Adaptability and subterranean plasticity of *Bokermannohyla martinsi* (Anura: Hylidae).

Maurício Carlos Martins de Andrade (1), Ítalo Moreira Martins (2), Tiago Castro Silva (1) & Paula Cabral Eterovick (3)

(1) Centro Nacional de Pesquisa e Conservação de Cavernas, Instituto Chico Mendes de Conservação da Biodiversidade (Cecav/ICMBio), Brasília, Brasil, mauricio.andrade@icmbio.gov.br (corresponding author)

(2) Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Brasil, italoomm@yahoo.com.br

(3) Leibniz Institute DSMZ - German Collection of Microorganisms and Cell Cultures GmbH, Science Campus Braunschweig-Süd, 38124 Braunschweig, Germany

Abstract

Bokermannohyla martinsi utilizes iron caves as shelter, especially during the dry season (autumn and winter), when external climatic conditions become adverse. During the rainy season, they seek external habitats for reproduction. In locations with suitable environmental conditions, the species exhibits continuous activity and reproduction throughout the year. Here, we investigate the ecological plasticity of *B. martinsi* in caves with perennial water bodies, examining whether it is active (including reproductive activity) year-round in these caves. We also list the environmental factors that, along with morphological, physiological, and behavioral adaptations, facilitate the colonization of caves by the species. *Bokermannohyla martinsi* is endemic to the Iron Quadrangle (Quadrilátero Ferrífero) region (Minas Gerais, Brazil), has a saxicolous habit, and occurs restrictively in rocky streams and creeks at high altitudes. The loss of quality and extent of its habitat is the primary threat faced by this vulnerable species. This study reinforces the importance of caves as habitats for *B. martinsi*, particularly due to mining, highlighting the need for the conservation of caves in Iron Quadrangle as well as the adjacent areas.

1. Introduction

Most amphibians exhibit an aquatic larval phase and a terrestrial adult phase (WELLS, 2007). Adult anurans, in addition to pulmonary respiration, also breathe through the skin (WELLS, 2007). Thus, maintenance of skin moisture is important for adequate gas exchange (WEBER, 2004; WELLS, 2007). Consequently, they are highly dependent on humid environments, being found in areas of high humidity or near water sites (WELLS, 2007). As ectothermic animals, the body temperature of anurans varies with ambient temperature, making them susceptible to changes in temperature and humidity in the environment (WEBER, 2004; WELLS, 2007). Most caves exhibit high humidity and mild temperatures (WEBER, 2004), and are also characterized by environmental stability, with little daily and annual variation in temperature and humidity (FERREIRA, 2005; ANDRADE et al., 2021). Thus, various species of anurans utilize natural cavities to shelter from unfavorable environmental conditions in the surrounding epigean environment, avoiding adverse temperatures and desiccation (WEBER, 2004).

Many anurans use caves to temporarily shelter from climatic adversities (WEBER, 2004). Species that return to the surface to complete their life cycle, such as for feeding or reproduction, can be classified as trogloxenes (SKET, 2008). However, when environmental resources are available, caves are also used as foraging and breeding sites by some species of anurans (WEBER, 2004), allowing them to complete their entire life cycle within the caves. In this case, some species may maintain permanent subterranean populations, being classified as eutroglophiles (SKET, 2008).

In this context, a study conducted in Serra do Gandarela National Park (SGNP) showed that *Bokermannohyla martinsi* utilizes iron caves year-round as shelter (ANDRADE et al., 2021). Increased usage was recorded during the dry and cold period (autumn and winter), when external climatic conditions become adverse (ANDRADE et al., 2021). In the upper part of the SGNP, where these caves are located, most streams are temporary and remain mostly dry during the dry season (ANDRADE et al., 2021). Thus, during this period, the species takes advantage of caves for shelter, as these have high humidity and are more environmentally stable (ANDRADE et al., 2021). Most iron caves in SGNP do not contain watercourses inside due to their altimetric positioning in the landscape, above 1,500 meters, being close to the top of the relief (PILÓ et al., 2015). During the rainy season, when temporary streams have water, most individuals leave the caves to reproduce in these streams (ANDRADE et al., 2021).

Ecological plasticity is the ability of organisms to respond differently to various environmental stimuli even with the same genetic background (NOVOPLANSKY, 2002). *Bokermannohyla martin*si is a territorial species that is normally active year-round in mountainous streams (MAGALHÃES et al., 2018). In the Santuário do Caraça Private Natural Heritage Reserve, another site within its distribution, *B. martinsi* tadpoles have been recorded throughout the year (AFONSO & ETEROVICK, 2007), indicating that the species has continuous reproduction in locations with suitable environmental conditions. At the Santuário do Caraça and the Itacolomi State Park, both tadpoles and adults of *B. martinsi* have been recorded in quartzitic caves with perennial water bodies (ANDRADE et al., 2021; 2023). Therefore, we aim to investigate the ecological plasticity of *Bokermannohyla martinsi* regarding the use of caves under different environmental conditions. Our hypothesis is that the species exhibits activity, including reproductive activity, throughout the year in caves with perennial water bodies. We also discuss whether morphological, physiological, and behavioral adaptations influence cave occupancy by the species.

2. Materials and Methods

We visited twenty caves distributed across two conservation units within the Iron Quadrangle (IQ), namely: (1) Serra do Gandarela National Park (SGNP) (20°06'03"S, 43°39'50"W), located in the central-northeastern region of the IQ; and (2) Itacolomi State Park (ISP) (20°26'32"S, 43°27'46"W), located in the southeastern region of the IQ (Fig. 1). The IQ is a geologically distinct area located in central-southeastern region of the state of Minas Gerais, Brazil, comprising iron-rich and quartzitic mountains and covering an area of approximately 7,000 km² (AZEVEDO et al. 2012).

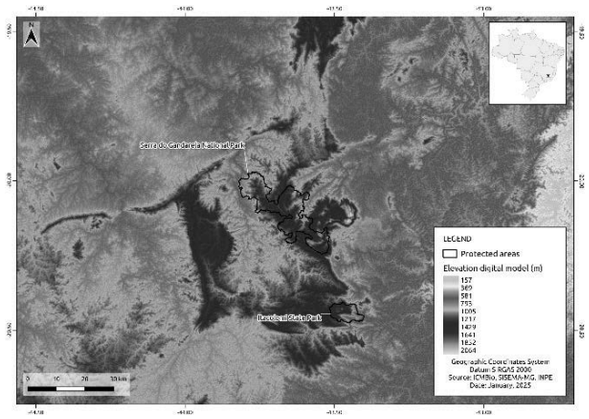

Figure 1: *Altimetric map showing the region of the Iron Quadrangle and the conservation units studied: Serra do Gandarela National Park (SGNP) and Itacolomi State Park (ISP). Author: Tiago Castro Silva.*

The area studied in the ISP is characterized by being drained by groundwater that flows between blocks, within caves, at the bottom of dolines, and in canyons (Fig. 2A and 2B) (GLÖCKNER, 1981). In contrast, the iron caves investigated in SGNP do not exhibit watercourses within them due to their altimetric positioning in landscape, as previously reported (Fig. 2C and 2D).

Each cave was visited four times between October 2022 and September 2023, keeping a minimum interval of two months between data collections. The sampling was undertaken within each of four three-month periods that we considered as early wet season (Spring: October–December), late wet season (Summer: January–March), early dry season (Autumn: April–June), and late dry season (Winter: July–September).

The search for anurans (adults and tadpoles) and reproductive activities (e.g., vocalization, amplexus, spawning) was carried out during daylight hours by two researchers, using flashlights, through active searching without time constraints, based on vocalization and visual observation. It is important to note that we did not employ any form of marking for individual identification of specimens. Thus, a specimen may have been recorded in more than one season.

We recorded the activity level of each adult anuran at the time of its location as (1) inactive: resting with eyes closed, unresponsive to the flashlight, body on the surface and limbs curled, with hands and feet beneath the body (sensu ANDRADE et al., 2021); (2) active: awake with limbs extended and responsive to the flashlight.

The light incidence at the location of the adult was classified into three categories: (1) photic: near the entrance, with direct sunlight incidence at some point during the day and the presence of photosynthesizing organisms; (2) dysphotic (twilight): with indirect light incidence (without direct sunlight); and (3) aphotic: without light incidence (adapted from SOARES et al., 2013). We classified the substrates of the microhabitat where the adults were found as: (1) rock, (2) soil, and (3) sand. To investigate the lithology of the caves, we utilized the National Register of Speleological Information (Canie) from the National Centre for Research and Conservation of Caves (ICMBio/Cecav) and bibliographic surveys, with subsequent validation of the information during field activities. The bodies of water present within the caves were classified as perennial or intermittent, as well as lentic or lotic.

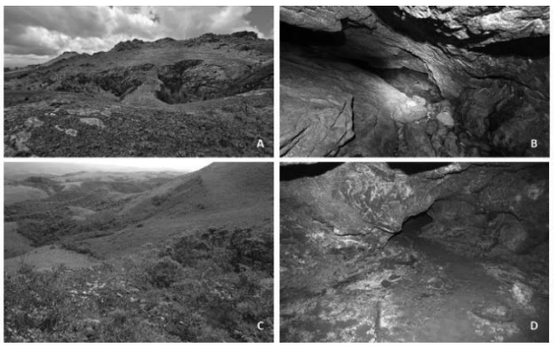

Figure 2: *(A) External environment in the Itacolomi State Park (ISP), showing the sinkholes where caves and underground watercourses are located; (B) Quartzite cave in the ISP, showing a lotic water body; (C) External environment in Serra do Gandarela National Park (SGNP), showing the ferruginous rock field (canga); (D) Ferruginous cave in SGNP. Author: Maurício Andrade.*

3. Results

We obtained 419 records (111 records of adults and 308 in the larval stage – tadpoles) in 16 (80%) of the 20 sampled caves, comprising nine caves in the ISP and seven in the SGNP. From these records, 75 (67.5%) were obtained in the SGPN and 36 (32.5%) in the ISP. Adults were observed in all seasons within the caves of both conservation units. The seasons with the highest number of adult records were autumn in the SGNP (n=24) and spring and summer in the ISP, both with ten records. Conversely, the seasons with the lowest number of adult records were summer in SGNP (n=15) and autumn and winter in ISP (n=8) (Fig. 3 and 4A). In caves of the ISP, seven adults were recorded vocalizing in spring, three in summer, one in autumn, and one in winter. We did not record any individual vocalizing in caves of the SGNP.

Tadpoles were recorded only in caves of the ISP and in all seasons of the year. Winter and summer were the seasons with the highest number of tadpole records (n=94 and n=93, respectively), while spring had the lowest number of records (n=43) (Fig. 3, 4B, and 4C). The tadpoles exhibited different sizes, suggesting multiple breeding events. No amplexus, spawning, or recently metamorphosed froglets were recorded within the caves.

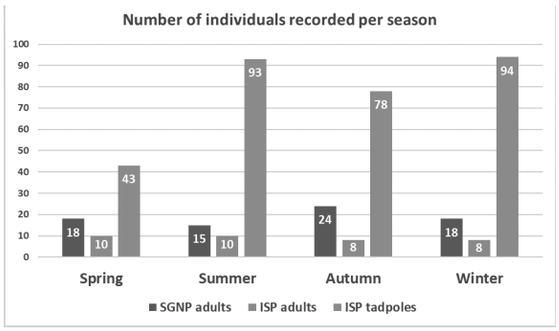

Figure 3: *Number of adults and tadpoles of Bokermannohyla martinsi recorded per season in caves of Serra do Gandarela National Park (SGNP) and Itacolomi State Park (ISP).*

Most adults (n=100; 90%) were found in the dysphotic zone of the caves. Ten individuals (9%) were found in the aphotic zone, and only one individual (1%) was recorded in the photic zone. In SGNP, 97% of the adults were found in the dysphotic zone and 3% in the aphotic zone. In ISP, 75% of adults were recorded in the dysphotic zone, 22% in aphotic zone, and 3% in photic zone (Fig. 5).

In SGNP, 98.5% of individuals were recorded on rocks and 1.5% on soil. In ISP, 69.5% were recorded on rocks, 8.5% on sand, and 2.5% on soil. In this conservation unit, we recorded seven (19.5%) individuals only acoustically. It was not possible to visualize the substrates due to unfeasible access to the places where they were positioned (Fig. 6).

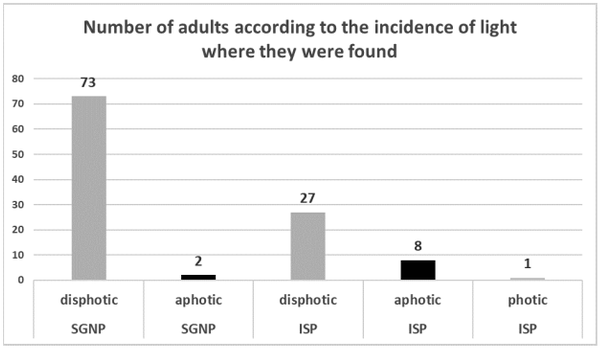

Figure 5: *Number of adults of Bokermannohyla martinsi found in caves of Serra do Gandarela National Park (SGNP) and Itacolimi State Park (ISP) according to the incidence of light in the location where they were found.*

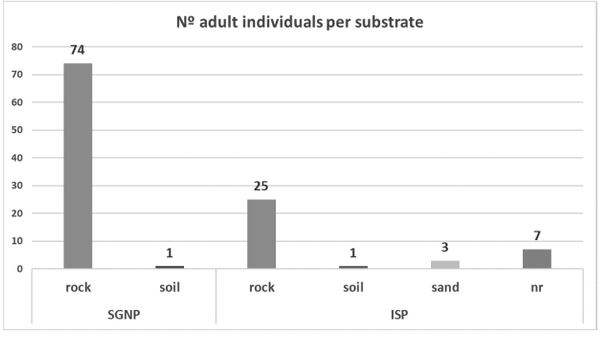

Figure 6: *Number of adults of Bokermannohyla martinsi found in caves of Serra do Gandarela National Park (SGNP) and Itacolimi State Park (ISP) according to substrate used. Legend: not recorded (nr).*

In SGNP, the majority of adult B. martinsi were inactive during both the rainy (85%) and dry (88%) seasons. In contrast, at ISP, most adults were active during the rainy period (65%) and exhibited both active and inactive states during the dry period (Fig. 7).

Regarding the lithologies of the surveyed caves, all caves at the ISP are composed of quartzitic rocks. At this location, we recorded bodies of water in eight caves, all classified as perennial and lotic. At the ISP, nearly all individuals were recorded in caves with watercourses, with only one individual recorded in a cave without any water body. In SGNP, half of the sampled caves are quartzitic, while the other half are composed of ferruginous rocks. At this site, we recorded individuals in four ferruginous caves and three quartzitic caves. However, in quartzitic caves, we recorded only five individuals (6.5%). Thus, ferruginous caves accounted for 93.5% of the adult records in SGNP. Water bodies were recorded in two quartzitic caves in SGNP, classified as intermittent and lentic. Four individuals of B. martinsi were recorded in these caves.

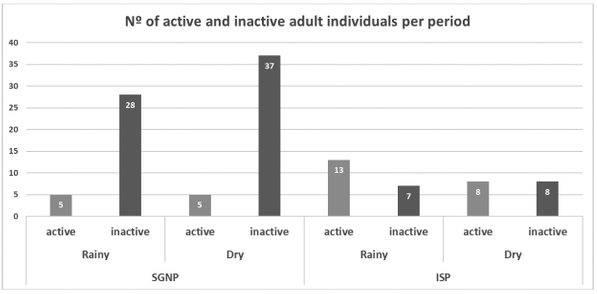

Figure 7: *Activity level of adults of Bokermannohyla martinsi, by dry and rainy season, found in caves of Serra do Gandarela National Park (SGNP) and Itacolimi State Park (ISP).*

4. Discussion

Bokermannohyla martinsi exhibited continuous use (throughout all seasons) of the ferruginous caves of the SGNP and the quartzitic caves of the ISP, either with or without water bodies. As recorded by ANDRADE et al. (2021), we also observed that the species utilized the ferruginous caves more during the dry period. Therefore, these caves represent a potential refuge for the species when the streams are dry and external climatic conditions become adverse (ANDRADE et al., 2021). The reduced use of these caves during the rainy season is likely related to the more favorable climatic conditions in the epigean environment and the search for streams for reproduction (ANDRADE et al., 2021). During this period, temporary streams retain water, allowing the reproduction and development of tadpoles (ANDRADE et al., 2021).

To avoid water loss during the day, nocturnal anurans typically rest in an "inactive" posture, thereby reducing the exposed surface area (e.g., ETEROVICK et al., 2020). Although we sampled during the day, adults varied in activity patterns, being predominantly inactive throughout the year in the SGPN, whereas in the ISP they were predominantly active in the rainy season and either active or inactive in the dry season. The record of activity in the ISP may be related to the availability of breeding habitats (with evidence of reproduction in these habitats, i.e., records of tadpoles in the bodies of water within the caves).

Fidelity to breeding, feeding, and estivating sites is a common characteristic among anurans (SINSCH, 1990). ANDRADE et al. (2021) demonstrated the fidelity of specimens of *B. martinsi* to the ferruginous caves of SGNP. Due to this fidelity and the territoriality of the species, we believe that specimens likely use the quartzitic caves of the ISP throughout the year.

The reproduction and feeding of anurans in caves are significantly influenced by the presence of water (SPERANDEI et al., 2024). In quartzitic caves of the ISP, which contain perennial and lotic water bodies, vocalizing adults and tadpoles have been recorded in all seasons. In these caves we observed a greater abundance of *B. martinsi* during the rainy period, as also recorded in epigean environments (AFONSO & ETEROVICK, 2007). Six caves surveyed in ISP have watercourses that are not connected upstream with other external water bodies. Thus, the hydromorphology of these caves prevents the transport of tadpoles

from outside. In these caves, although we did not record any spawn or couples in amplexus, we did observe tadpoles, females, and calling males, indicating the occurrence of reproduction. Therefore, we can conclude that the species exhibits ecological plasticity, remaining active and reproducing throughout the year in caves that provide the required environmental conditions.

The degree of association of species with the cave environment is intrinsically linked to the combination of morphological, physiological and behavioral adaptations (HOWARTH & MOLDOVAN, 2018). The saxicolous habit, the presence of digital discs, interdigital membranes, and nocturnal activity pattern are eco-physiological characteristics found in some anuran species that utilize caves (BISWAS, 2014) and are also present in *B. martinsi*.

In our study, the species showed a preference for the disphotic zone of the caves, followed by the aphotic zone, as also observed by ANDRADE et al. (2021). Most troglophilic and trogloxenic species, including anurans, are found in twilight (disphotic) zones of caves, characterized by high humidity and mild temperatures, favorable microclimatic conditions (OSEEN & WASSERSUG, 2002; WEBER, 2004; LUNGHI et al., 2018). In these areas, which have lower visibility, anurans are also better protected from predators that rely on visual orientation (OSEEN & WASSERSUG, 2002).

Regarding the microhabitat, most recorded adults were found on rocky substrates, as observed by LIMA et al. (2013) in epigean environment. Records of males vocalizing in rock crevices in streams demonstrate their adaptation and strong association with the rocky environment (SILVEIRA et al., 2019). The presence of rocky substrates in both epigean and hypogean microhabitats, combined with the saxicolous and nocturnal habits of the species, are factors that enable its use of caves and adaptability to the cave environment.

Anurans exhibit a sedentary habit, with migratory behavior limited by the demands of water balance and thermoregulation (SINSCH, 1990). To date, studies conducted in the SGNP have characterized *B. martinsi* as a trogloxene species (ANDRADE et al., 2021). However, given its sedentary habit and a favorable environment for reproduction, thermoregulation, and maintenance of water balance, it is possible that some individuals may complete their entire life cycle in caves and could be classified as eutroglophilic, what remains to be tested.

Although foraging in caves has been reported for anurans (LURÍA-MANZANO & RAMÍREZ-BAUTISTA, 2017), there is currently no data demonstrating that the species feeds on cave-dwelling invertebrates. Nevertheless, it is highly likely that it does so due to the availability of prey in this environment, as noted by FERREIRA (2005).

Bokermannohyla martinsi is an endemic species of the Iron Quadrangle (IQ), with an estimated range of occurrence of 3,816 km² (BASTOS et al., 2023), occurring restrictively in rocky streams at high altitudes (SILVEIRA et al., 2019). Thus, given the species' limited range and restricted habitat preferences, caves constitute an environment that the species has colonized, thereby increasing its niche within its small distribution area.

In addition to being endemic, *B. martinsi* is classified as "Vulnerable" (VU) due to its limited range of occurrence (< 20,000 km²) and the ongoing decline in the extent and quality of its habitat (IUCN, 2023). The primary threat to the species is mining, which is responsible for the continuous decline in the quality and extent of its habitat (BASTOS et al., 2023). The IQ is one of the world's major iron mining areas (PINHEIRO et al., 2014), posing an increasing threat to the caves and the species' habitat. Furthermore, wildfires, urban expansion, and agricultural development in the region also contribute to the degradation and fragmentation of its habitat (IUCN, 2023). The species does not adapt well to disturbed environments, and some subpopulations are no longer found, possibly being locally extinct (BASTOS et al., 2023). Therefore, this study corroborates the importance of conserving the areas where the species occurs as a whole, including the caves.

Bokermannohyla martinsi, like other anurans, is negatively affected by global warming, which is causing droughts and rising temperatures in its distribution range (IUCN, 2023). However, habitat loss is the most urgent threat faced by this species, affecting approximately 70% of its distribution area (IUCN, 2023), less than 30% of which is protected by conservation units (IUCN, 2023). Thus, we strongly recommend the establishment of fully protected conservation units in IQ to preserve caves, breeding habitats, and populations of this sedentary species. Monitoring populations is also essential for the ongoing assessment of anthropogenic impacts on the species and its risk of extinction.

5. Conclusion

Our study provides new insights into the ecology of *Bokermannohyla martinsi* and contributes to the understanding of the use and adaptation of anurans to caves, highlighting the importance of this environment in their life history and generating support for the planning and implementation of conservation actions that take into account caves and their inhabitants.

Acknowledgements

We would like to express our gratitude to the managers and staff of Serra do Gandarela National Park and Itacolomi State Park. We also thank the teams from SISBio/ICMBio and IEF-MG for the authorizations for activities conducted for scientific purposes. The project utilized financial resources from the Term of Commitment for Speleological Compensation (TCCE ICMBio/Vale No. 01/2018), established between Vale S.A. and Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), with operational management carried out by Instituto Brasileiro de Desenvolvimento e Sustentabilidade (IABS), to whom the authors also extend their thanks.

References

ANDRADE M.C.M., COSTA J.C.R., ETEROVICK, P.C. (2021) Fidelity in the use of iron caves by Bokermannohyla martinsi (Anura: Hylidae): a step further in unveiling the importance of Brazilian caves for the herpetofauna. Salamandra 57(4):502-512.

ANDRADE M.C.M., MARTINS I.M., SILVA, T.C., ETEROVICK P.C. (2023) Reprodução de pererecas endêmicas (Anura: Hylidae) em cavernas da Serra do Espinhaço Meridional, Brasil. In: MISE K.M., GUIMARÃES G.B. (orgs.) CONGRESSO BRASILEIRO DE ESPELEOLOGIA, 37, 2023. Curitiba. Anais... Campinas: SBE, p.292-300.

AFONSO L.G., ETEROVICK P.C. (2007) Spatial and temporal distribution of breeding anurans in streams in southeastern Brazil. Journal of Natural History 41(13-16):949-963.

AZEVEDO U.R., MACHADO M.M.M., CASTRO P.T.A., RENGER F.E., TREVISOL A., BEATO D.A.C. (2012) Geoparque Quadrilátero Ferrífero (MG): proposta. In: SCHOBBENHAUS C., SILVA C.R. Geoparques do Brasil: propostas. CPRM, Rio de Janeiro.

BASTOS R.P., MARTINS M.R., BATAUS Y.S.L., CÔRTES L.G., GUIMARÃES-

-JUNIOR R.V., RODRIGUES J., BRANDÃO R.A., FERRÃO M., GORDO M., HOOGMOED M.S., KAEFER I.L., LEITE F.S.F., MACIEL N.M., PRADO V.H.M., SANTANA D.J., SILVANO D.L., SOUZA M.B., TOLEDO L.F. (2023) Bokermannohyla martinsi. Sistema de Avaliação do Risco de Extinção da Biodiversidade - SALVE.

BISWAS, J. (2014) Occurrence and distribution of cave dwelling frogs of peninsular India. Ambient Science 1:17–25.

ETEROVICK P.C., SOUZA A.M., SAZIMA I. (2020) Anfíbios anuros da Serra do Cipó, Minas Gerais – Brasil. Belo Horizonte. 292p.

FERREIRA R.L. (2005) A vida subterrânea nos campos ferruginosos. O Carste 17:106–115.

HOWARTH, F.G.; MOLDOVAN, O.T. (2018) The ecological classification of cave animals and their adaptations. Cave ecology, p.41-67.

IUCN SSC Amphibian Specialist Group & Instituto Boitatá de Etnobiologia e Conservação da Fauna. (2023) Bokermannohyla martinsi. The IUCN Red List of Threatened Species 2023.

GLÖCKNER R.H. (1981) Lithostratigraphie, sedimentologie, tektonic und metamorphose der proterozoischen Itacolomi Serie bei Ouro Preto, Minas Gerais, Brasilien. Clausthaler Geowissenschaftliche Dissertationen 10:221p.

LIMA N.G.S., LIMA R.C.L., DIAS J.E.M., TORRES P. F., ETEROVICK P.C. (2013) Spatial niche variation in two sympatric species of Bokermannohyla (Anura: Hylidae) in southeastern Brazil. Journal of Natural History 48:229-240.

LUNGHI E., BRUNI G., FICETOLA F.G., MANENTI R. (2018) Is the Italian stream frog (Rana italica Dubois, 1987) an opportunistic exploiter of cave twilight zone? Subterranean Biology 25:49-60.

LURÍA-MANZANO R., RAMÍREZ-BAUTISTA A. (2017) Diet comparison between rainforest and cave populations of Craugastor alfredi (Anura: Craugastoridae): does diet vary in contrasting habitats? Journal of Natural History 51:2345-2354.

MAGALHÃES R.F., LACERDA J.V.A., PAULA REIS L., GARCIA P.C.A., PINHEIRO P.D.P. (2018). Sexual dimorphism in Bokermannohyla martinsi (Bokermann, 1964) (Anura, Hylidae) with a report of male–male combat. South American Journal of Herpetology 13(2):202-209.

NOVOPLANSKY A. (2002). Developmental plasticity in plants: implications of non-cognitive behavior. Evolutionary Ecology 16(3):177-188.

OSEEN K.L., WASSERSUG R.J. (2002) Environmental factors influencing calling in sympatric anurans. Oecologia 133:616-625.

PILÓ L.B., COELHO A., REINO J.C.R. (2015) Geoespeleologia em Rochas Ferríferas: Cenário Atual e Conservação. In: CARMO F.F., KAMINO L.H.Y. (Org.). Geossistemas Ferruginosos do Brasil: áreas prioritárias para conservação da diversidade geológica e biológica, patrimônio cultural e serviços ambientais. Belo Horizonte: 3i Editora, 5:125-148.

PINHEIRO P.D.P., TAUCCE P.P.G., LEITE F.S.F., GARCIA P.C.A. (2014) The advertisement call of the endemic Bokermannohyla martinsi (Bokermann, 1964) (Anura: Hylidae) from southern Espinhaço range, southeastern Brazil. Zootaxa 3815(1):147-150.

SILVEIRA A.L., RIBEIRO A.S.V.B, FERNANDES T.N., DORNAS T.T. (2019) Anfíbios do Quadrilátero Ferrífero (Minas Gerais): atualização do conhecimento, lista comentada e guia fotográfico. Belo Horizonte: Editora Rupestre 448p.

SINSCH U. (1990). Migration and orientation in anuran amphibians. Ethology Ecology & Evolution 2(1):65-79.

SKET B. (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42(21–22):1549–1563.

SOARES L.G.S., VAN DE KOKEN A.F., TIMO M., SILVA R.P. (2013) Fauna de invertebrados em cavernas de calcário na região de Córrego Fundo, Minas Gerais, Brasil. Revista Eletrônica de Biologia 6: 8-68.

SPERANDEI V.D.F., VAZ-SILVA W., TEJERINA-GARRO F.L. (2024) Characterization of anuran fauna inside caves in Brazil. Biota Neotropica 24(3):e20241657.

WEBER A. (2004) Amphibia. In: Gunn J. Encyclopedia of caves and karst science. Routledge p.125-128.

WELLS K.D. (2007) The ecology and behavior of amphibians. University of Chicago press. 1400p.