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REVIEW

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Historical and current knowledge of the Magellanic tuco-tuco *Ctenomys magellanicus* in Patagonia and Tierra del Fuego, South America

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Abstract

Background I review the natural history of the tuco-tuco *Ctenomys magellanicus* in Patagonia and Tierra del Fuego, southernmost geographic regions shared by Argentina and Chile. By natural history I mean both historical records and ecological features of this gregarious burrowing rodent.

Methods and results I conducted a selective review of the natural history of *C. magellanicus*, as recorded in mainstream journals and proceedings, landmark monographs and books, and internet sources. I report results on: (a) Original description, (b) Diversity and distribution, (c) Life history, (d) Interactions with plants and herbivorous competitors, (e) Interactions with predators other than humans, (f) Interactions with humans, and (g) Abundance and conservation. I also enter the anthropology field, but I only touch the archeology field. Although this review is not on the systematics of *C. magellanicus*, I do provide an updated overview of the phylogenetics-based taxonomy of the genus where it belongs.

Discussion There is a rather large body of literature on *C. magellanicus,* comprising the fields of anthropology, archeology, biogeography, biology, ecology, and systematics. These areas are broadly covered but thinly treated, offering interesting opportunities for further research. For instance, on adaptation, evolution, and environmental impact of the southernmost burrowing rodent in the world and its cultural impact on vanishing native peoples, especially the Selk'nam.

Keywords Argentina, Chile, *C. m. dicki*, *C. m. fueginus*, *C. m. magellanicus*, *C. m. obscurus*, *C. m. osgoodi*

Background

Ecologists have been slow to recognize the importance of historical accounts for understanding the current status of any given species in the world. Only recently there were formal calls to ecologists to incorporate a historical perspective into their pursuits [74, 75] and some of them have taken heed. To cite recent examples concerning animals in Chile, Correa-Cuadros [15] compared the history, control, epidemiology, ecology, and economy of the introduction of European rabbits in Chile and Australia, thus providing a framework to contrast the different values associated with English versus Spanish colonization and with the use of these two territories. Jaksic [34] studied the southernmost lizard in the world, *Liolaemus magellanicus,* on the large Tierra del Fuego Island shared by Argentina and Chile at the tip of South America and found surprising insights emerging from

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none other than Darwin [17]; (see [91] for his overall contribution on Chilean vertebrates). Zurita et al. [85] analyzed the introduction history, motivations, and predator-rancher conflicts brought about by the translocated Chilla fox (*Lycalopex griseus)* also on Tierra del Fuego. And Andrews et al. [3] addressed the introduction history and motivations behind the several translocations of the California quail (*Callipepla californica*) within and between Chile and Argentina. Aware of its shortcomings [16], I followed this synthetic path, connecting historical accounts of the Magellanic tuco-tuco (*Ctenomys magellanicus*) with its current status.

This review is not on the systematics of *Ctenomys magellanicus* (see Species disambiguation below); it is on the natural history of this species in Patagonia and Tierra del Fuego, geographic regions shared by Argentina and Chile (see Geographical disambiguation below). Therefore, I comment rather cursorily those aspects related to phylogenetics and taxonomy. By natural history I mean both historical records and ecological features of the species. Among the latter, specifically to: (a) Original description, (b) Diversity and distribution, (c) Life history, (d) Interactions with plants and herbivorous competitors, (e) Interactions with predators other than humans, (f) Interactions with humans, and (g) Abundance and conservation. In dealing with the latter two aspects, I entered hesitantly in the anthropology field (see Fuegian and Patagonian peoples disambiguation below), and decided to touch only lightly the archeological field for my lack of qualifications. A good recent entry to the latter literature on *C. magellanicus* is in Pardiñas et al. [58].

Methods

Literature search

I back-tracked references from current to older sources, using mainstream journals, monographs, and books, and relevant grey literature. Some new sources emerged when engine-searching the internet without time or language constraints for vernacular key words such as *apen* (as in Bridges' [9, 10] spelling); coruro (as in Osgood's [55] and Markham's [44] spelling) or cururo (as in and Gusinde's [29], Señoret's [70], and Wolffsohn's [84] spelling) or cururu (as in Massoia and Chebez's [49] and Prosser-Goodall's [63] spelling); *tukem* (as in Massoia and Chebez's [49] spelling); tucotuco or tuco-tuco (as in Mann's [43], Ohlin's [53], and Skottsberg's [73] spelling), and tucutuco or tucu-tuco (as in Darwin's [17], C. R. Gallardo's [25], Gusinde's [29], Housse's [30], and Godoy's [28] spelling), tucutucu or tucu-tucu (as in Bridges' [9, 10], Fitz Roy's [23], and Payró's [59] spelling); or tucutztco (as in C. R. Gallardo's spelling [25]) both as singular an plural names. Osgood [55, page 120] commented that "The vernacular name coruro is universally applied to this animal on Tierra del Fuego as well as elsewhere in the vicinity of the Straits of Magellan, evidently having been brought there from northern and central Chile where it is used for a different animal of similar habits, belonging to the genus *Spalacopus*. In northern Patagonia and Argentina generally the name tuco tuco is more frequently applied to it." Throughout this text, I keep the common name used by any given author (e.g., not hyphened as in [55], above), but I myself use tuco-tuco and tuco-tucos (with a hyphen), as most authors do.

I searched scientific keywords such as *Ctenomys,* either *dicki* or *fueginus* or *magellanicus* or *obscurus,* or *osgoodi* or sp. I noted that computer searches are often defeated by misspellings of scientific names. In my queries I detected several of them: *fueguinus* for the correct *fueginus* (a common mistake made by Housse [30], Markham [44], Reig and Kiblisky [67], Teta et al. [78], Texera [79], and Venegas and Sielfeld [82]), *magallanicus* for *magellanicus* (by M. Gallardo [26] and Housse [30]), *magallenicus* for *magellanicus* (by Simonetti and Stipicic [72]), and dickii for dicki (by Simonetti and Stipicic [72]). Sometimes the specific name was capitalized (*Magellanicus).* Curiously, *Ctenomys* was never spelled wrong. When such misspellings or egregious meanings were expressed, I attached to them the adverb *sic* in brackets [*sic*]. Another surprise I found was that translations were not exactly symmetrical: For example, Bridges' [9] original book in English of 1949 is rendered slightly different in its Spanish version of 1952 [10]. I understand that both Bridges and his translator were not zoologists, and thus I used my best judgment to interpret the original meaning of Bridges taking English as the base original and Spanish as the derivative that may have misinterpreted the former. The same applies to Prosser-Goodall's [63] book, which is bilingual. Here, one has to consider that her native language was English, and that the translation was aided by Spanish speakers. Darwin's [17] classic book is another case. It has had so many small variations over the years that one has to be carefully in citing which exact edition was used to make quotations.

I distinguished between first-hand information and secondary use of literature sources to avoid redundancies; instead of quoting review papers or books, I preferred to read and cite the original source and not the compilation one. In quoting authors, I did not correct grammar or taxonomic mistakes, nor did I feel obligated to list in the references those citations made by any quoting author (chiefly because I could not locate the original source). This literature search is undeniably non-systematic (e.g., the grey literature is not usually archived electronically). Currently, the most updated compilations of peer-reviewed and grey literature for

Ctenomys magellanicus in Chile are in MMA (Ministerio del Medio Ambiente) [51] and in Argentina are in Bidau [7] and Sánchez and Lizarralde [99]. This review updates that information. For the record, I did not find mention to tuco-tucos in the accounts of Byron [12, 13], de Bougainville [18], Laming [39], Milne-Edwards [50], in Martial [45], Molina [92], Olrog [54], Pigafetta ([61], see also [14]), or Pine et al. [62].

Species disambiguation

A general overview of *Ctenomys* is in Patton et al. [103] and I hereby follow the orientations of Parada et al. [57] as updated by D'Elía et al. [20] (see also [76, 100]) in recognizing several phylogenetic groups of species of *Ctenomys* with varying support from biogeographic [21, 40, 41], evolutionary [20, 57, 76–78], physiological [42], genetic [21, 26, 37], and sperm-morphologic data [22]. (a) The "*mendocinus*" group, comprising at least *Ctenomys mendocinus* Philippi, 1869 (including *azarae* and *porteousi* as synonyms); *C. bergi* Thomas, 1902; *Ctenomys coludo* Thomas, 1920 (including *famosus* as a synonym; see [101]); *C. johannis* Thomas, 1921; and *C. australis* Rusconi, 1934; all these species are widely distributed in central Argentina, excluding northern Patagonia provinces. Within this "*mendocinus*" group there are also two geographically disconnected species: *C. flamarioni* Travi, 1981 in southern Brazil and *C. rionegrensis* Langguth and Abella, 1970 in Entre Ríos province and Uruguay. Teta et al. [100] recently described two new species from the Andean slopes of west-central Argentina: *C. eileenae* and *C. verzi.* Perhaps other species are part of this group as well (e.g., *C. emilianus* and *C. fochi*), but they have not yet been analyzed phylogenetically (D'Elía, personal communication April 2023). (b) Southward, in Argentinian and Chilean Patagonia, is found the "*magellanicus*" group. I follow the lead of Teta et al. [78] in recognizing that the nominal forms *Ctenomys fueginus* Philippi, 1880 [60]; *C. colburni* Allen, 1903 [1]; *C. osgoodi* Allen, 1905 [86]; *C. m. dicki* Osgood, 1943 [55]; and *C. m. obscurus* Texera, 1975 [79] are all subjective junior synonyms of *Ctenomys magellanicus* Bennett, 1835 [6]. Recently, [77] added three new species of Patagonian *Ctenomys,* all belonging to the "*magellanicus*" species group and distributed in Chubut province, Patagonian Argentina: *Ctenomys bidaui*, *C. contrerasi*, and *C. thalesi*. They also placed *C. coyhaiquensis,* Kelt and Gallardo in 1994 [36] under the synonymy of *C. sericeus* Allen, 1903 [1]. Other known species of the *magellanicus* group are *C. haigi* Thomas, 1919 [80, 81] and *C. lentulus* Thomas, 1919 [80, 81]. Surprisingly, a new species in this group was recently described from southern Buenos Aires province, well outside Patagonia: *C. pulcer* [83]. (c) Additional species of Patagonian *Ctenomys* are *C. fodax* Thomas, 1910 [95]; *C. maulinus* Philippi, 1872 [94]; *C. sociabilis* Pearson and Christie, 1985 [93]; and the recently described *C. plebiscitum* [11], which is sister of *C. sociabilis*.

Geographical disambiguation

Patagonia is a rather imprecise geographical term than nonetheless is attributed to lands in the southern section of the Andes Mountains, in both Argentina and Chile, with lakes, fjords, temperate rainforests, and glaciers in the west and deserts, tablelands, and steppes to the east. Patagonia is bounded by the Pacific Ocean on the west, the Atlantic Ocean to the east, and bodies of seawater that connect them, including the Strait of Magellan and sometimes the Beagle Channel and the Drake Passage to the south. The Colorado and Barrancas rivers, which run from the Andes Ranges to the Atlantic Ocean, are commonly considered the northern limit of Argentine Patagonia while the northern limit of Chilean Patagonia is at Huincul Fault, in Araucanía Region. The archipelago of Tierra del Fuego, south of the Strait of Magellan is sometimes included as part of Patagonia but I prefer to keep it separate. In continental Argentina the central part is known as the Pampean or Pampas geographical region [102] (https://en.wikipedia.org/wiki/Pampas) while the southern part is called the Patagonian or Patagonia geographical region, https://en.wikipedia.org/wiki/Patagonia). In Chile, the name Patagonia stops at the Strait of Magellan, and anything outside is considered part of the Tierra del Fuego archipelago.

Tierra del Fuego is also an ambiguous geographic term: It may refer to the archipelago (Archipiélago de Tierra del Fuego or Archipiélago fueguino) or to the island proper (Tierra del Fuego Island, or Fireland, or Isla Grande de Tierra del Fuego). The Fuegian archipelago contains the large Tierra del Fuego Island (ca. 48,000 km^2), seven medium-sized islands (Hoste, Santa Ines, Navarino, Dawson, Aracena, Clarence, and Staten, ranging from 4,100 to 500 km^2 in the same sequence), and ca. 3,000 smaller islands and islets, the best-known being Cape Horn, Lennox, Nueva, Picton, and Riesco. Most of these smaller islands are located to the southwest of Tierra del Fuego Island, separated by the Strait of Magellan and the Beagle Channel. The large island is split east–west between Argentina and Chile (40:60), respectively, at meridian 68°34' W, and most other islands (Staten Island excepted) are in Chilean territory. Tierra del Fuego Island is the largest island in South America, ranks 29 in size worldwide, and amounts to ca. 70% of the area of Tasmania in southernmost Australia (https://en.wikipedia.org/wiki/Listofislandsbyarea).

From the above, the proper adjectives for the names Patagonia, Tierra del Fuego, and Fuego-Patagonia should

be Patagonian, Fuegian, and Fuegian-Patagonian. San Roman et al. [68] provided a colorful map that represents these regions well.

Fuegian and patagonian peoples disambiguation

The Fuegian archipelago hosted until the twentieth century four different peoples [24, 25]: Kawesqar or Alacalufe, Manek'enk or Haush, Selk'nam or Ona, and Yahgan or Yamana; the former denominations being more favored. The Selk'nam branched out from the "Patagones" (=Aonikenk or Telhuelche people) on the South American (Patagonian) mainland, and migrated across the Strait of Magellan to the large Tierra del Fuego Island (Fuegian), where they concentrated on the northeastern area of the island, although they sporadically reached southward to the Beagle channel. The Manek'enk lived on the Mitre peninsula in southeastern Tierra del Fuego Island, and were culturally and linguistically related to the more northerly Selk'nam. Unlike the three previous peoples (all being "foot indians"), the next three were nomadic seafaring, or "canoe indians." The Chonos were found in the archipelagos of Chiloé, Guaitecas, and Chonos, roughly spanning from Calbuco and southernmost Chiloé Island to Taitao peninsula. The Kawesqar concentrated mostly on islands to the south of the Gulf of Penas, around Wellington, Desolación, and Santa Inés islands, and around Brunswick peninsula. The Yahgan traditional territory included the islands south of the Strait of Magellan and the Beagle Channel, extending their presence into Cape Horn, making them the world's southernmost human population. All these peoples overlapped geographically to some extent and traded goods among them. Further details may be found in https://en.wikipedia.org/wiki/Fuegians With regard to the use of *Ctenomys* for food, fur, or trade, up to now only the Aonikenk and Selk'nam (the Manek'enk to a lesser extent) "foot indians" have been reported to be involved. And for the specific Tierra del Fuego setting, good entries to that literature are in [52, 64, 68].

Results and discussion

Original description

The first description was by Bennett ([6], pages 189–190): "December 22, 1836 [the year printed is 1836, but the number 6 is crossed out and above it a 5 is penciled, giving the impression that the minutes were read in December 1835 but that the typist mistakenly dated them the year he was printing, i.e., 1836. Indeed, he previous minutes are dated December 8, 1835, pp. 185–188]. E. S. Hardisty, Esq., in the Chair. Specimens were exhibited of several *Rodent* animals collected during his survey of the Straits of Magalhaens, by Capt. P. P. King, R. N., Corr. Memb. Z. S., and presented by him to the Society. They were accompanied by some notes by Capt. King, which were read. In bringing the animals severally under the notice of the Meeting, Mr. Bennett first directed particular attention to one of them, which constituted, in his estimation, a new species in the genus *Ctenomys*, Blainv. … The characters distinguishing the new species of *Ctenomys* are chiefly those of colour. The *Cten. Brasiliensis* is described by M. de Blainville as being shining rufous above, and reddish white below. The new species may be characterized as the CTENOMYS MAGELLANICUS [*sic*]. *Cten. flavescenti-fusco-griseus, subtus pallidior; pedibus caudaque albescentibus. Long. corporis cum capite 7½ unc.; caudae, 2¾; capitis, 2. Hab. apud Portum Gregory dlctum, ad Fretus Magellanici ostium orientale*. [My translation from Latin: "A yellowish-brownish-greyish *Ctenomys*, paler underneath, and with whitish feet and tail. Head and body length is 7½ inches; tail is 2¾ inches; head is 2 inches. It is said to inhabit Port Gregory, at the eastern mouth of the Strait of Magellan"]. Captain King states that this 'little animal is very timid; feeds upon grass; and is eaten by the Patagonian Indians. It inhabits holes, which it burrows, in the ground: and, from the number of the holes, it would appear to be very abundant.'".

Thus, the minutes of the Zoological Society of London were read on December 22, 1835, by Edward Turner Bennett (1797–1836) under the chairmanship of E. S. Hardisty and aided with complementary notes provided by Captain Phillip Parker King (1791–1856) –of the British Royal Navy and a Corresponding Fellow of the Society— who collected the type specimen near the port then existing at San Gregorio Bay (52°35'S, 70°10'W) in continental Magallanes, Chile. It is interesting that King noted that the local natives (Aonikenk people) ate this tuco-tuco (see below for more on this).

For Chile, Gay [88], pages 105–106; see [89, 90] for his overall contribution on Chilean vertebrates] gave his Latin description of *C. magellanicus* as *C. fusco-cinnamoneus, pedibus setiferis, cauda brevi, auriculis mediocribus, dentibus molaribus exiguis*. [My translation from Latin: "Brownish-cinnamon, feet with bristles, short tail, medium-sized ears, small molar teeth."]. He also provided its first morphological description in Spanish, which in comparison to Bennett's (1835), highlights that *C. magellanicus* has curved claws in its forefeet and longer in its hindfeet, which are covered by strong and straight bristles (stiff hairs). He finally stated (page 106) that: "Esta especie, descubierta en el Puerto Gregory en el estrecho de Magallanes, difiere del *C. brasiliensis*, conocido muy anteriormente por diversos caracteres, y entre otros por sus muelas mucho más pequeñas y por el color del cuerpo algo más oscuro, de un flavo claro por bajo y no blanco rojizo. Hace agujeros en la tierra, a donde se va

a ocultar al menor ruido. Los patagones los cazan para comerlos." That is, he concurred with Bennett's (1835) rendition, but adding a comparison with *C. brasiliensis.* Thomas [[96], page 6], tersely reported "A spirit specimen from Pechett [Peckett] Harbour."

Diversity and distribution

The first distributional map of the Magellanic tuco-tuco was that by Osgood ([55], page 121): *Ctenomys magellanicus osgoodi* appeared as the northernmost subspecies, on the western fringe of the Andes Ranges, in the provinces of Chubut and Santa Cruz in Argentina. Southwards it was replaced by *C. m. magellanicus* in Santa Cruz province (Argentina) and Magallanes province (now Region, Chile). Across the Strait of Magellan, in Tierra del Fuego Island (shared by Argentina and Chile), *C. m. fueginus* was distributed. On Riesco Island, *C. m. dicki* was represented by a single locality. Texera ([79], page 164) displayed on a map the type locality of the newly named *C. m. obscurus,* from southern Tierra del Fuego Island, on the Chilean side. Kelt and Gallardo [36] described a new species, *C. coyhaiquensis* in Aysén province (Chile), across from Santa Cruz province (Argentina). In their map, two Chilean collecting localities face rather closely the type locality of *C. colburni* in Argentina. Lizarralde et al. ([40], page 14) showed the distribution of *C. m. fueginus* on the Argentinian side of Tierra del Fuego Island. They distinguished between the northerly San Sebastian subpopulation (2n = 34) and the southerly Río Grande subpopulation (2n = 36). See [21, 41], below, for other genetic information.

Chile's MMA (Ministerio del Medio Ambiente) [51] mapped all Chilean records of *C. m. magellanicus, C. m. dicki,* and *C. m. fueginus.* They were all from Magallanes Region in Chile. Bidau [7] showed a distributional map of *Ctenomys magellanicus* (without discriminating subspecies) across Argentina, encompassing the provinces of Chubut on the north, Santa Cruz in the middle, and Tierra del Fuego in southernmost Argentina. Barquez and Pardiñas ([5], page 13) displayed the localities visited by Emilio Budin in 1927–1928 [80, 81], from one of which (Arroyo de los Perros, Santa Cruz province, Argentina) *C. magellanicus* was collected. Teta et al. ([78], page 3) mapped collecting localities of *C. magellanicus* (with *C. colburni* as part of it) and *C. fodax,* from Chubut, Santa Cruz, and Tierra del Fuego provinces in Argentina, and from Aysén and Magallanes Regions in Chile. Teta and D'Elía ([77], page 5) mapped collecting localities of *C. haigi, C. lentulus, C. bidaui, C. contrerasi* (two subspecies recognized), *C. thalesi, C. sericeus,* and *C. magellanicus.* Most recently, Tammone and Pardiñas ([76], page 483) mapped the distribution of Argentinian *Ctenomys* species into the northerly "*mendocinus*" group and the southerly "*magellanicus*" group. The first was distributed mostly in Mendoza, San Luis, Córdoba, Buenos Aires, La Pampa, and Río Negro provinces. The latter, in Neuquén, Río Negro, and Chubut provinces. The map was truncated, and thus the more southerly distribution of the "*magellanicus*" group in Santa Cruz and Tierra del Fuego provinces in Argentina was not shown. Fasanella et al. ([21], page 699) provided a distributional map of *C. magellanicus* in Tierra del Fuego Island, showing two genetically distinct populations (by both chromosome number and haplotype): A northerly one centered at San Sebastian Bay, and a southerly population south of Río Grande city.

The oldest known *C. magellanicus* fossil record in southern Patagonia came from the Cueva del Milodon site in continental Magallanes Region (Chile), with a radiocarbon dating of 13,500 ± 470 and 10,400 ± 300 years before present ([71], see also [69, 98]). A late Quaternary distributional map of *C. magellanicus* was recently published by Pardiñas et al. ([58], page 101). In it, the species is shown to have been distributed all over Tierra del Fuego Island, expect for the southern, wetter, higher-relief, and forested part. Fasanella et al. [21] studied the genetic-demographic structure of *C. magellanicus* in the same island *and* discussed that the species is currently fragmented into two populations: A southerly one, firmly structured genetically, including the basal haplotype, and representing the ancestral population, which apparently lived in a biogeographical refuge through the adverse Pleistocene environmental conditions [64]. And a northerly population, with low genetic structure, derived, and spanning the most recently occupied area in northern Tierra del Fuego Island.

Life history

The following is a synthesis of original observations by Darwin [17] on *Ctenomys brasiliensis* and by several other authors [9, 10, 49, 84, 97] on *Ctenomys magellanicus.* It must be noticed that the latter authors took extensively from Mann [43]. The Magellanic tuco-tuco is an inhabitant of the Patagonian steppe [65], where it occupies both flat or rolling plains, with a dense cover of grasses or bunchgrasses (*Festuca, Hordeum, Poa*), and landscapes of gentle hills covered by plant associations in which low shrubs predominate, such as *Baccharis magellanica*, *Berberis empetrifolia*, *Berberis microphylla*, *Chiliotrichium diffusum*, *Empetrum rubrum,* and *Senecio* of various species. This tuco-tuco is absent from forests, peatlands, swamps, and stony soils. Darwin [17] visited the Fuegian archipelago in December 1832-February 1833, January-March 1834, and May–June 1834) in a footnote in page 51 stated "The wide plains north of the Rio Colorado are undermined by these animals; and

near the Strait of Magellan, where Patagonia blends with Tierra del Fuego, the whole sandy country forms a great warren for the tucotuco." Jaksic et al. [35] reported that the mean weight of tuco-tuco on the island was 272 g, based on [4].

The Magellanic tuco-tuco is a fossorial gregarious animal that excavates burrows and galleries for feeding, sheltering, and reproduction, completely undermining the soil. Grass roots are the most important food in their diet, but shrub roots may be eaten in shrub-covered steppes. As a consequence of these feeding activities, extensive patches of grass may die out. Galleries are superficial on account of the root depth of their food plants, but they are also said to cut the grass around their outlets, let it dry, and then transport it underground, being thus suspected of storing food in deeper chambers for overwintering. They spend daytime underground but leave their burrows at night to look for new favorable feeding places when the roots of the sector occupied by its network of galleries is exhausted. Thermoregulation problems are reduced to a minimum in their southern temperate locations, by building their galleries at 30–40 cm deep and by their nests being upholstered by thick straw mattresses. Plus, the exterior openings of the burrows are oriented downwind, and their own "dejection cones" of excavated materials prevent the entry of the cold winds so frequent at high latitudes. They are very difficult to observe leaning out at the entrance of their burrows, but they are easy to hear. Their vocalizations underground may be described as a short, but not rough, nasal grunt, which is repeated about four times in quick succession; the first grunt is not so loud but a little longer, and more distinct than the three following. The musical time of the whole is a constant "drumming" or "hammering" like *Spalacopus cyanus* utters in central Chile (although the latter seems softer and more melodious). Indeed, the name tuco-tuco is given in imitation of the sound produced. There is a puzzling footnote in Darwin ([17], page 58): "At the R. Negro, in Northern Patagonia, there is an animal of the same habits, and probably a closely allied species, but which I never saw. Its noise is different from the Maldonado kind [*Ctenomys brasiliensis*]; it is repeated only twice instead of three or four times, and is more distinct and sonorous: when heard from a distance, it so closely resembles the sound made in cutting down a small tree with an axe, that I have sometimes remained in doubt concerning it." Similarly, Fitz Roy ([23], page 107) reported "This Indian name [tucu-tucu], gutturally pronounced, expresses the curious sound made by these creatures while under ground—a noise somewhat like the blow of a distant hammer."

When set on the ground, the tuco-tuco moves slowly and clumsily, which apparently owes to the outward action of their hind legs; they are likewise quite incapable of jumping even the smallest vertical heights. When eating aboveground, they rest on their hind legs and hold the food in their forepaws and also attempt to drag it into some corner. They do not usually make any attempt at escaping; when angry or frightened, they utter their tuco-tuco vocalization, and –according to Darwin ([17], page 58)—do not defend themselves even if offered an offending finger to bite on. An anonymous referee of this paper, familiar with *C. magellanicus* wrote "their aggressiveness varies among the genus but a *magellanicus* would definitely bite you if you hold it for a long time. In addition. hearsay referred to Osgood ([55], page 118), was that tuco-tucos take a stand against approaching sheep and even bite them.

Their current presence in a landscape is revealed by the higher degree of humidity and loose compaction of the mounds deposited outside the entrance hole to their galleries, as well as by their voices. Recently started colonies have a few exit holes to rather superficial galleries, which allow them to be captured by opening them with pikes and shovels. Their past presence in a landscape is told by the land being covered by small undulations, reminiscent of mima-mound formations in North America caused by the burrowing actions of Geomyidae rodents that represent ecological equivalents of Ctenomyidae rodents in South America.

[42] examined comparatively the energetics of nine species of *Ctenomys* at different altitudes from 0–4600 m elevation, ranging in body mass from 120–325, and distributed from latitudes 26°-53°S, with *C. magellanicus* being a low-altitude, mid-sized (=263.1 g) species with the southernmost distribution in South America. They observed that only body mass affected the variability in basal metabolic rate (BMR), with climate, soil conditions, habitat productivity, and net primary productivity not being correlated with BMR variability. Because BMR and maximum metabolic rate (MMR) was correlated, the low BMR among *Ctenomys* species could also be determined by factors that affect MMR rather than BMR. The parasitology of *C. magellanicus* is poorly known [19]; indeed, a single record of a helminth endoparasite was wrongly attributed to it instead of to an unspecified Uruguayan *Ctenomys* species.

Interactions with plants and herbivorous competitors

There are no quantitative studies of the diet of the Magellanic tuco-tuco. All authors cited in the Life history section above agree that it is herbivorous, and that it is eats grass roots and sometimes shrub roots, and even herb foliage outside its exit tunnels but fail to identify species, much less preference of consumption. A typical statement by Bridges [9, page 452] is: "I believe they are

strictly vegetarian and probably eat many roots from underground, thus causing the plants to die." Or this by Mann [43, page 307] (my translation from Spanish): "According to our observations in *Ctenomys magellanicus fueginus*, in the southwest of Tierra del Fuego, grass roots play the most important role in their diet. However, it is very possible that the populations in steppes covered by shrubs find their forage in their roots." This is a sore piece of missing information for understanding not only life history traits of this species but also its role in communities and ecosystems of Patagonia and Tierra del Fuego. Therefore, it is difficult to gauge any type of potential competition between *Ctenomys magellanicus* and either native (Lama guanicoe) or introduced herbivores such as sheep (*Ovis aries*), cattle (*Bos taurus*), and horses (*Equus ferus caballus*). Even though livestock are all surface grazers and tuco-tucos are underground root eaters, they may still interfere with each other. Removal of aboveground plant tissues may result in lower root development, and vice versa. Perhaps in the past Magellanic tuco-tucos competed for food more with native guanacos than with introduced sheep, cattle, or horses, which may have led the former to decline over time only to be compensated by the incoming alien herbivores. This research topic is still open.

Interactions with predators other than humans

My search of the published literature on predator food habits in Chile [32, 33], specifically in the Magallanes Region, rendered the scarce positive information (I am not reporting predators whose published diet I scrutinized but yielded no occurrence of *Ctenomys* among their prey). There are no quantitative records of predation on Magellanic tuco-tuco before the 1900s (when these herbivores were more abundant than now). And the few later additions show relatively low consumption of this prey.

The first record of predation on a *Ctenomys* from somewhere in the Tierra del Fuego archipelago was reported in a footnote by Oustalet ([56], page B 42) stating (my translation from French): "A female of this species whose autopsy was carried out by Dr. Hyades had rodent hairs in her stomach which appeared to belong to the genus *Ctenomys*." "Her" was a Magellanic Horned Owl (*Bubo magellanicus*). Humphrey et al. ([31], page 159) reported that Crawshay (1907, page 14), when referring to *Geranoaetus polyosoma* recorded"Five examples examined by me contained the remains of *Ctenomys magellanicus*." Also, in page 169, Humphrey et al. [31] reported verbatim an original observation by Cunningham ([97], page 190), made in Quartermaster Island [Isla Contramaestre] with regard to *Caracara plancus* "On arriving at the place where they had been sitting, we found an accumulation of bones of the *Ctenomys Magellanicus [sic]*, including several hundred fragments of crania…" Indeed, Cunningham ([97], page 195) near Philip Bay [Bahía Felipe] made the following observation: "We saw several specimens of the burrowing owl [*Athene cunicularia*], one flying about our heads and uttering its peculiar note as we returned to camp in the dusk, and many broken crania of *Ctenomys* enveloped in a ball of hair were lying about, bearing evidence as to the nature of their destroyer." Finally, in page 241, Humphrey et al. [31] implied that *Athene cunicularia* was a main predator of *C. magellanicus,* but because the latter were trampled out by sheep, this may have led to the disappearance of that owl from the island in the mid 1920s.

In describing a new subspecies in Tierra del Fuego Island, *Ctenomys magellanicus obscurus* Texera ([79], page 163) reported that its potential predators were *Polyborus plancus plancus, Geranoaetus melanoleucus,* and *Buteo polyosoma polyosoma*. Currently, *Polyborus* = *Caracara,* and *Buteo* = *Geranoaetus.* Jaksic et al. ([35], see also 4) compared the diets of the foxes *Lycalopex culpaeus* and *Lycalopex griseus* between continental Magallanes and Tierra del Fuego Island, and detected that *C. magellanicus* made up 11.7% of the diet of the Grey fox by numerical frequency, but it was preyed on only in the island. The Culpeo fox did not consume this prey in either location. Kusch and Donoso [38] reported that an albino Magellanic Horned Owl (*Bubo magellanicus*) had among its regurgitated pellets numerous remains of *C. magellanicus*.

Interactions with humans

The existing literature on the Magellanic tuco-tuco touches on essentially two topics: (a) The use of *Ctenomys magellanicus* for food, fur, or trade, by the Aonikenk, Selk'nam, and Manek'enk "foot indians" of Patagonia and Tierra del Fuego. (b) The competition for herbage with – and interference by and with– sheep (*Ovis aries*), cattle (*Bos taurus*), and horses (*Equus ferus caballus*).

Magellanic tuco-tuco use for food, fur, or trade, by native peoples

These tuco-tucos were reported to be eaten by "Patagones" (Aonikenk) as early as 1835 by Bennett ([6], page 189) and in 1847 by Gay ([87], page 106). Philippi in 1880 [60], page 276; see [86] for his overall contribution on Chilean vertebrates], when describing *Ctenomys fueginus*, reported that (my translation from German): "This mouse is the main food of the inhabitants of that island –just as before the arrival of the Spaniards, the Chileans took their meat mainly from the degu, Octodon Degus [*sic*] Waterhouse. The inhabitants of eastern Tierra del Fuego catch this rodent mainly with their dogs." He was

reaffirmed by Ohlin ([53], page 177), who stated that "It forms one of the chief articles of food of the Onas Indians, whose women are very skilful [*sic*] in catching it." Onas are more properly named Selk'nam. Señoret ([70], page 21) also stated (my translation from Spanish): "The cururo, a species of mouse, used to be their main food." Carlos Gallardo ([25], page 71) reported (my translation from Spanish): "The tucutuco, together with fish and birds, is the basis of the diet of the ona [*sic*] of the north and northeast." Wolffsohn ([84], pages 62–64) stated (my translation from Spanish):"The *ctenomys* are considered good to eat, not only by the 'ona' indians who live almost exclusively on their meat, but also by some Europeans, who consider it better than that of rabbits and hares." Bridges ([9], page 444), when referring to the "Aush" (=Manek'enk) reported that "For food they relied more on seal and shell-fish, which were abundant round the coast, and less on the *apen* (tucu-tucu), which was comparatively scarce in their swampy country." And also that (page 452) "As food the tucu-tucu were a delicious change from guanaco meat, but their tiny bones were so brittle that one had to be careful when eating, lest the splinters got into one's tongue or gums." Gilmore ([27], page 373) stated that "This animal is a burrower in colonies, is of rat size, and can be captured by hand. It was used for food by the *Ona* and *Tehuelche*." (meaning Selk'nam and Aonikenk, respectively).

Gusinde ([29], page 92) stated (my translation from Spanish): "As indispensable for the economy of the northern Selk'nam, two species of rodents (*Ctenomys*) are pivotal, known by the names of tucutuco and cururo; they are properly steppe animals. Similar to the grey rat, although a little finer, it burrows a wide expanse of land and lives underground. Since sheep ranching began in this region, these rodents headed south [*sic*]. Much more important than the cururo for the indigenous people of the northern half of the Isla Grande is the guanaco for those of the southern half, where there are no cururos, and from these profound differences emerge economic consequences." He ([29], page 95) also stated "Although the Selk'nam constitute a single tribe, they are subdivided into three local groups. Said subdivision has its origin in economic causes, coming from the particularities of the land. The groups of families settled in the flat area of the north lived preferentially from the numerous small rodents, for which they were nicknamed by their neighbors to the south with the adjective 'cururo-eaters.' The second, southeastern group, also called 'Haus,' may represent the core of the first wave of settlers on the continent. Because they live on rocky shores, their dependence on marine animals is greater than that of the third group, the 'people of the south,' who feed solely on guanaco." By Haus he meant Manek'enk. Almost in closing ([29], pages 170–171), he reiterated "The interior of the Isla Grande is home to the cururo in the north and the guanaco in the south as usable game animals. For the sustenance of the indians, the different species of birds found in the swamps and on their long coasts scarcely come into consideration, and plant-based foodstuffs are completely lacking. Guanacos and cururos determine, therefore, the guiding characteristic of the Tierra del Fuego economy. The hunting and use of these animals absorbs the life of the Selk'nam and ensures the existence of each and every one in particular." And finally, Gusinde ([29], page 183) stated: "Only free hunting makes it possible for our indians to exist on the Isla Grande. Because the flora can offer them absolutely nothing, they live exclusively depending on their game animals. Therefore, food is as simple as possible: the meat of the guanaco or cururo is roasted over the fire in the hut, without the slightest preparation."

The use of tuco-tuco furs is scarcely mentioned in the literature. Only Gusinde ([29], pages 178–179) reported (my translation from Spanish): "The indian women make their large fur cape with several pieces of the same material [skins], sewn together with sinew threads. The people of the north need about 40 to 60 skins of the small cururo for such a coat." He is referring to the Selk'nam people. Indeed, in the Museo Histórico y de Ciencias Naturales Monseñor Fagnano in Río Grande city, Argentina, there is a cape or "quillango" made of such skins. The use of tuco-tuco as trade currency is also reported only by Carlos Gallardo ([25], page 272) (my translation from Spanish): "In each tribe there is an indian who, due to his greatest skill, perseverance, and patience, has become a specialist in the making of bows and arrows; it is to him that friends go to obtain the weapons they need, rewarding his service with gifts consisting of meat, leather, etc. Such is the fame acquired by those made from woods of the south, that the indians of the north offer smoke-and wind-dried tucutztcos wind in exchange for half-finished arrows, a trade that the indians of the south carry out with pleasure." Tucutztco is a strange rendering of tucutuco.

The consumption of *C. magellanicus* may be quite old. Santiago et al. [69] found that in Las Vueltas 1 archeological site in Argentine Tierra del Fuego (between San Sebastian Bay and Río Grande city; see map in page 214), out of 2191 skeletal elements recorded, 1488 remains belonged to this species. They commented that, from a taphonomic perspective, a large number of those remains may have entered the archaeological assemblage through actions by avian raptors, mammalian carnivores, or as a result of natural death in burrows. Nevertheless, although to a lesser extent, they also detected evidence of human consumption and discard of tuco-tucos by early settlers from as far back as 3220 to 539 years before present.

Andrade and Boschín [2] framed most of the above within an anthropological-ethnographic perspective. They made taphonomic analyses of Patagonian and Fuegian small mammal assemblages (which included tuco-tucos in high proportion) and reviewed historical and ethnographical documents. They proposed that some species of *Ctenomys* were rather intensively exploited by hunter-gatherer societies who lived in Fuego-Patagonia since the late Holocene. Bones, meat, and skin of tucotucos were used, and Andrade and Boschín (2015) considered it likely that this use continued until last century (see above paragraphs for the evidence I gleaned). In addition, they verified that such activity was differentiated by sex and age of Aonikenk and Selk´nam peoples, and linked with biological and social aspects of their lives. Indeed, the use of small mammals (including tuco-tucos) and its predilection by Fuegian-Patagonian populations was recorded since the first contact episode back to 1520 ([61]; see [14]). Andrade and Boschín [2] further affirm that for Selk'nam people in northern Tierra del Fuego, the Fuegian tuco-tuco *C. magellanicus* was not only one of the main food items, but it was considered a delicacy.

Magellanic tuco-tuco interference by and with sheep, cattle, and horses

As stated above, no assessments of exploitative competitive interactions have ever been made among tuco-tucos, sheep, cattle, and horses, which all are introduced herbivores. But there is a wealth of anecdotal evidence on interference interactions between the native and the aliens.

As early as 1896, Señoret ([70], page 11) in his report on Tierra del Fuego Island stated (my translation from Spanish): "The cururo used to populate all the flat regions of Tierra del Fuego. Due to the establishment of sheep and cattle ranches, it is rapidly being destroyed." A few years later, Wolffsohn ([84], pages 62–64), referring to both *Ctenomys magellanicus magellanicus* in Patagonia and *Ctenomys magellanicus fueginus* in Tierra del Fuego, reported that the introduction of sheep in these two regions resulted in the extermination of tuco-tucos in many parts, where all that was left were their empty burrows. And that on Tierra del Fuego Island, where sheep had been removed during one or several seasons, the fields were rapidly repopulated by tuco-tucos.

The travels of Emilio Budin in 1927–1928 along Argentina were narrated by Barquez and Pardiñas ([5], page 25). With reference to *Ctenomys magellanicus* in arroyo de los Perros, Santa Cruz province, they cited Thomas verbatim ([81], page 43): "Sr. Budin states that this species is now almost exterminated, owing to the fact that the introduced sheep, by piercing with their pointed feet the crust of snow above the burrows, have caused the death of the tuco-tucos by the resulting wet and cold thus allowed to enter." Barquez and Pardiñas ([5], page 25) also commented that (my translation from Spanish): "Everything seems to indicate that, in vast portions of Patagonia, this fossorial rodent has been deeply damaged, with special impact in sub-Andean and southernmost sectors (Tammone et al. 2018). Our recent surveys in the area of Arroyo de los Perros, as well as in the entire upper basin of the Santa Cruz River, are consistent in pointing out the absence (or, at least, rarity) of *Ctenomys* populations."

Osgood ([55], pages 117–118) was the first to make explicit statements about potential competition for forage between the Magellanic tuco-tuco (*Ctenomys magellanicus magellanicus)* and sheep (*Ovis aries*): "Practically the whole of southern Patagonia east of the mountains is now in private ownership completely fenced and devoted to sheepraising. That the extinction of an animal like *Ctenomys* is welcomed by the sheep owners is natural, not only because of its effect on the forage, but because its burrows are a hazard to horsemen. The extinction, however, has required no effort on their part, the mere presence of the sheep being sufficient to accomplish it. It might be supposed that the rodents would retreat into the few areas not frequented by the sheep, but there is little evidence that this has taken place with much success. During the summer season a certain number may be trampled to death by the sheep, but the burrows, in most cases, seem too deep to fail to give considerable protection. In drives of sheep as many as 50,000 closely packed animals often passed over long stretches of grassland, and, in such cases, according to report, the pugnacious *Ctenomys* sometimes came out of their burrows and actually attempted to attack the sheep. It is related as not uncommon to see a sheep with a wriggling *Ctenomys* dangling from its nose, probably to the great discomfort of the sheep and doubtless with ultimate fatality for the rodent. No doubt the highest mortality comes in winter and early spring when the passing hoofs would open up the burrows sufficiently to let in snow water, and what this did not accomplish directly would soon be finished by alternate freezing and thawing."

Gusinde ([29], page 92) reported: "Desde que empezó en esta región la cría del carnero, se encaminaron estos roedores hacia el sur." Meaning that in Tierra del Fuego Island since the beginning of sheep farming, Fuegian tuco-tuco "moved" to the southern part of that island. The wording is problematic, implying that the rodent fled away from stocking sheep. In page 100, he further stated: "Cuando los hambrientos indios se aproximaban a los cercados, eran recibidos a tiros por los guardas y pastores. Los guanacos y cururos habían sido ahuyentados por los intrusos blancos y en su mayoría aniquilados; en su lugar pastaban ahora miles y miles de carneros

-los "guanacos blancos", como se les llamaba-." That is (my translation from Spanish): "When the hungry indians approached the fenced sheep enclosures, they were greeted with shots by the guards and herdsmen. The guanacos and tuco-tucos had been driven off by the white intruders and mostly wiped out; in its place now thousands and thousands of sheep grazed -the 'white guanacos'- as they were called."

Bridges ([9], page 452) stated "They burrow fairly deep, but come up near the surface for their sleeping-quarters. This is their undoing, for once the land is stocked with sheep or cattle, the nests –unless they happen to be beneath a rock or under the roots of strong bushes or trees– are trodden in and destroyed, together with their occupants." Godoy ([28], page 208), from quite a contrasting perspective stated that: "En la Patagonia, en donde son conocidos por cururú, al parecer han aumentado considerablemente sus colonias en algunas zonas, especialmente en Neuquén y Santa Cruz, causando una justificada preocupación de los ganaderos." That is, tuco-tucos have increased considerable their colonies in Neuquén y Santa Cruz, causing justified concern from livestock ranchers.

Mann ([43], pages 304–307) stated (my translation from Spanish): "Sheep farming, which reaches such extreme extension and intensity in many sectors of the Patagonian steppe, is responsible for the disappearance of *Ctenomys magellanicus* over large sectors that once harbored it. Thus, since 1920, the Magellanic tuco-tuco is no longer found in the pampas that surround Punta Arenas. Its armies of hundreds of thousands of individuals, which undermined the land until they transformed it into true sieves, dangerous traps for the horseman, were eliminated by the trampling of the flocks of sheep, which clogged the entrance holes to their galleries." He then added: "Day by day the importance of *Ctenomys magellanicus* for humans decreases, due to the rapid extermination it suffers due to the action of flocks of sheep that block and destroy with their thousands the entrance holes to the underground galleries of theses rodents. With this, the problem posed by the land undermined by its galleries for horses and riders alike has already completely disappeared." Finally, Massoia and Chebez ([49], page 121) stated (my translation from Spanish): "… currently the Fuegian tuco-tuco faces serious setbacks in vast sectors of its distribution area due to sheep."

Milton Gallardo ([26], page 77), visited Riesco Island in 1976 and contemplating the absence of *Ctenomys magellanicus dicki* discussed (my translation from Spanish): "Probably the intense grazing to which these areas are currently subjected, in addition to other factors, have influenced the disappearance of the colonies that Osgood already described as scarce." Prosser-Goodall ([63], page 88) writing about Tierra del Fuego Island declared "A small rodent, the cururu or tuco-tuco (*apen* in Ona), nearly became extinct because of the sheep, but is now becoming common again on the plains." One wonders if the sheep had declined in the Tierra del Fuego of the 1970s and this had resulted in a recovery of tuco-tuco populations.

Particularly for horses and horse riders, the tuco-tuco was a nightmare of old. Darwin ([17], page 50) stated "Considerable tracts of country are so completely undermined by these animals, that horses, in passing over, sink above their fetlocks." Similarly, Fitz Roy ([23], page 107) reported "Many accidents happen to the horses in these hunts, owing to the ground being so undermined, in some places, by the 'tucu-tucu,' a little animal like a small rabbit; but the riders are so skilful [*sic*], that they generally save themselves, however awkwardly their horses may fall." Skottsberg ([73], page 189) narrated "Without suspecting anything you come along at a canter; suddenly the horse goes through with his front legs. You had better proceed cautiously or you will easily get your horse hurt." But later, Massoia and Chebez ([49], page 121) stated (my translation from Spanish): "Although up to a few years ago horse and horse-rider falls in the land filled with its burrows were common, currently the Fuegian tuco-tuco faces serious setbacks in vast sectors of its distribution area due to sheep." This implies that because sheep had led tuco-tucos to decline, this has resulted in less risk for horses breaking their legs.

Abundance and conservation

In Chile, MMA [51] considered that *Ctenomys magellanicus dicki* is extinct, and that *C. m. fueginus*, *C. m. magellanicus, C. m. obscurus,* and *C. m. osgoodi* are all vulnerable. In Argentina, Bidau [7] listed *Ctenomys magellanicus* as a whole in the Least Concern category, essentially because of its large geographical range and many currently occupied localities. Nevertheless, he commented that there was concern about its population decline inferred from over-exploitation, shrinkage in distribution, and habitat destruction and degradation due to sheep grazing. But he added that the latter disturbance was not currently occurring at a rate enabling to qualify this species in the Threatened category.

Was the Magellanic tuco-tuco a more abundant species in the past? Witness the following writings: Ohlin ([53], page 177) declared "The troublesome little 'tuco-tuco' (*Ctenomys magellanicus*) is extremely abundant in the northern and eastern parts of Tierra del Fuego, and in the pampas of southern Patagonia…" But Señoret [70] already raised a red flag by stating (my translation from Spanish): "The cururo used to populate all the flat regions of Tierra del Fuego. Due to the establishment of sheep and cattle

ranches, it is rapidly being destroyed." Wolffsohn ([84], pages 62–64), referring to both *Ctenomys magellanicus magellanicus* in Patagonia and *Ctenomys magellanicus fueginus* in Tierra del Fuego, stated that (my translation from Spanish): "Despite the introduction of sheep having exterminated this rodent in many parts, there are always in both parts, countless burrows that reveal their presence. On the Island of Tierra del Fuego, there are parts left without their endowment of sheep during one or several seasons, which are rapidly populating with 'cururos,' as these species are commonly called there."

From an anthropological perspective, Carlos Gallardo ([25], page 71) felt confident to state (my translation from Spanish): "The tucutuco, together with fish and birds, is the basis of the diet of the ona [*sic*] of the north and northeast." Gusinde [29] went even further, declaring that the tuco-tuco were the chief sustenance of the Selk'nam in northern Tierra del Fuego, and that their southern relatives laughed at them for being "cururo eaters" while they were "guanaco-eaters" [9, 10]. Indeed, Martinic ([47], page 233) puts forth that the same techniques for hunting *Ctenomys* used by both Aonikenk and Selk'nam peoples speak to their common ancestry.

Osgood [55] collected small mammals in continental Magallanes and Tierra del Fuego Island from December 1939 to February 1940 and thus provided an exceptional state-of-the-art for the distribution and abundance of the then four recognized subspecies of *Ctenomys magellanicus*. This is an unusual benchmark, issued simultaneously by the same researcher.

He ([55], pages 117–118), speaking of *Ctenomys magellanicus magellanicus,* described "Range. Extreme southern Patagonia east of the mountains, from the Straits of Magellan northward to the vicinity of the Santa Cruz River on the east and Lake Argentine on the west. Rare or extirpated over most of this area. This animal, the first Chilean *Ctenomys* to be described, is now either quite extinct or so near it that its preservation beyond a few years is very unlikely. As late as the summer of 1927–28 when Budin collected at Punta Arenas and elsewhere within its range it had become so scarce that he was unable to find it except at one locality considerably north of the Straits at Rio Perro, at the north end of Lake Argentine," … "In 1940 Mr. Sanborn and myself made every effort to find it at various localities but without success. Everywhere we received reports of its former abundance and, in some cases, explicit testimony as to its occurrence in small numbers at specific localities within five years, but on visiting these places only abandoned burrows were found. One such place was on the bay of San Gregorio, the type locality, where it seems to have persisted until very recently. According to report, one of the regions where it was once excessively numerous was toward the northern end of the Straits near the boundary between Chile and Argentina, on the estancia Monte Dinero. Practically the whole of southern Patagonia east of the mountains is now in private ownership completely fenced and devoted to sheepraising. That the extinction of an animal like *Ctenomys* is welcomed by the sheep owners is natural, not only because of its effect on the forage, but because its burrows are a hazard to horsemen. The extinction, however, has required no effort on their part, the mere presence of the sheep being sufficient to accomplish it. It might be supposed that the rodents would retreat into the few areas not frequented by the sheep, but there is little evidence that this has taken place with much success."

Osgood ([55], pages 119–120), this time speaking of *Ctenomys magellanicus fueginus,* described "Range. Northern and eastern Tierra del Fuego, now reduced to small, scattered, and greatly isolated colonies. Although *Ctenomys* were not found on the north side of the Straits in 1940, they were discovered in some numbers at a few localities on Tierra del Fuego. Here they have persisted longer than on the mainland but their fate is sealed and within a very few years doubtless they will be gone. A small colony of some two dozen burrows was found occupying a gravel ridge just back of the beach between Cape Penas and Via Monte on the north shore of the island. Another group, slightly smaller, was encountered near the road leading from Via Monte to Lake Fagnano and about ten miles north of the east end of the lake. Signs of considerable numbers were seen also just west of San Sebastian on the road leading to Cullen. Otherwise, during several hundred miles of travel on Tierra del Fuego no signs of *Ctenomys* were seen. According to the testimony of residents of the island their numbers in former years were incalculable."

He ([55], pages 120–123), now speaking about *Ctenomys magellanicus osgoodi*, reported: "Range. Valleys along the eastern base of the Andes from westcentral Santa Cruz, Argentina, northward to west-central Chubut, passing locally into Chilean territory. This form has heretofore been regarded as a species distinct from *C. magellanicus*, but its obviously close relationship seems best indicated by the subspecific status. It differs mainly and rather markedly in color, but this, as noted by Allen in his report on the original series of 23 specimens, is subject to some variation. A considerable area, unrepresented by specimens, lies between the southernmost localities for *osgoodi* and the northernmost ones for *magellanicus*." In this case, Osgood did not refer to its abundance, as above.

Osgood ([55], pages 123–124), finally referring to *Ctenomys magellanicus dicki*, stated: "Type from Estancia Ponsonby, east end of Riesco Island, Magallanes, Chile. No. 50734 Field Museum of Natural History.

Adult male. Collected February 2, 1940, by Colin C. Sanborn. Orig. No. 2401. Diagnosis. Similar in general to *C. m. magellanicus*, but differing widely in color, being wholly mixed blackish and buffy Smoke Gray both above and below." … "Remarks. This very distinct form is doubtless confined to the eastern part of Riesco Island where it is already rare and difficult to obtain. Although this part of the island is not forested, it has but little open grassland, being largely covered with a heavy growth of the "mata negra" or black brush (*Chiliotrichum diffusum*). During a few days' stay in this region we were able to obtain only two specimens, an adult male and female, these apparently being the only occupants of a small area where about a dozen burrows were found." … "The channel separating Riesco Island from the mainland is deep and permits the passage of vessels of considerable size, but at one or two points it is quite narrow, perhaps not more than a few hundred feet."

Less than four decades later, Milton Gallardo [26] reported (my translation from Spanish): "*Ctenomys magellanicus dicki* Osgood. The locality for which Osgood describes this subspecies was visited in January 1976. Although there was a guide who remembered the places that Osgood visited on Riesco Island, it was not possible to find any footprints, even old ones, indicating the existence of *Ctenomys* on the island. Probably the intense grazing to which those areas are currently subjected, in addition to other factors, have influenced the disappearance of the colonies that Osgood already described as scarce. For these reasons, *Ctenomys magellanicus dicki* Osgood is considered extinct." Complementing the preceding, Simonetti and Stipicic ([72], page 12) discussed (my translation from Spanish): "Osgood (1943) describes the subspecies *Ctenomys magallenicus dickii* [*sic*] with two specimens collected at Estancia Ponsonby in 1940, which he describes as confined to the eastern sector of the island, where he indicates that they are rare despite the existence of their numerous burrows. Carlos Hoffmann reports observing a dead specimen in the same area in 1928 (Martinic, 2005). The presence of burrows but the scarcity of specimens was already observed in 1877, on the continental coasts of the Otway and Skyring inlets (Ibar, 1878; see also Latorre, 1879), where *C. magallenicus* [*sic*] has not gone extinct as would the *dickii* subspecies on Riesco Island. Thus, while Miller et al. (1983) indicate that *C. m. dickii* would be rare, without providing further information; Gallardo (1979) in 1976 found no trace of *Ctenomys* in the same area where Osgood (1943) obtained the specimens on which he described *C. m. dickii*, thus declaring it extinct. Gallardo (1979) attributes its disappearance to intense grazing and other possible factors. The subspecies has been declared Extinct in the Classification of Species according to their Conservation Status (MMA, 2013)."

Almost six decades after the report by Osgood [55], Venegas and Sielfeld ([82], page 89) issued their own status report (my translation from Spanish): "*Ctenomys magellanicus* Bennett, 1835. Magellanic Tucotuco, Magellan Tucotuco. Patagonia. In the region, represented by four subspecies. The nominal, in low and high steppe environments on the eastern slope of the provinces of Ultima Esperanza and Magallanes. Listed as 'Endangered' by Glade (1993), but apparently in recovery. The subspecies *C. m. dicki* Osgood, 1943, from Riesco Island corresponds to a taxon in the 'Extinct' category (Glade, 1993). The subspecies *C. m. fueguinus* [*sic*] Philippi, 1880, from Tierra del Fuego, is very common and abundant in the north and central area of the island. Finally, the subspecies *C. m. obscu*rus was described by Texera (1975) on the basis of specimens from the center-south zone of Tierra del Fuego." It should be noted that the latter subspecies is now considered to be part of *C. m. fueginus*. In a nutshell, according to Venegas (Sielfeld [82], *C. m. magellanicus* was recovering from past population lows, while *C. m. fueginus* was thriving.

More recently, MMA [51] considered that *Ctenomys magellanicus dicki* was extinct, and that *C. m. fueginus*, *C. m. magellanicus, C. m. obscurus,* and *C. m. osgoodi* were all vulnerable: (a) Because of their reduction in population size and because this reduction has been ca. 30% in the last 10 years (as inferred from a reduction in habitat quality due to sheep trampling). (b) Because their occupation area is less than 2,000 km^2; because they exist in fewer than 10 locations; and because their decrease in habitat quality is due to degradation by human endeavor (shepherding and subsequent trampling). This is a bleaker picture than that painted 16 years before by Venegas and Sielfeld [82]. Similar conclusions were reached by Sánchez and Lizarralde [99] for *Ctenomys magellanicus* in Argentina.

The final straw for the survival and conservation of this species may be climate change. Lazo-Cancino et al. [104] showed that under different modeling scenarios of temperature and precipitation the spatial distribution of the Magellanic tuco-tuco would always shrink, essentially disappearing from the continental region and surviving in Tierra del Fuego Island, but concentrated in the northeastern part.

Conclusion

What lessons can we draw from incorporating a historical perspective to the study of any chosen species? In this case study on the Magellanic tuco-tuco I dare venture that eye-opening perspectives were gained with the discovery of new populations, subspecies, or species in

little-explored places; but more importantly, on revisiting those same places to witness the changes brought about essentially by human action. The introduction of sheep in 1877 to Isabel Island in the Strait of Magellan [8] and its ensuing spread to surrounding Patagonia and Tierra del Fuego, the killing of guanacos suspected of competing with livestock, and the persecution of native peoples (especially Selk'nam) left important imprints in those regions [46–48]. The entire food web shifted from humans and other predators of tuco-tucos, exploiting an abundant herbivore that presumably competed with native guanacos and kept at some equilibrium with its food plant resources, to an overstocked range, sheep-dominated system that not only competed for gasses with tuco-tucos but also trampled their habitations. Sheep in the whole Magallanes Region (which includes Chilean Tierra del Fuego) increased steadily for a century, from 1877 to 1975, reaching a peak of ca. 3 million and slowly declining for the next 45 years to a current total of ca. 1.5 million [66]. Surely, the decimation of the Selk'nam people by diseases, deportations, and killings was not enough of a predation relief for the rodents: In the mid-nineteenth century there were about 4000 Selk'nam, by 1919 there were 297, and by 1930 just over 100 [29, 48]. The 1906 livestock census revealed the existence of 850,000 sheep, which continued to increase [46]. So, fewer than 4,000 Selk'nam were replaced by ca. 1 million sheep only in Tierra del Fuego! Incidentally, the sheep stocks in that large island have been decreasing because of forage overgrazing, ensuing erosion, and climate change toward less precipitation. But despite that sheep decline, the Magellanic tuco-tuco has not rebound, much less to its original nineteenth century levels. I fear it never will.

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