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Historical account and current ecological knowledge of the southernmost lizard in the world, Liolaemus magellanicus (Squamata: Liolaemidae)

Fabian M. Jaksic[1*]

Abstract

Background The systematics of *Liolaemus magellanicus* has been relatively well researched, but despite its recognition as the southernmost lizard in the world, scant attention has been paid to the discovery, distribution, biogeography, and ecology of this lizard at the southern tip of South America. I hereby research such aspects and collate the most relevant information reported in the primary literature.

Methods and Results I conducted a selective review of the history of discovery, distributional records, biogeography, and ecological features of *L. magellanicus*, as recorded in mainstream journals and landmark monographs and books. I specifically omitted the work on the systematics of the species and genus because its complexity warrants separate treatment. I found scattered references to this lizard starting with the chronicles of several overseas expeditions (British, French, and Swedish), with Darwin, Jacquinot and Guichenot, and Anderson and Ohlin acting as informers; and culminating with Skottsberg, a traveler, and Bridges, an early settler in Tierra del Fuego Island. Modern treatment of this species started with Hellmich in the 1930s and Donoso-Barros in the 1960s in Chile, and with Cei in Argentina in the 1960s and has continued chiefly in the latter country until today.

Discussion I propose this species as a model ectothermic vertebrate that may serve to test hypotheses about: (a) Resource allocation strategies to deal with a harsh environment that affords limited opportunities for foraging and reproductive activities of a lizard. (b) Behavioral strategies for dealing with thermoregulation, food, and mate acquisition, and care –if any—of offspring. (c) Its place within the rather impoverished food web of which this species forms part of. This relatively new species, which persisted in glacial refuges before being cut off into two subpopulations—one mainlander, another islander—also offers fertile ground for testing population genetic, evolutionary, and phylogeographic hypotheses. I think that biogeographers, systematists, evolutionists, physiologists, and ecologists should take advantage of this uniquely positioned species in the southernmost margin of the world.

Keywords Patagonia, Argentina, Chile, Santa Cruz Province, Magallanes Region, Straits of Magellan, Tierra del Fuego Island, Darwin

*Correspondence:
Fabian M. Jaksic
fjaksic@bio.puc.cl

[1]Departamento de Ecología, Facultad de Ciencias Biológicas, Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, 8331150 Santiago, Chile

Background

This is a selective review of aspects concerning the history of discovery, distributional records, biogeography, and ecological features of *Liolaemus magellanicus*, as recorded essentially in mainstream literature and landmark monographs of old. Specifically omitted is the abundant output of work on the systematics of the species and genus, a discipline in which I am not well versed. My intent is to highlight the most salient aspects of this southernmost lizard in the world, aimed at profiling this species as a model organism that may throw light on how small ectothermic vertebrates deal with a harsh environment such as that found in Patagonia, a rather cold, windy, and certainly remote area of the world. This review is organized into three parts: (a) A historical account of the discovery and expanding records of distribution of *L. magellanicus*. (b) A state-of-the-art status of current ecological knowledge on the species. (c) A preliminary synthesis and prospects for further research on a possible model organism.

Methods

I back-tracked references from current to older sources, using mainstream journals, monographs, and books, and not grey literature. No new sources emerged when searching the internet. I specifically discarded work on the systematics of the species and genus, unless it provided natural history observations, distinguishing between first-hand information and use of literature sources.

Results

Historical account

Darwin [1] (p. 301-02) in his chapter on Tierra del Fuego noticed that "The absence of any species whatever in the whole class of Reptiles is a marked feature in the zoology of this country, as well as in that of the Falkland Islands. I do not ground this statement merely on my own observation, but I heard it from the Spanish inhabitants of the latter place, and from Jemmy Button with regard to Tierra del Fuego. On the banks of the St. Cruz in 50° south, I saw a frog; and it is not improbable that these animals, as well as lizards, may be found as far south as the Strait of Magellan, where the country retains the character of Patagonia; but within the damp and cold limit not one occurs. That the climate would not have suited some of the orders, such as lizards, might have been foreseen; but with respect to frogs, this was not so obvious." Darwin was mistaken, there were lizards on Tierra del Fuego, though represented by a single species, *L. magellanicus* (see below).

Jacquinot and Guichenot [2] provided the first morphological description of a new species of lizard collected by J. Hombron and H. Jacquinot in 1847 at "Havre-Pecket, détroit de Magellan" (Peckett Harbour, ca. 52°54'S, 71°01'W in continental Magallanes; see [3], which they named Proctotrete magellanique (later *Proctotretus magellanicus*). Williams et al. [4] (p. 6) narrated that: "The southernmost lizard in the world, *Liolaemus magellanicus* (Fig. 1.1d), was described in 1847 by two French surgeons and naturalists, Jacques Bernard Hombron and Honoré Jacquinot. We can still find today in Patagonia (in both countries) this species that was collected by them in the expedition Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée (Trip to the South Pole and Oceania on corvettes Astrolabe and Zélée)." Indeed, Plate 2, Fig. 2 of Sauriens in the Atlas of the book depicts quite faithfully an individual of that species.

Boulenger [5] (p. 148–49) in the Catalogue of lizards in the British Museum described morphologically *Liolaemus magellanicus* (sic.) and reported specimens from Cape Gregory, Philip Bay, and Straits of Magellan; the first locality communicated by "C. Darwin, Esq." and the latter two by "Dr. Cunningham." Cape Gregory must refer to San Gregorio, a vague locality centered at 52°19'S 69°41´W about 120 km N of Punta Arenas city (53°10'S, 70°56'W). Philip Bay must refer to Bahía Felipe, a bay on Tierra del Fuego Island, centered at 52°50'S, 69°50'W. Notice the presence of this species in both continental Magallanes and the large island across the Straits.

Ohlin [6] (p. 174) stated that "Again, among vertebrates I should like to call attention to the singular distribution of a lizard, doubtless identical with *Ptygoderus pectinatus*, Dum. and Bibr. (=*Proctotretus magellanicus*, Hombr. and Jacquin.). Darwin remarks that no reptiles have been found at Tierra del Fuego, though they may exist, he says, as far south as the Strait of Magellan. Indeed, even Hombron and Jacquinet mention in their "Voyage au Pole Sud," Zoologie, t. iii., p. 6, the occurrence of a small lizard at Peckett Harbour, on the northern shore of the Strait. Cunningham procured specimens of the same species at Rio Gallegos and many other places in eastern Patagonia, and afterwards observed it for the first time at Philip Bay, on the northern coast of Tierra del Fuego. I myself found it fairly often along the northern and eastern coasts of this great island within the pampas region, and secured two specimens as far south as Rio Grande, lat. 53° 50' S., the most southerly spot on the globe where reptiles are as yet known. Darwin, in fact, advanced the entire absence of reptiles south of the Strait as an argument in favour of his theory that the Strait was to be regarded as the distinct boundary between two entirely different faunas, and that Tierra del Fuego had no, or very few, species of insects, spiders, and other terrestrial animals occurring in Patagonia. In regard to insects, especially Coleoptera, it is mainly by the examination of the valuable collections brought back by the French "Mission scientifique du Cap Horn, 1882-83," that Darwin's view is

proved erroneous. The observations of Cunningham and of myself also contradict his view as to the distribution of reptiles. Although the lizard referred to above evidently belongs to the pampas, it occurs as far west as Punta Arenas, where Cunningham found a specimen, though I was not successful in my search for it." *Proctotretus magellanicus* is an old synonym of *Liolaemus magellanicus*. Peckett Harbour must refer to a harbor on Otway Sound centered at ca. 52°54'S, 71°01'W, facing Riesco Island on the western side of Brunswick Peninsula, about 65 km west of Punta Arenas.

Anderson [7] provided a list of Reptiles and Amphibians (Batrachians or Anurans) collected by the Swedish expedition to Patagonia and Tierra del Fuego conducted in 1895–1896, under the direction of Otto Nordenskjold. Anderson (p. 461) recorded the presence of 3 specimens of *Liolaemus magellanicus* (after Boulenger [5]) collected in continental Patagonia and of other 3 from Río Grande (53°47'S, 67°42'W) in Argentinian Tierra del Fuego Island. Simultaneously, Koslowsky [8] (p. 173] included *L. magellanicus* as part of the Argentinian herpetofauna, reporting its presence in Patagonia from the Strait of Magellan northward to Neuquén Province, but somehow skipping Río Negro Province. He was unaware of its presence in Tierra del Fuego Island, reported by Anderson.

Skottsberg [9] (p. 210−11) travelling at the latitude of Lake Buenos Aires (46°26'S) in Argentinian Patagonia reported that "Between the tussocks many-coloured lizards scurried to and fro, black and yellow, brown with red and white markings or with a copper lustre --always making me think of Pagels, who entertained an inextinguishable passion for these animals. All of a sudden we would see him stop, jump from his horse, and pursue some speedy lizard, that often was caught in his cap, to be afterwards transferred to an old pickle- bottle he carried in his maletas." This is a very generic description of a lizard, which loosely fits *Liolaemus lineomaculatus* on account of the yellow markings and location.

Quijada [10] (p. 29) reported the animal specimens held at the Museo Nacional de Historia Natural in Santiago, Chile, and listed one of *L. magellanicus* from Magallanes and another from Puerto Montt. He did not specify where from Magallanes (then a Chilean province) the former came, and surely the latter is either misidentified or misplaced, as no *L. magellanicus* has ever been recorded so far north or west. Burt and Burt [11] (p. 275) reported the South American lizards held in the collection of the American Museum of Natural History in New York (USA), and listed one *L. magellanicus* from Punta Arenas.

Current ecological knowledge

The first natural history notes on *L. magellanicus* seem to be those made by Hellmich [12] (p. 44): "Distribution and Ecology: *L. magellanicus* inhabits the entire Patagonia from Tierra del Fuego to the territory of Neuquen, according to Koslowsky perhaps with the exception of the Territorio del Rio Negro; the typical habitat is undoubtedly the Patagonian xerophytic steppe. *L. magellanicus* is thus to be regarded as a Patagonian, east-Andean faunal element that invades Chilean territory within the xerophyte steppe itself. How far up the western side of the Andes *magellanicus* occurs is unknown. From the ecologist's point of view, the long Chilean-Patagonian coast can still be regarded as *terra incognita*. Insect remains and flowers of a Patagonian composite were found in the stomach of one examined specimen." [My free translation from the German original]. Noteworthy is the use of the novel term "ecology" and that Hellmich reported specimens from Porvenir (53°18'S, 70°22'W) in Chilean Tierra del Fuego Island.

Bridges [13] (p. 457) stated that "En la Tierra del Fuego, en una extensión de novecientos kilómetros a la redonda, no hay víboras. Las más próximas están en el territorio del Chubut, en la Argentina. Pequeños lagartos hay sólo en la tierra ona, y no existen en ningún otro lugar de la isla principal." That is, there are no snakes on the island, but small lizards are found in Ona (=Selk'nam) land, meaning the grassy steppes of northern Tierra del Fuego Island.

Donoso and Codoceo [14] (p. 32–36) studied the presence of lizards in the Aysén and Magallanes Regions of Chile. They noted that "*Liolaemus magellanicus*, que es la más frecuente, y *Liolaemus lineomaculatus* viven en los bultos de *Festuca*. En cambio *d'orbignyi*, *Leiosaurus darwini* y *Leiosaurus bibroni*, que parecen alcanzar allí su límite más austral, prefieren el matorral constituido por la comunidad *Colliguaya-Berberis*." That is, *L. magellanicus* is more frequent in the open steppe with *Festuca* bunch grass." En cuanto a las adaptaciones homocrómicas, se observa que las especies de *Liolaemus magellanicus* que viven en las proximidades de la costa, tienen una tonalidad más oscura que los que habitan más al Norte. En relación a la temperatura que en esta región es más baja que en Aysén, llama la atención el aumento del melanismo ventral cuyo papel sería semejante, a lo que hemos sugerido con respecto a la pigmentación abdominal de *Liolaemus fitzingeri*. Igualmente vale señalar la constancia de la viviparidad en las especies de esta región." That is, coastal specimens are darker than those from the northerly interior, which is associated to the lower temperature in the latter area. In addition, viviparity is a constant feature. Finally, "Los *Liolaemus* de Magallanes, tienen inclinaciones distintas, *Liolaemus magellanicus* y *Liolaemus d'orbignyi* son insectívoros. *Liolaemuslineomaculatus* es de tendencia vegetariana." That is, the former two are insectivorous while that latter is herbivorous. Donoso and Codoceo specifically reported one specimen

each from Caleta Josefina (4.5 km E of Porvenir town 53°18'S, 70°22'W) and Manantiales (52°37'S, 69°26'W) on Tierra del Fuego Island, and 15 others from continental Magallanes, collected between 1952 and 1956.

Donoso [15] (p. 277–81) provided the following account on the biology of *L. magellanicus*: "La especie es caracterlstican1ente patagónica; se extiende en el territorio chileno desde Balmaceda (Provincia de Aysén) hasta Punta Arenas. Ha sido colectada en Manantiales, Bahía Catalina, Última Esperanza, Laguna Azul, Tierra del Fuego, etc. Es predominantemente insectívora, aunque suele ingerir algunos trozos vegetales. Sus habitat preferidos en la estepa patagónica y magallánica son los cojines de *Mulinun spinosum* y los paquetes de coirón *Festuca*, cuyas variaciones de colorido permiten los fenómenos crípticos." Apart from the collecting localities mentioned, it is worth noting that the species is labeled as insectivorous but with some plant consumption, and that its preferred habitat is *Festuca* bunch grass and *Mulinun* cushion plant. He added that "Las formas distribuidas en las proximidades de la costa son más oscuras. Algunos ejemplares colectados en Balmaceda (Aysén), tenían tonos amarillento claros. De reproducción vivípara, la hembra pare dos hijuelos en el verano." That is, coastal specimens are darker than those from the interior, and they are viviparous, producing two young during summer. Finally, that "Las poblaciones de esta lagartija tienen grandes variaciones. En El Paine y Última Esperanza, zonas menos rígidas climáticamente, son más abundantes. En Tierra del Fuego son extraordinariamente escasas; la mayoría de los habitantes ignora incluso su existencia." They are more abundant in continental Magallanes than in Tierra del Fuego Island, where they are so scarce that most inhabitants ignore their existence.

Cei [16] (p. 423–24), based on his expeditions to Santa Cruz Province in Argentina (conducted 1969–1970) stated that "Las formas del grupo *magellanicus* viven en Santa Cruz en las estepas frías de *Stipa y Festuca* alternadas con verbenales *(Verbena tridens)*, propias del sur patagónico. Son relativamente resistentes al frío, escondiéndose bajo piedras y troncos en los días más lluviosos. Frecuentan a menudo los alrededores muy húmedos de los arroyos como hemos observado en el arroyo Las Vizcachas, a pocos kilómetros de los nevados permanentes de los cerros fronterizos. La alimentación es omnívora, pero prevalece una dieta de insectos y otros artrópodos. El contenido estomacal de un ejemplar de *Liolaemus magellanicus* (Bellavista, Santa Cruz, 20-1-1970) indicaba restos de coleópteros (curculiónidos, cuatro individuos; carábidos, escarabeidos), ortópteros, otros restos de artrópodos no reconocibles, y residuos vegetales (fibras, etc.). Ambas formas son ágiles y agresivas, mordiendo sin excitación cuando son agarradas o provocadas. That is, they live in cold steppes populated by bunch grasses and verbena herbs, take refuge under rocks or logs when it rains, frequent wet areas along streams, are omnivores but with preponderance of insects and other arthropods in their diet. One specimen examined had beetles, grasshoppers, unidentified arthropods, and plant fibers in its stomach. They are agile and aggressive, biting their captor. Cei went on to say that "Estos *Liolaemus* son vivíparos, como es natural en reptiles de aquellas latitudes. La mayoría de las hembras capturadas entre el 15 y 22-1-1970 se encontraba en estado de preñez, y aproximadamente 15–20 días después, en febrero, aparecieron sus crías, en nuestro laboratorio. Es asombroso el número de neonatos en cada parto, en relación con el tamaño de estas especies. Dos hembras de *L. magellanicus* procedentes de arroyo Vizcachas parieron el 30-1-1790 y el 3-II-1970, respectivamente, 9 y 5 lagartijas… Los recién nacidos, apenas liberados de las envolturas embrionarias, son ágiles y activos, manifestando de inmediato su natural agresividad." That is, they are viviparous and quite prolific, with 5 to 9 young each of two females. The just born lizards are active and agile and already aggressive.

Bottari [17] (p. 211–13) reported the presence of *L. magellanicus* on the Argentinian side of Tierra del Fuego Island, based on field observations made during January 1974 essentially around the Atlantic-facing coastal city of Rio Grande (53°47'S, 67°42'W): The inland locality of Estancia San José (65 km to the SE, at the Chilean border). And the coastal localities of Misión Salesiana La Candelaria (10–13 km to the NW), Estancia Las Violetas (20–25 km to the NW), and Cabo San Pablo (85–90 km to the SE). The latter represented the southernmost distribution (54°17'S) recorded in Argentina for *L. magellanicus.* The inland habitat was a steppe with *Festuca* bunch grass and scarce *Empetrum* crawling shrubs on a black soil with little sand. The coastal habitats had *Acaena* dwarf shrubs, *Empetrum* crawling shrubs, and *Azorella* cushion plants, under which the lizards took shelter. The soil was grey and finely sandy. Bottari commented "De todas maneras, se ha podido confirmar que la especie, aun en la opinión de los observadores, es de muy baja frecuencia, manteniéndose probablemente en esos especializados parajes, por estar provista de mecanismos fisiológicos de adaptación que merecen ser particularmente estudiados como la resistencia a temperaturas bajas extremas y elevado índice de humedad." That is, the species is scarce, and able to survive in such harsh environment because of adaptive physiological mechanisms (needed to be studied) that enable it coping with such low temperature and high humidity.

Jaksic and Schwenk [18] reporting on *L. magellanicus* stated that "This species is distributed in Chile from Balmaceda (45°55'S, 71°41'W) south to Punta Arenas (53°09' S, 70°55' W) and to Tierra del Fuego Island, where it is the

only lizard present (Donoso-Barros, 1966; see Instituto Geográfico Militar, 1970, for a map). Most of the records from neighboring Argentina are in Santa Cruz Province (Cei, 1971), but Bottari (1975) reported the presence of *L. magellanicus* also on the Argentinian side of Tierra del Fuego Island, between latitudes 53°35'S and 54°17'S. Both Donoso-Barros (1966) and Bottari (1975) suggested that this species is extremely scarce on the island. Its presence on Tierra del Fuego is of particular interest due to the stringency of the environment; cold temperatures prevail nearly all year and snow cover is present half the year." They went on to report that "This species is patchily distributed in areas of coastal scrub and coastal steppe, reaching high local densities. Two color morphs are described: grey-olivaceous and green. Color dimorphism is not related to sex or body size of adults; all neonates are grey olivaceous. Reproductive maturity appears to occur at snout-vent lengths of >48 mm for males and 60 mm for females. Females are ovoviviparous, having a relative clutch mass of 0.322 (mean for five specimens) and a mean litter size of 5.5 neonates (range 3–8). Birth occurs during the midsummer (January and February), probably 1 year after copulation. Based on a sample of feces and a single stomach, *L. magellanicus* appears to be largely or entirely herbivorous, despite its small size (ca. 6 g). Field cloacal temperatures (mean for 20 specimens=27 C) are significantly lower than for central Chilean species of *Liolaemus*." Finally, that "*Liolaemus magellanicus* was found at only two localities on Tierra del Fuego, Onaisin (53°24'S, 69°19' W, about 2 m above sea level, 98 km east of Porvenir city), and Cabo Espiritu Santo, at the lighthouse (52°40'S, 68°37' W, 67 m above sea level, 70 km east of Cerro Sombrero city). Both collecting sites (about 91 km apart) are less than 200 m from the coastline, but differ in their physiognomy, vegetation and soil. The vegetation at Onaisin is coastal scrub with sparse dwarf shrubs and cushion plants dominated by *Mulinum* sp.; the soil is sandy and heavily mined by the fossorial rodent *Ctenomys magellanicus* (Ctenomyidae). Cabo Espiritu Santo supports a coastal steppe homogeneously covered by the bunchgrass *Festuca* sp.; the soil is sandy-clayish and fossorial rodents are absent."

Cei [19] (p. 264) pointed out: "Distribución - En gran parte de la prov. de Santa Cruz y en Tierra del Fuego, donde nunca llega a ser abundante. De las cercanías de la Cordillera hasta la costa. Biología - Lagartija típicamente patagónica, prefiere ambientes esteparios, con vegetación baja y espinosa, o coironal de *Festuca*. Insectívora, pero puede integrar su dieta con vegetales; vivípara, llega a dar a luz hasta 7–9 crías en una sola postura (lám. 12)." That is, largely distributed in Santa Cruz Province, Argentina and in Tierra del Fuego, where it is never abundant. From the Andes Ranges to the Atlantic coast. It prefers steppe environments, with dwarf and spiny shrubs or *Festuca* bunch grasses. It is insectivorous, but it also takes plant material, and viviparous, producing up to 9 young in a single clutch. Indeed, Plate 12 shows a picture of a female surrounded by nine newborn lizards. After this report, almost a 20-yr hiatus occurred before a new publication even mentioned biological aspects of *L. magellanicus.*

Pincheira-Donoso and Núñez [20] reviewed the systematic status of the genus *Liolaemus* in Chile and provided the following natural history statement (p. 302-03) about *L. magellanicus*: "La historia natural de esta especie ha sido estudiada en detalle por Cei (1971) y Jaksic y Schwenk (1983), artículos a los que remitimos a los lectores. En términos generales, la biología de esta lagartija se caracteriza por sus hábitos típicamente patagónicos; selecciona hábitats esteparios constituidos por biocenosis de vegetación baja, de coironal de *Festuca* o cojines del género *Mulinum*. Según Donoso-Barros (1966) su abundancia poblacional muestra notables diferencias, siendo en Última Esperanza muy frecuentes, y decayendo hacia Tierra del Fuego, donde su hallazgo es muy ocasional, habiendo desconocimiento de su existencia aún por los lugareños. De reproducción vivípara, las hembras paren entre dos y nueve crías en una sola postura, la que se efectúa en verano. Dieta constituida principalmente por insectos, aunque consume también vegetales." Thus, they reported previous findings by the authors cited above, but did not provide further natural history information.

In Argentina, Breitman et al. [21, 22] examined the phylogenetic relationships of the *Liolaemus lineomaculatus* section wherein *L. magellanicus* belongs (see also Abdala et al. [23]), but apart from providing maps of collection sites, they did not report natural history observations on the latter species. It took until Ibargüengoytía et al. [24] to add further ecological context to knowledge of *L. magellanicus*. They studied the thermal biology of 16 specimens of this species captured in February 2007 and 2009 in two localities (50°28'S, 72°16'W and 51°56'S, 70°24'W) of Santa Cruz Province in Argentinian Patagonia. They determined the efficiency of thermoregulation of this species by measuring activity body and ambient temperatures in the field, as well as preferred body temperatures in the laboratory. The species was found to be a constrained thermoconformer, which had the lowest body temperature among all known species of the genus when tested in the field, but its preferred body temperature was similar to that of other species within *Liolaemus*. According to the authors, these data indicated that *L. magellanicus* had not yet evolved appropriate physiological adjustments to face the extreme thermal challenges of its environment. Indeed, the climate at 51–52°S latitude imposes a relatively short activity season that challenges the ability of lizards to compensate for low temperatures by lengthening their activity time, thus forcing the use of behavioral thermoregulation to raise body temperature

above that in the environment. *L. magellanicus* did not show noticeable color shifts either, as other *Liolaemus* species do, to enhance the absorption of radiant heat. Instead, the only possibility left for these lizards seems to be an opportunistic thermoregulatory behavior taking advantage of sunny spots whenever possible. See Medina et al. [25] for a review of *Liolaemus* thermal biology, which briefly covers *L. magellanicus*.

Along the same vein, Fernández et al. [26] studied the performance and thermal sensitivity for sprinting at different body temperatures, of *L. magellanicus* collected at the same two localities as above. The speed of sprints and of sustained runs was measured in the field to determine the physiological performance of lizards at different air temperatures and their speed increased with ambient temperature in both cases. The difference between normal speed and that at higher temperature suggests that this species has colonized its current environs recently, and that it has not had enough time for its physiological mechanisms to evolve and achieve a maximum performance at the low temperatures it has to normally face.

Fernández et al. [27] analyzed the reproductive traits of *L. magellanicus*, focusing on the females of the species, collected at the same study sites as above. They presented data on body size at sexual maturity, litter size, and fat-body cycle. They reported that females were active for a period restricted to spring and summer, when vitellogenesis, pregnancy and birth take place. Females started vitellogenesis in late spring, probably arrested or continued at very low rates during brumation, and resumed in the spring of the following year. Pregnancy started in spring and births of 3 to 4 offspring occurred over one month in midsummer. Females that gave birth earlier could then start a new vitellogenic cycle before autumn and thus performed an annual reproductive cycle. Instead, females that give birth later, delayed the start of a new vitellogenic cycle until the following spring, thus performing a biennial reproductive cycle. Accordingly, females had the potential to adjust their frequency of reproduction depending on the energetic restrictions imposed by their environmental conditions.

Fernández et al. [28] retook the issue of reproductive traits of *L. magellanicus*, but this time focusing on the males of the species. Using gonadal histology and morphological analyses in the laboratory, they described the male reproductive biology, fat storage, and sexual dimorphism of specimens collected within the same area as before. They showed that the lizards were reproductively available during the entire five-month activity season. Males exhibited greater body size than females, while females showed larger inter-limb length, which the authors interpreted as selection for fecundity, by increasing abdominal space available for a larger litter size. The continuous sperm production throughout the activity season allowed males to mate at any time when females happened to ovulate, thus representing a selective advantage to deal with the short activity season and the adversities of the cold environment these lizards inhabited. All of the above papers by Fernández (including that by Ibargüengoytía et al. 2010) were part of her doctoral training at Universidad Nacional del Comahue, Centro Regional Universitario Bariloche, Rio Negro Province of Argentina. See also Fernández [29].

The most recent contributions to Patagonian lizard diversity, systematics, biogeography, and biology are to be found in the book edited by Morando and Ávila [30], but only two chapters touch very briefly on *L. magellanicus*: That by Minoli et al. [31] on biogeography, ecology, and spatial patterns of Patagonian lizards, and that by Williams et al. [4] on the history of discovery of Patagonian lizards; the chapter by Kacoliris et al. [32] on conservation concerns about the southernmost lizards of the world does not even mention the species. Ignacio Minoli, a coauthor of the latter chapter communicated to me (July 2022) that this omission was not for lack of interest but for lack of data.

Finally, regarding the most updated conservation status of *L. magellanicus*, in Chile it is categorized as Near Threatened (NT) by Ministerio del Medio Ambiente [33] on account of its marginal and restricted distribution in the country. In Argentina, according to the Sistema de Información de Biodiversidad [34], it is categorized as Not Threatened (NA) by the Asociación Herpetológica Argentina and Not Threatened (NA) by Resolution N° 1055 of Secretaría de Ambiente y Desarrollo Sustentable. According to International Union for Conservation of Nature [35] it is of Least Concern (LC).

Discussion

Preliminary synthesis

As I stated in the beginning, I am not prepared to offer a diagnosis, much less a critique, of systematic studies on *Liolaemus magellanicus* or its position in Liolaemid clades. This requires treatment by trained systematists with knowledge of genetic, genomic, and phylogeographic approaches. But on surveying the existing literature, I can offer my perspectives on other natural history aspects of *L. magellanicus*: (a) Its area of distribution has not been well established, especially in Chile. Detailed georeferenced maps are needed before biogeographic analyses may be contemplated by overlaying distributional datapoints with topographic, vegetation, soil, and microclimatic filters. Niche modelling may be used as an exploratory tool for directing population surveys to specific localities. (b) At the level of organismal biology, we know preciously little of the physiological features that enable these lizards to survive in their harsh environment. Indeed, reproductive aspects have been more

deeply analyzed than thermoregulation, feeding, parasites, diseases, and behavior. (c) At the level of population biology, we do not have estimates of their density fluctuations over seasons or years, or their habitat and food selection. (d) At the level of community biology, we ignore their place in food local webs, their predators, competitors, and food base, and the strength of their interactions with sympatric organisms. (e) At the level of ecosystems biology, we surely do not know how much material and energy passes through these lizards in the relatively simple ecosystem they take part thereof.

Prospects for further research

From the selective review above it is clear that *Liolaemus magellanicus* may be proposed as a model ectothermic vertebrate that may serve to test hypotheses about: (a) Resource allocation strategies to deal with a harsh environment that affords limited opportunities for foraging and reproductive activities of a lizard. (b) Behavioral strategies for dealing with thermoregulation, food and mate acquisition, and care –if any—of offspring. (c) Its place within the rather impoverished food web of which this species forms part of. It does not escape my attention that this rather new species, which persisted in Patagonian glacial refuges before being cut off into two subpopulations—one mainlander, another islander—offers fertile ground for testing population genetic, evolutionary, and phylogeographic hypotheses. I think that biogeographers, systematists, evolutionists, physiologists, and ecologists should take advantage of this uniquely positioned species in the southernmost margins of our changing world.

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Data analysis: FMJ. Manuscript preparation: FMJ. FMJ read and approved the final version of the manuscript.

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Data Availability
Not applicable; this is a literature review of published sources.

Declarations

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