellín 050034, SB-C, Colombia

D.A. Caraballo and S.L. Lopez contributed equally to this paper.

Correspondence — D.A. Caraballo, dcaraballo@ege.fcen.uba.ar

Abstract
South American subterranean rodents of the genus *Ctenomys* (Rodentia, Ctenomyidae, tuco-tuco) are one of the most diverse genera among mammals. Recently described species, new taxonomic revisions, and new distribution range delimitation made the revision of distribution areas and conservation status of these mammals mandatory. Implementing the first part of the DAMA protocol (document, assess, monitor, act), here we compile updated sets of species distribution range maps and use these and the number of collection localities to assess the conservation status of ctenomyids. We integrate potential for conservation in protected areas, and levels of habitat transformation

Published in *Journal of Mammalogy*, 104(3):466–478, 2023.
doi:10.1093/jmammal/gyac099

Submitted 27 January 2022; accepted 15 September 2022; published January 13, 2023.

to revise previous conservation status assessments and propose the first assessment for all Data Deficient or not evaluated species of tuco-tucos. Our results indicate that 53 (78%) of these species are threatened and that 47 (69%) have little or no overlap with protected areas, emphasizing the urgent need to conduct conservation efforts. Here, 18 of 22 species previously classified as Data Deficient resulted in them being put in an at-risk category (VU, EN, CR). In addition, nine species that have not been previously evaluated were classified as threatened, with these two groups comprising more than 47% of the known species. These results posit that the Ctenomyidae are the rodent family with the greatest number of species at risk of extinction. Finally, a total of 33 (49%) species have been reported from three or fewer localities; all considered threatened through the approach implemented in this study. These geographically restricted taxa should be given more attention in conservation programs since the richness of this genus relies on the survival of such species.

Keywords: conservation status, *Ctenomys*, habitat transformation, protected areas

Resumen

Los roedores subterraneos sudamericanos del genero *Ctenomys* (Rodentia, Ctenomyidae, tuco-tuco) pertenecen a uno de los generos mas diversos de mamiferos. Especies descritas recientemente, nuevas revisiones taxonomicas y nuevas delimitaciones del rango de distribucion hicieron obligatoria la revision de las areas de distribucion del genero y su estado de conservacion. Implementando la primera parte del protocolo DAMA (documentar, evaluar, monitorear, actuar), compilamos una serie de mapas actualizados de los rangos de distribucion de especies que, conjuntamente con el numero de localidades de colecta, se utilizaron para evaluar el estado de conservacion de los ctenomidos. Tambien integramos el potencial de conservacion en areas protegidas, asi como la transformacion del habitat para examinar las evaluaciones del estado de conservacion anteriores y proponemos la primera evaluacion para todas aquellas especies de tuco-tucos con datos deficientes o que no fueron evaluadas. Nuestros resultados indican que 53 (78%) de las especies se encuentran amenazadas y que 47 (69%), tienen solapamiento nulo o escaso con areas protegidas, resaltando la necesidad de conservacion. Dieciocho de las 22 especies anteriormente clasificadas como 'Con datos insuficientes' calificaron en alguna categoria de riesgo: vulnerable (VU), amenazada (EN), o en peligro critico (CR). A su vez, nueve especies que no habian sido evaluadas previamente, tambien clasificaron como amenazadas, ambos grupos abarcando mas del 47% del genero. Estos resultados ubican a la familia Ctenomyidae como al grupo de roedores con el mayor numero de especies en riesgo de extincion. Por ultimo, un total de 33 (49%) especies ocurren en tres o menos localidades, que mediante el abordaje implementado en este estudio, todas ellas califican como amenazadas. Estos taxones restringidos geograficamente requieren una mayor atencion en los programas de conservacion, debido a que la riqueza del genero depende de la supervivencia de tales especies.

Palabras claves: areas protegidas, *Ctenomys*, estado de conservacion, transformacion de habitat

There is an increasing global concern about the loss of biodiversity and, ultimately, about the potential loss of ecological services and sustainability of the biosphere (Diaz et al. 2019). Present global extinction rates are exceptionally high, likely a thousand times greater than the background rate that would occur in the absence of human action (Pimm et al. 2014). Although phenomena such as climate disruption, introduced species, and diseases are important causes of extinction, the destruction and degradation of natural habitats have been the predominant factors affecting biodiversity loss in the Anthropocene (Pereira et al. 2010). Fortunately, habitat preservation, as well as other conservation interventions, can ameliorate these trends. For example, a quantitative analysis showed that the rate of extinction of mammals, amphibians, and birds would have been one-fifth higher in the absence of conservation efforts (Hoffmann et al. 2010). Nonetheless, biological knowledge, starting with sound systematic hypotheses, followed by deep understanding of geographic distributions, population structure, and ecological information are necessary to prioritize species and areas for these interventions and design effective conservation strategies. Many mammal groups—including rodents, the most speciose mammalian lineage—lack these data.

Conservation of small mammals requires knowledge of meaningful spatial scales at which species respond to habitat modifications. Alterations in small mammal community assemblages may lead to cascading effects across the environments they inhabit (Manning and Edge 2004). Among small mammals, subterranean rodents are pivotal for the maintenance of ecosystems due to their ability to modify the availability of resources directly or indirectly for other species (Reichman and Seabloom 2002; Hagenah and Bennett 2013). As a result of moving, mixing, or bringing soil to the surface from lower levels, subterranean rodents affect the texture, water-holding capacity, soil nutrient dynamics, and vegetation composition and abundance throughout the habitats they occupy (Hole 1981). Through their burrowing activity, subterranean rodents generate a dynamic mosaic of nutrients and soil conditions that promote diversity and maintain disturbance- dependent components of plant communities (Reichman and Seabloom 2002). In addition to the modification of physical and chemical soil properties, subterranean rodents can increase soil patchiness by enriching it with endophytic fungal propagules (Miranda et al. 2019). Because of their species diversity, abundance, and expansive distributional range, and their ecological importance, subterranean rodents of the genus *Ctenomys* constitute a high-priority study case for small mammal conservation.

Popularly known as tuco-tucos, rodents of the genus *Ctenomys* comprise more than 60 species inhabiting the southern cone of South America (D'Elia et al. 2021), from Peru and Brazil in the north to the Tierra del Fuego in the south, and from the Atlantic Ocean to the west coast of the Pacific (Bidau 2015; de Freitas 2016). The origin of species allocated to this genus has been estimated to be from 10 to 3 Ma, depending on the study (Parada et al. 2011; Roratto et al. 2015; Upham and Patterson 2015; Caraballo and Rossi 2018b; de Santi et al. 2021), but it is clear that extensive and rapid cladogenesis took place around 3–1 Ma with the development of at least eight different species groups (Parada et al. 2011; de Santi et al. 2021). Although these species groups are quite stable working hypotheses, it is worth noting that these lineages were recovered via phylogenetic analysis using only a single genetic marker (mitochondrial *Cytb*), and no further studies (including mitochondrial and nuclear data, or at the genomic level) have been carried out to test the phylogenetic relationships among species of *Ctenomys*. What is clear is that rapid speciation and perhaps geographic dispersal gave rise to a large number of allopatric species (Bidau 2015; de Freitas 2016), with only a few known cases of sympatry (Galiano and Kubiak 2021). As subterranean rodents, species of *Ctenomys* are generally characterized by ecogeographic features that include: low vagility, high habitat specificity, and high levels of population subdivision, which appears to result in low within-species genetic variability (Reig et al. 1990; Lacey et al. 2000).

These attributes, together with factors such as anthropogenic habitat fragmentation and habitat degradation, climatic change, urbanization, and limited knowledge of the geographic occurrence of these rodents increase the risk of extinction at both the population and the species levels (Gallardo et al. 1996; Gomez Fernandez et al. 2016). In a recent study of all known Bolivian species of *Ctenomys*, Gardner et al. (2021) quantified large-scale habitat transformation within each species range and assessed the potential effect of climatic change on five of these species. Most Bolivian tuco-tuco species have suffered significant range contractions due to anthropogenic land cover change, which will be most likely be exacerbated in the near future by rapidly changing climatic conditions.

Because of their potential or confirmed vulnerability, a survey of the occurrence of *Ctenomys* species in protected areas (PAs) is crucial for their conservation. In a previous study, the conservation status and the potential occurrence of *Ctenomys* in PAs were analyzed, showing that 34 out of 67 (50.75%) species of tuco-tucos had significant overlapping distributions with PAs (Caraballo et al. 2020). In contrast, 27 (40.30%) species presented some degree of extinction risk (or were not evaluated) and would require closer surveillance because they had no significant overlap with PAs (Caraballo et al. 2020). Remarkably, most not evaluated (NE) species are known only from their type locality or its surroundings (Teta and D'Elia 2019), which makes it very likely that they are threatened species.

Since the publication of the study by Caraballo et al. (2020), several important modifications in the knowledge about *Ctenomys* conservation status and species distributions have taken place. The conservation status and distribution areas (DAs) of all *Ctenomys* species from Argentina had been reassessed in a recent contribution coordinated by the Argentinean Society of Mammalogists and the Argentinean National Ministry of Environment and Sustainable Development (MAyDS; http://cma.sarem.org.ar). Since most of the species of *Ctenomys* (45 out of 64, see below) occur in Argentina, the outcome of this effort is a crucial advancement toward having more precise information on distributional ranges and to study the potential for conservation of these species in PAs. Similarly, Gardner et al. (2021) have updated information on distributions of each species and provided a preliminary assessment of the preservation or conservation status of tuco-tucos within Bolivia. Despite these valuable efforts, around half of the species of *Ctenomys* have been categorized by the IUCN as Data Deficient (DD) due to insufficient information for a proper assessment of their conservation status, or remain NE. This reflects the fragmentary nature of the knowledge of *Ctenomys*, and that the assessment of the conservation status of these rodents is still a work in progress.

Ctenomys is a taxonomically dynamic group, with several species being recently synonymized, and new species being described. Although there have been several recent advances using integrative approaches (Lopes and Freitas 2012; Gardner et al. 2014; Caraballo and Rossi 2018a; Teta and D'Elia 2020; Teta et al. 2020), the taxonomic status of a number of populations and nominal forms is still dubious, either because they have not been assessed or results are inconclusive. A total of 64 living species of tuco-tucos have been recognized in a recent revision, although the authors point out that the taxonomy of the genus *Ctenomys* is far from stable (D'Elia et al. 2021). Narrow geographic coverage, nomenclatural synonymy, and the presence of unnamed or undescribed species are some of the factors contributing to taxonomic instability. Changes in taxonomy in turn influence knowledge of distributional range delimitation and conservation status assessment.

Recent profound changes in taxonomy combined with detected gaps in assessment of conservation status, together with new information on geographic ranges of many species of *Ctenomys*, make updated evaluations of conservation status for these species imperative. Included in these assessments will be a necessary interpretation of the impact of habitat loss, actual extinction risk, and future potential for implementing programs for conservation of critical habitat in PAs in which these animals still occur. In this study we compiled the updated conservation status, DAs, and overlap with PAs, as well as quantified large-scale habitat transformation within each species range of *Ctenomys*. Based on determinant variables such as species ranges and the number of localities, but also integrating potential for conservation in PAs, as well as habitat transformation, we revised previous conservation status assessments and proposed the first assessment for all DD or NE species of tuco-tucos.

One of the general methods that have been proposed to begin to ameliorate the biodiversity crisis is to implement the DAMA protocol (Brooks et al. 2014)—document, assess, monitor, act—that aims to document organismal distributions and biodiversity, then to assess detected diversity by study and investigation, followed by longer-term field-based monitoring by looping back and checking diversity in areas that were surveyed to determine if species assemblages and communities are changing through time (Brooks et al. 2019). It is not enough to simply document and assess; long-term monitoring is necessary to determine if there are changes occurring in any parts of the ecosystems under study and changes in one area may portend similar changes at other sites. Once data are accumulated and information is available, conservationists can then act to make positive effects on preservation of species of tucos. Here we illustrate the implementation of the first half of the DAMA protocol in which we are both summarizing the documented occurrence records of ctenomyids in the southern Neotropics and providing assessments of species viability through space and time.

Materials and Methods

Species distribution shapes.—In this study, we used data generated by the reassessment of Argentinian species performed by MAyDS and SAREM (http://cma.sarem.org.ar), as well as those of Bolivian species evaluated by Gardner et al. (2021), and we provide a detailed justification of any departure in the use of this material that could result from ulterior taxonomic definitions or the discovery of unstudied populations. In the case of Argentinean species, DAs were created based on extent of occurrence polygons (EOOP), extrapolated by expert criteria around habitats considered as suitable for the species, considering other factors that may limit distribution in geographic space such as elevation, temperature, or natural physical barriers. For five Bolivian species, the estimated DA was further refined using the ecological niche modeling approach detailed in Gardner et al. (2021), and considering environmental variables such as soil composition, elevation, and temperature. Some of the DAs for these species result in disjunct polygons, and others show empty spaces within polygons. Only polygons with corroborated data of occurrence and those <30 km away from these were retained, while areas within these polygons that were considered unsuitable for the species and larger than 2,000 km^2 were removed from the DA estimation. This 2,000 km^2 threshold was selected as a compromise to ensure that the final maps reflect the extent of occurrence while reducing substantial overestimation of the range.

The distributional ranges of non-Argentinean/Bolivian species used are the same as in Caraballo et al. (2020) unless specified. The distributional range of *C. ibicuiensis* was extended by including new occurrence points reported by Medeiros et al. (2020). The Argentinean portion of species occurring in more than one country was modified based on the mentioned reassessment. This was the case for *C. opimus*, *C. conoveri*, *C. pearsoni*, *C. rionegrensis*, and *C. frater*. Namely, the Argentinean part of the distribution was joined to the previous shape beyond Argentina following Gardner et al. (2021) or Caraballo et al. (2020), if available, or IUCN distribution shapes. The distribution of *C. torquatus* was extended to the south considering new sampling localities (Tomasco I., Universidad de la Republica, Montevideo, Uruguay, personal communication, 2022) while the distribution polygon for *C. maulinus* was built joining the Chilean distribution data provided by the IUCN with the Argentinean distribution data from MAyDS and SAREM, and extending it to the northeast following Tammone et al. (2021). According to the Argentinean species recategorization, *C. pontifex* occurs in two disjunct population nuclei, but this was later questioned by Tammone et al. (2021), who state that this species has a very narrow area of occurrence, restricted to the western nucleus that includes Valle Hermoso, the proposed type locality (Tammone and Pardinas 2021). Indeed, after thorough sampling near this area, no tuco-tucos resembling this species were confirmed, suggesting that it is either extremely rare, or now extinct. We followed Tammone et al. (2021) and, thus, retained only the data comprising the western nucleus in our analysis. The distribution of *C. fodax* was extended to include the population of Rio Nireguao, Chile, following Teta et al. (2020). The distribution of *C. bicolor* was estimated based on information provided by Stolz et al. (2013), while that of *C. brasiliensis* was estimated following de Freitas (2016). The shape distribution estimation of *C. dorsalis* was built according to Londono-Gaviria et al. (2019). The shape distribution of *C. lessai* was made based on the collection point informed by Gardner et al. (2014), while that of *C. paraguayensis* was made following Bidau (2015). The shape map for *C. rondoni* was made following Bidau (2015) and de Freitas (2016), while the shape distribution of *C. famosus* was extended according to Tammone et al. (2022a), totaling three disjunct populations (Sanchez et al. 2019; Tammone et al. 2022a).

Species geographic distribution shapes were inspected using QGIS v3.16-Hannover (QGIS Development Team 2021) and modified according to recent literature in case of discordance or corrected according to the criteria specified in this section. Those species with one or two known localities were assigned a circular distribution of 20 km^2 around each locality point (radius = 2.5 km). For species with ≥3 localities, we followed the IUCN Red List guidelines (IUCN 2021) to construct EOOP. The EOOP is defined as the minimum convex polygon that contains all the sites of occurrence of a species (IUCN 2021). The reason for choosing an area of 20 km^2 around each point is that this value corresponds to the smallest range defined by expert criterion for a tuco-tuco species reported at a single locality (*C. tulduco*). We consider that the selected buffer sizes are conservative, particularly for species with few reported localities.

Distribution areas, PAs, water bodies, and their intersections were measured and manipulated using the sf package on R and RStudio (Pebesma 2018; RStudio Team 2020; R Development Core Team 2021). Water bodies were subtracted from *Ctenomys* species DAs using the SRTM

(Shuttle Radar Topography Mission) world surface water body data set (available at http://gis.ess.washington.edu/data/vector/worldshore/). An interactive map was created with the R package leafletR (Graul 2016) enabling exploration of the geospatial analysis presented in our study, alternating and identifying DAs, PAs, and their intersections (Supplementary Data SD1). For this purpose, the shapefiles were simplified to reduce file size using MapShaper.org (Harrower and Bloch 2006).

Taxonomic considerations.—Since our main goal is to study the presence of species or forms of *Ctenomys* in PAs and revisit their conservation status, we had to adopt some taxonomic definitions in cases where data are either scarce, contradictory among studies, or both. To indicate that some names are no longer valid or acceptable under the zoological code (ICZN), but we are using the name to indicate extant populations of tucos, we use quotations around the species name to avoid confusion and to affirm that these are not fully validated species. The forms *C. goodfellowi*, *C. colburni*, and *C. coyahiquensis* were synonymized, respectively, under *C. boliviensis*, *C. magellanicus*, and *C. sericeus* (see: Gardner et al. 2014; Teta and D'Elia 2020; Teta et al. 2020). In these cases, we joined their respective polygons. The polygon of *C. magellanicus* was made following Lazo-Cancino et al. (2020) and was extended to include northern occurrence points as reported by Teta and D'Elia (2020). The forms *C. azarae*, *C. porteousi*, and *C.* "*chasiquensis*" are here considered part of *C. mendocinus* (see D'Elia et al. 2021 and references therein) with an ample distribution in central Argentina through the provinces of Buenos Aires, Cordoba, La Pampa, and San Luis. Similarly, *C. lentulus* was preliminarily maintained as a synonym of *C. haigi* by Teta and D'Elia (2020), and we follow their proposal, extending the shape provided by MAyDS–SAREM and including two localities reported by Tammone et al. (2022b). We modified the geographic shape provided by MAyDS–SAREM for *C. talarum* in order to exclude the segment of the coastal distribution that extends from Pehuen-Co to Monte Hermoso, which belong to a lineage different from *C. talarum* (Cutrera and Mora 2017). The shape of the distribution of *C. yatesi* was made based on the point recorded by Gardner et al. (2014).

There are three recently described species, whose conservation status is still pending and for which we created distribution polygons: *C. bidaui*, *C. thalesi*, and *C. contrerasi* (Teta and D'Elia 2020; Tammone et al. 2022b). The distribution polygon of the recently described *C. plebiscitum* was created based on the locality points provided by Brook et al. (2021).

In addition, we included some unnamed candidate species, with evidence supporting their distinction, but lacking a formal description, which has a direct impact in conservation. The IUCN Red List of Threatened Species includes only named species. So, until a group of populations with undefined taxonomic status is recognized as a species, there would be no assessments of its risk of extinction, and probably fewer chances to enter these unnamed populations into conservation programs. One of these cases is *C*. "*yolandae*," a form from Santa Fe Province in Argentina, which shows considerable karyotypic differentiation as well as a complex asymmetric sperm type relative to other nearby species of tucos (Vitullo et al. 1988). The form *C.* "*rosendopascuali*," endemic from Cordoba, Argentina, was excluded from the list of valid species by D'Elia et al. (2021), because the name is unavailable; however, we included it in our analysis for the abovementioned reasons. Finally, the Ibera lineage of *Ctenomys*, which include populations occurring in Corrientes Province in Argentina, is also considered here as a candidate species, since Caraballo and Rossi (2018a) demonstrated that these populations had definite karyotypic and molecular uniqueness from other species. There is an important number of extant tuco-tuco populations that have no taxonomic assignment and, hence, were excluded from our analysis. This should be addressed by the research community before long in order to have a more complete assessment of the distribution of *Ctenomys* species, and more importantly, to contribute to the conservation of these populations. Supplementary Data SD2 and SD3 show the locality points used to construct/modify polygons, and all *Ctenomys* distribution polygons, respectively.

Protected areas and intersection with DAs.—The distribution shapes of PAs were retrieved from the World Database on Protected Areas (WDPA; UNEP-WCMC and IUCN 2021) available at the Protected Planet website (https://www.protectedplanet.net). To maintain the maximum amount of data available for our analysis, we decided to include PAs with both "designated" and "inscribed" status. Designated PAs are those areas that are *recognized or dedicated through legal means*, implying specific binding commitment to conservation in the long term (UNEP-WCMC and IUCN 2021). Inscribed PAs are those geographic areas designated as protected under the World Heritage Convention (UNEP-WCMC and IUCN 2021). We discarded proposed PAs because they lack concrete conservation actions at present. Only PAs depicted as polygons were kept and we discarded points that correspond to PAs that have no defined boundaries.

We constructed polygons of the intersection of *Ctenomys* species DAs (minus water bodies) and PAs. The three sets are all vector-based data taken from the Geographic Coordinate System: World Geodetic Survey (WGS) 1984, a projection that prioritizes shapes but also produces some distortions in area estimations (Snyder 1997). To decrease this potential distortion, we transformed data sets and performed calculations using the Molleweide projection, which sacrifices accuracy of angle and shape but maximizes the accuracy of proportions in area (Snyder 1987). However, we decided to use the WGS 1984 projection in the design of our figures because it is more extensively used in regular visualized map products such as the OpenStreetMap, or the IUCN Red List. Since there is a high degree of overlap between PAs in the WDPA (e.g., the same area may be a National Park and at the same time being a Ramsar site under international legislation), we created a flat layer (merging overlapping polygons) to avoid coverage overestimation. For this reason, our flattened areas rather than the absolute number of PAs may constitute a more informative measure of the potential for conservation of a species. To create more realistic mapping, we established two coverage measures to consider that a species distribution has a significant overlap with PAs: (1) the areas within PAs and (2) the areas within PAs for a species divided by the species DA. We adopted a double criterion because there are specific cases where the use of one of them could lead to erroneous conclusions. For example, a species DA could have 100% overlap with PA but be confined to an extremely restricted area. Conversely, a widespread species might have a small percentage of its DA within PAs, nonetheless depicting high absolute values.

Analysis of habitat transformation.—To explore the magnitude of recent intense anthropogenic land cover changes within the range of each species, we used the land cover classification of the Copernicus Climate Change Service for the years 2000 and 2020 at a scale of 300 m pixel size (https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-landcover?tab=overview). Given that detailed data on habitat use and anthropogenic tolerance are lacking for most of the described species of tuco-tucos, our aim was to quantify large-scale and intense anthropogenic habitat transformation coinciding with the ranges of each species of *Ctenomys*. To do this, we classified urban, rainfed, and irrigated/post-flooding agriculture, and permanent ice or snow land cover categories as anthropogenic intensive or unsuitable habitat land covers, and the remaining land cover types as natural/seminatural, which beside natural land covers, included mosaics of cropland, natural vegetation, and pastures. These categories were designated as seminatural because at least some species of tuco-tucos can survive in these habitats, including *C. boliviensis* and *C. erikacuellarae* (see Gardner et al. 2014), and at the scale of this analysis suitable patches of habitat can occur in pixels classified as seminatural. In this way, a conservative estimate was obtained that included large-scale, intensive changes within the geographic range of the species of interest. We report the net percentage of natural/seminatural habitat within each species range in the year 2020, as well as the percentage of natural/seminatural habitat change between the years 2000 and 2020 as a measure of more recent and/or ongoing loss of habitat. The used code for data preparation, processing, analysis, and visualization is available at https://github.com/SLLDeC/Ctenomys_conservation_status_2022 .

Results

Distribution areas and number of localities in conservation status assessment.—The DAs, typically measured as the extent of occurrence, and the number of localities at which individuals of a certain taxon occur, are two key variables in defining the conservation status of a species under criterion B (IUCN 2012). We plotted DAs versus number of localities to inspect previously evaluated species, as well as to assess the risk of DD or NE taxa (**Fig. 1**, Supplementary Data SD4). Considering the IUCN thresholds for Red List assessments, the extent of occurrence

Fig. 1.—Distribution areas (DAs) versus number of localities of extant *Ctenomys* species. Shapes represent previous conservation status assessments (stars = Least Concern, Near Threatened; squares = Vulnerable, Endangered, Critically Endangered; circles = data deficient, not evaluated). Dotted lines represent IUCN thresholds for DAs (20,000 km^2, 5,000 km^2, and 100 km^2) and for the number of localities (10). The bottom panel corresponds to the enlargement of the quadrant defined by species with DA ≤ 20,000 km^2 and 10 or fewer localities. Each quadrant defined by the thresholds corresponds to a specific threat category.


Distribution area (Km^2)
Number of localities
Threat category
LC, NT
VU, EN, CR
Not Evaluated
NT
LC
VU
EN
CR
C. mendocinus
C. opimus
C. magellanicus
C. torquatus
C. argentinus
C. conoveri
C. fulvus
C. sericeus
C. nattereri
C. contrerasi
C. frater
C. maulinus
C. haigi
C. pearsoni
C. rionegrensis
C. "yolandae"
C. boliviensis
C. flamarioni
C. australis
C. lami
C. talarum
C. minutus
C. perrensi
C. fodax
C. knighti
C. "rosendopascuali"
C. tucumanus
C. famosus
C. leucodon
C. thalesi
C. bidaui
C. steinbachi
C. erikacuellarae
Iberá
C. pontifex
C. bergi
C. peruanus
C. saltarius
C. fochi
C. lewisi
C. osvaldoreigi
C. bonettoi
C. validus
C. johannis
C. scagliai
C. pilarensis
C. juris
C. coludo
C. latro
C. tuconax
C. occultus
C. sociabilis
C. ibicuiensis
C. roigi
C. emilianus
C. pundti
C. andersoni
C. bicolor
C. brasiliensis
C. paraguayensis
C. tulduco
C. yatesi
C. dorbignyi
C. viperinus
C. rondoni
C. plebiscitum
C. dorsalis
C. lessai

(equivalent to DAs in this study) and the number of locality thresholds to consider a species as threatened should be <20,000 km^2 and ≤10 localities, respectively. According to these thresholds, four quadrants can be established (Fig. 1) wherein the upper-right portion of the quadrant corresponds to 11 nonthreatened species, while the lower-left corresponds to 46 threatened species. Remarkably, most species of *Ctenomys* fall within the threatened category. The other two quadrants represent 11 species that should be considered at-risk to some extent and will be further discussed jointly with other results. As expected, most species that were evaluated are located congruently within quadrants according to their conservation status, while the majority of NE or DD species fall within the *Threatened* quadrant (Fig. 1).

Overlap with PAs.—From a total of 68 *Ctenomys* species analyzed, 26 have null overlaps with PAs (**Fig. 2**, Supplementary Data SD5). Together with these, 17 additional species have DA–PA overlaps <1,000 km^2 and <25% of their range area. Except for *C.* "*yolandae*," these species are also threatened. The number of PAs, their names, and the countries where they occur are given in Supplementary Data SD6.

Habitat transformation in the past 20 years.—Our results show that 56 species of tuco-tucos have low overlap with anthropogenic intensive land covers (less than 30% of total DAs; Supplementary Data SD5, Supplementary Data SD6). Nonetheless, there are some species with a high percentage of overlap with these cover types. *Ctenomys boliviensis*, *C. brasiliensis*, and *C. steinbachi* have 50–58% of their DAs in such habitats, while *C.* "*rosendopascuali*" has an overlap of about 65%. The most extreme case is the remnant population of *C. pundti*, with 92% of its geographic range under anthropogenic intensive use. Together with the restricted total DA, this species is confined to the borders of intensive agriculture systems of the Pampas Region in Argentina. Forty-one species of *Ctenomys* have lost to some extent their natural or seminatural land cover during the period from 2000 to 2020, although the more extreme loss values are those of *C. argentinus*, *C. conoveri*, *C. frater*, and *C. mendocinus*, with losses greater than 1,000 km^2. The species *C. nattereri*, *C. boliviensis*, *C. pearsoni*, *C. torquatus*, *C. tucumanus*, *C. opimus*, and *C. fulvus* depict moderate values of habitat loss. The majority of these species inhabit grasslands and lowlands, habitats that have been severely affected

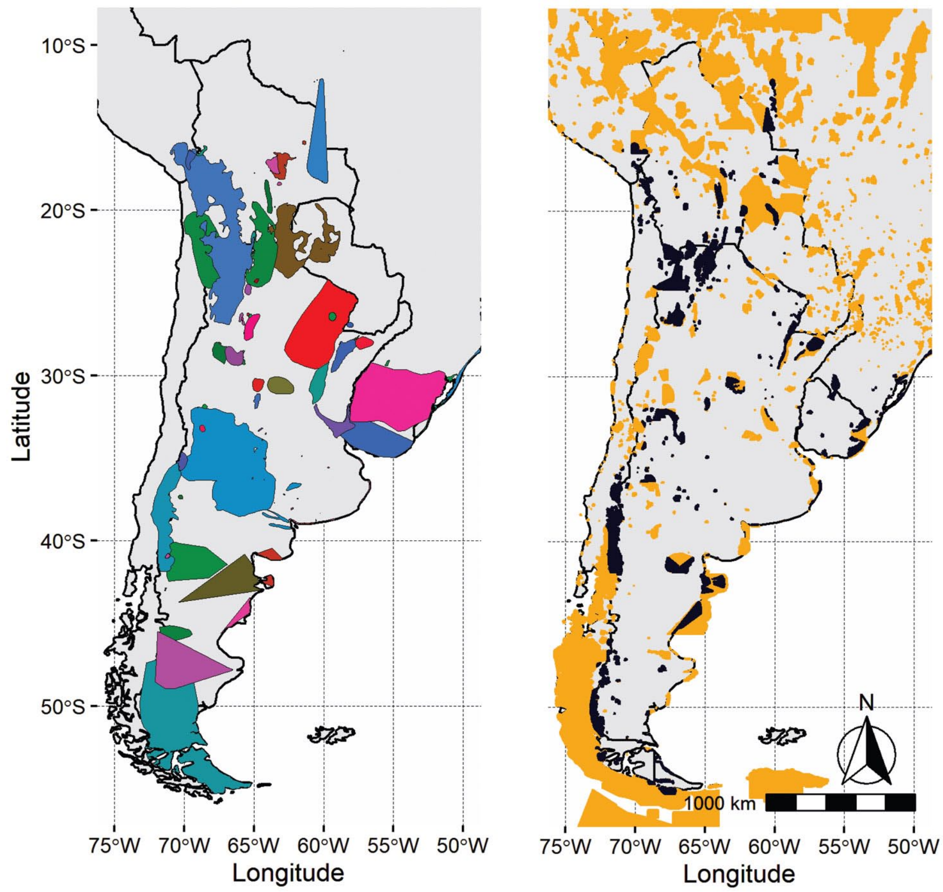

Fig. 2.—Geographic distribution of 68 extant *Ctenomys* species (left panel), protected areas (PAs) retrieved from the World Database on Protected Areas (right panel, light), and overlap between *Ctenomys* and protected areas (right panel, dark). Water body surface was subtracted from the area of overlap between tuco-tuco distribution areas (DAs) and PAs (right panel).

by anthropogenic causes, such as unsustainable agricultural practices, overgrazing, and forest clearing. When considering this loss relative to the natural cover in the year 2000, the species *C. boliviensis*, *C. pundti*, *C. juris*, *C. roigi*, *C. conoveri*, and *C. brasiliensis* depict the more extreme values (3–7%), again being mostly grassland-associated species.

Discussion

The dynamic taxonomy of *Ctenomys*, as well as the high proportion of NE or DD species in this group, made a reevaluation of the conservation status of species in the genus mandatory. Here, we provide an updated set of species distribution ranges which, together with other relevant information, can both aid in revision of previous conservation assessments and provide a provisional estimate of the risk of extinction of an important proportion of NE and DD species. As noted above, the DA and number of localities are two of the most important variables considered by the IUCN to determine whether a species belongs to a category of threat. To enrich this evaluation, we also quantified the degree of overlap of species ranges with PAs, as well as measured the level of natural–seminatural habitat loss over the past 20 years. In this section we discuss both previous assessments and NE taxa, to determine the level of threat of *Ctenomys* species, integrating the abovementioned lines of evidence. Supplementary Data SD7 is an interactive table where all the information used for proposing/revising the conservation status of species of *Ctenomys* can be explored.

Eleven species of *Ctenomys* have DA > 20,000 km^2 and are known from more than 10 localities, being the group under a lesser level of threat, which would correspond to the category of Least Concern (LC; Fig. 1). Concurrently, eight of these have been previously categorized as LC, while *C. argentinus* was classified as Near Threatened (NT). The status proposed for *C.* "*yolandae*" was DD, but following our analysis, we propose to recategorize it as LC. *Ctenomys pearsoni* has been previously classified as NT (Bidau 2019) and EN (Tomasco and Caraballo 2019), but the addition of previously unrecorded localities (this study; Tomasco I., Universidad de la Republica, Montevideo, Uruguay, personal communication, 2022) with the concomitant expansion of the species range (from 312 to 82,558 km^2), enable us to consider this species as LC—the overlap of its geographic range with PAs (4,833 km^2, 5.85%) as well as low to moderate levels of natural–seminatural habitat loss, support the conservation status proposal of LC for this species.

Four previously unassessed (NE or DD) species have DA > 20,000 km^2 but are known from fewer than 10 localities (Fig. 1, Supplementary Data SD4). These species have high absolute and intermediate relative levels of overlap with PAs (Supplementary Data SD4, Supplementary Data SD6) and low rates of natural–seminatural habitat loss over the past 20 years (Supplementary Data SD5, Supplementary Data SD6). We propose to treat these species as NT since they do not meet the number of localities to be considered LC (Supplementary Data SD4).

The NT category includes those species with DA < 20,000 km^2 and more than 10 localities. Seven species fall into this quadrant (Fig. 1), but these should be categorized as EN or VU, for the reasons outlined below. Five species correspond to coastal forms, including: *C. australis*, *C. flamarioni*, *C. minutus*, *C. lami*, and *C. talarum* (mostly coastal, although it has continental relictual populations) and except for *C. minutus*, which has a slightly higher value, all of these species have DA < 5,000 km^2 which corresponds to the threshold below which a species should be considered at least as Endangered (EN). Coastal species have been historically used as models for population genetics studies (Fernandez-Stolz et al. 2007; Mora et al. 2007; Lopes and Freitas 2012), and have been subject to intensive sampling, surveying a high number of close sampling locations. Thus, the number of locations is likely to be inflated by considering sampling points as synonyms of collection localities. However, there are cases in which localities have been proven to represent different populations, as occurs in *C. australis*, which has 13 genetically distinct populations (Austrich et al. 2020). The IUCN defines the term location as "a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present" (IUCN 2012). This definition implies that sampling sites in close geographic proximity should not be considered as different collection localities. This issue could be solved by establishing a minimum distance to consider two sampling points as part of the same locality. For example, Meiri et al. (2018) established that lizard species could be considered restricted to a single locality if they occupied an area with a lineal extent ≤ 10 km or 0.1 of a degree. In addition to restricted DAs, all coastal species have DA–PA overlap <1,000 km^2, and moderate to low relative overlap. Thus, the five coastal species should be considered EN. We think that *C. boliviensis* and *C. rionegrensis* should be categorized as Vulnerable (VU) since they have DAs near the 20,000 km^2 threshold. *Ctenomys rionegrensis* has been previously categorized as EN, but the expansion of its estimated geographic distribution (Caraballo et al. 2020), allows us to allocate this species in a lesser risk category. *Ctenomys boliviensis* is near the limit between NT and VU, but the fact that it is the species with the highest rate of natural–seminatural habitat loss supports the more conservative classification as VU.

The VU category includes species with 5,000 km^2 < DA < 20,000 km^2 and 10 or fewer localities. Fifteen species fall within this quadrant (Fig.

1). Four species, *C. fodax*, *C. tucumanus*, *C. pontifex*, and *C. knighti*, are known only from their type localities or their local surrounding area and, thus, should be considered at a higher risk of extinction category. We suggest treating these species as EN (see below for a discussion of species occurring at one locality). Two species from this group, *C. leucodon* and *C. peruanus*, have been previously assessed as LC, but under this criterion should be categorized as VU. Two additional species, *C. bergi* and *C. perrensi*, were previously evaluated, and coincide with the classification under the criterion applied in this study. *Ctenomys steinbachi* was suggested to be NT or at higher threat. The remaining four species were DD or NE, and are proposed as VU herein, although it is worth noting that many of these species are known to occur in less than five localities. Ten of the 15 species (including those occurring only at the type locality) have little (<1,000 km^2) or no overlap with PAs, underlining the need for conservation outside PAs. The five remaining species have moderate to high PA/DA overlaps, with the highest ratios corresponding to *C. thalesi* and the undescribed forms in the Ibera wetlands, with 97% and 80% of their distribution located in PAs, respectively. The majority of species in this group (eight) have suffered natural–seminatural habitat reduction in the past 20 years, although both absolute values and relative rates are low.

The EN category includes a total of 19 species with 100 km^2 < DA < 5,000 km^2 and five or fewer localities. We decided to include in this category two additional species, *C. ibicuiensis* and *C. pundti*, with eight reported localities, because the location points are proximal to each other and these species occupy small areas of <700 km^2. These two species have no overlap with PAs, and *C. pundti* has the aggravating condition of possessing one of the highest rates of natural–seminatural cover loss, denoting a significant level of threat. Remarkably, *C. lewisi*, a species with only two reported collection localities and a DA of 2,000 km^2, has been previously categorized as LC. Fifteen species, including *C. lewisi*, have 100 km^2 < DA < 5,000 km^2 and have been reported at only one or two localities. These species should be treated as EN, taking also into account that 13 have little (<600 km^2) or no overlap with PAs, and that most of them have experienced natural–seminatural habitat loss (Supplementary Data SD5, Supplementary Data SD6). The four remaining species of this group have 3–5 reported localities (Fig. 1, Supplementary Data SD4), and have been previously categorized as EN, which is in agreement with our proposal. *Ctenomys sociabilis* is an exception that occurs entirely in a PA, but the rest have no overlap with PAs and none have suffered important habitat reduction. The species *C. dorbignyi* has been categorized as CR, but according to both thresholds applied in this approach, it should be recategorized as EN.

Eight species should be considered as Critically Endangered (CR), a category defined by a DA < 100 km^2 and occurrence in one locality. The species *C. dorsalis* and *C. rondoni*, reported at two localities, were included also in this category since their distributions are extremely narrow, and the occurrence in two localities is as serious as that of taxa occurring in a single locality. *Ctenomys roigi* has experienced moderate rates of habitat reduction in the past 20 years, but all species included in this group require urgent conservation actions, since they have no overlap with PAs.

Twenty-two out of 36 previously evaluated species maintained their conservation status after the approach implemented in this study (**Fig. 3**). This corroborates the applicability of the use of DAs, and number of localities, complemented with relevant information such as DA–PA coverage and habitat transformation, as a proxy for assessing the conservation status of NE species. Remarkably, in 9 of the 14 species where there were discrepancies, our approach yielded more conservative categories, suggesting that threat levels were underestimated in previous assessments. More importantly, 27 NE and DD species were categorized under threat in this study (Fig. 3, Supplementary Data SD4).

Before this study, approximately half of the species of *Ctenomys* (32/68) had never been evaluated or were categorized as DD. One of the main outcomes of the use of the DD category is that usually these species receive less attention in management or conservation programs than those categorized as CR, EN, or VU (Amori et al. 2016). The IUCN's Red List categories are internationally utilized by governments for prioritizing conservation actions upon threatened species (Parsons 2016 and references therein). The IUCN defines as DD a species where "there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/ or population status" (IUCN 2021:11). Hence, the true conservation status of a DD species could be anything from "Least Concern" to "Threatened," or even "Extinct." This category is mostly uninformative, limiting the chances to take conservation measures or to support additional scientific research

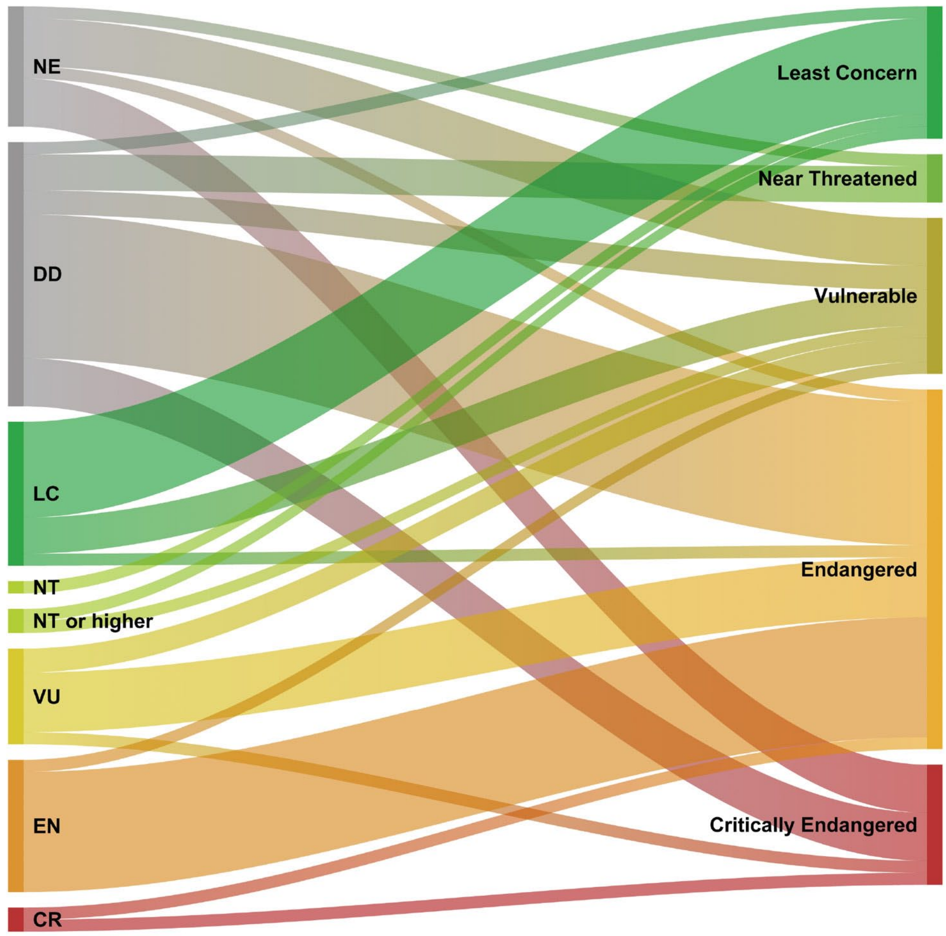

Fig. 3.—Sankey diagram showing previous ctenomyid conservation status (left) and conservation status resulting from the approach implemented in this study (right). Acronyms: NE (not evaluated), DD (Data Deficient), LC (Least Concern), NT (Near Threatened), VU (Vulnerable), EN (Endangered), CR (Critically Endangered).

on these species. Even when the widespread use of the DD category is explicitly discouraged by the IUCN (2021), one in every five South American rodents is included in it (Teta et al. 2021), *Ctenomys* being the genus with the highest number of species classified under this category (Teta et al. 2021). The majority of *Ctenomys* species categorized as DD (15 out of 22) have been reported only at one or two localities, very likely because their geographic ranges are extremely restricted, and as such, they are under a high risk of extinction. Despite the gaps in the study and survey of *Ctenomys* species, the assumption that rarity arises mainly by suboptimal research efforts rather than by low population numbers and sizes, and their concomitant categorization as DD, may be detrimental for species conservation. It is true that one of the most difficult problems is actually accessing areas in which these rodents live, and also, because of their fossorial habits, tuco-tucos are many times difficult to detect. However, the perceived rarity of a given rodent species cannot be easily distinguished from actual low levels of abundance in nature. According to indirect predictions based on spatial and phylogenetic information, Jarić et al. (2016) estimated that 35–69% of mammal species categorized as DD are potentially threatened. Several proposals have been made to alert researchers, land managers, and conservation biologists that most DD species should be considered, at least as a precaution, under some category of threat (Jarić et al. 2016; Parsons 2016; Roberts et al. 2016), particularly in those species with small known ranges and few actual collection localities (Roberts et al. 2016). We adopted this provisory criterion, expecting to contribute to the conservation of an elevated number of *Ctenomys* species categorized as DD. The application of objective criteria (e.g., DAs and the number of localities, but also overlap with PAs and habitat transformation measures) can help to overcome this issue. Remarkably, 18 out of 22 DD *Ctenomys* species are evaluated and deemed at-risk (VU, EN, CR). In addition, 9 out of 10 species that have not been previously evaluated are also threatened, these two groups totaling more than 47% of the species in the genus. To put the real conservation problem of these species into perspective it is important to consider that 53 (78%) of the known species are threatened and that 47 (69%) have known geographic ranges that share little or no overlap with PAs, emphasizing the need for conducting additional research and implementing new conservation efforts for these rodents. Finally, our summary shows that 33 species, representing 49% of known-extant tuco-tucos, have been recorded from three or fewer collection localities, and all are considered threatened through the approach implemented in this study. The conservation of geographically restricted species is of great relevance since these species may function as "singletons" in ecological communities and may be pivotal to understanding biogeographical processes and speciation (Gardner et al. 2014; Teta and D'Elia 2019; Teta et al. 2021).

Acknowledgments We are especially grateful to Sebastian Cirignoli and Diego Varela for facilitating the shapes generated in the framework of the reassessment of Argentinian species by SAREM. The authors thank Federico Brook, Mauro Tammone, Pablo Teta, Andres Parada, and Ivanna Tomasco for the information provided for Mendoza's, Patagonian, Chacoan, and Uruguayan tuco-tucos. We thank Matias Mora for the information regarding *C. talarum*, the *C. pundti* complex, and *C. mendocinus*. Thank you also to Gabor Racz for assisting with the web page on Lamarck and to Sue Gardner for assistance with the tables. Part of this study was supported by United States National Science Foundation (NSF) grants no. BSR-9024816, DEB-9496263, and DBI-145813, to SLG, and PICT-2020- 01989 (Agencia Nacional de Promocion de la Investigacion, el Desarrollo Tecnologico y la Innovacion, Argentina) to DAC.

Supplementary Data Supplementary data are attached to the archive record for this paper; they are also available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Interactive map showing *Ctenomys* geographic distribution areas (DAs), protected areas (PAs), and their intersection. To avoid an excessively large file, we retained PAs within the limits of the distribution of the genus. The file can be accessed at: https://lamarck.unl.edu/Tuco-2/SD1.html

Supplementary Data SD2.—This is a CSV spreadsheet that is downloadable and contains locality points used in the construction/ modification of species distribution polygons. The file can be accessed at: https://lamarck.unl.edu/Tuco-2/SD2.csv

Supplementary Data SD3.—Polygons of all *Ctenomys* species distributions that can be opened by any ARC-GIS compatible software. The file can be accessed at: https://lamarck.unl.edu/Tuco-2/SD3.zip 476 Journal of Mammalogy

Supplementary Data SD4.—Distributional information, previous conservation status assessments, and revised conservation status according to updated distribution areas, number of localities and auxiliary information (overlap with protected areas and habitat transformation), of extant Ctenomys species. https://lamarck.unl.edu/Tuco-2/SD4-tuco-dist-info.pdf

Supplementary Data SD5.—Distribution areas, extent of overlap with protected areas (expressed in km^2, as a percentage and also the number of PAs), and measures of natural, seminatural and anthropogenic land cover changes in the period for the years 2000–2020 for all extant Ctenomys species. https://lamarck.unl.edu/Tuco-2/SD5-tuco-dist-info2.pdf

Supplementary Data SD6.—An interactive list of protected areas that overlap *Ctenomys* geographic distributions. This is available as a web-based table that can be searched. The file can be accessed at: https://lamarck.unl.edu/Tuco-2/SD6-new.html

Supplementary Data SD7.—Interactive table showing distribution areas, conservation status, overlap with protected areas, and habitat transformation in the past 20 years for 68 extant *Ctenomys* species. The file can be accessed at: https://lamarck.unl.edu/Tuco-2/SD7.html

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