The Imperiled Giant Armadillo: Ecology and Conservation

Arnaud LJ Desbiez[a,b,c] **and Nina Attias**[a], [a]Instituto de Conservação de Animais Silvestres (ICAS), Campo Grande, Mato Grosso do Sul, Brasil; [b]Instituto de Pesquisas Ecológicas (IPÊ), São Paulo, Brasil; [c]Royal Zoological Society of Scotland (RZSS), Edinburgh, United Kingdom

Abstract

The giant armadillo *Priodontes maximus* is by far the largest of the 20 extant armadillo species with adults weighing well over 30 kg and measuring 1.50 m from the tip of the nose to the tip of their tail. Giant armadillos' range over much of South America from Colombia and Venezuela south to Paraguay and Northern Argentina, but they are rare over their entire distribution range. Giant armadillos feed mainly on termites and ants. The species is cryptic, solitary, nocturnal, and have large exclusive home ranges. Forests are fundamental for the species survival, especially during early life stages. Giant armadillos play an important role as ecosystem engineers (e.g., over 70 species have been described using their burrows). Due to their late sexual maturity (7 years), single pup litters, and long interbirth rates (approximately 3 years), the population growth rate of giant armadillos is very low, and the species can therefore easily be locally extirpated. The giant armadillo is classified as "Vulnerable" to extinction by the IUCN with local extinctions and population declines due to habitat loss, and fragmentation, hunting, road kills, and wildlife trade.

Introduction

Armadillos are terrestrial mammals with unique morphological attributes easily distinguishable from other groups by the presence of a carapace formed by ossified dermal tissue (Fig. 1). They are fossorial, excavating soil both to forage and to build burrows where they can rest and shelter from unfavorable conditions (Eisenberg and Redford, 1999). Armadillos provide a diversity of ecosystem services and are important resources to top predators and indigenous and rural communities. The giant armadillo *Priodontes maximus* is unmistakable as it is by far the largest of the 20 extant armadillo species (Carter et al., 2016; Desbiez et al., 2019).

Morphology

Average mass of an adult giant armadillo exceeds 30 kg, but can vary between eco-regions (Desbiez et al., 2019). Morphometric differentiation between sexes has been described and adult males are generally larger and heavier than females (Desbiez et al., 2019; Silveira et al., 2009). Adult dorsal body length is 70–100 cm from the tip of the nose to the base of the tail, while the tail is about 50–60 cm long (Carter et al., 2016; Desbiez et al., 2019). Prepubescent individuals or subadult individuals, defined as animals that

Fig. 1 An adult giant armadillo *Priodontes maximus* at the sand mound formed in front of its burrow. Credit: *Kevin Schafer*.

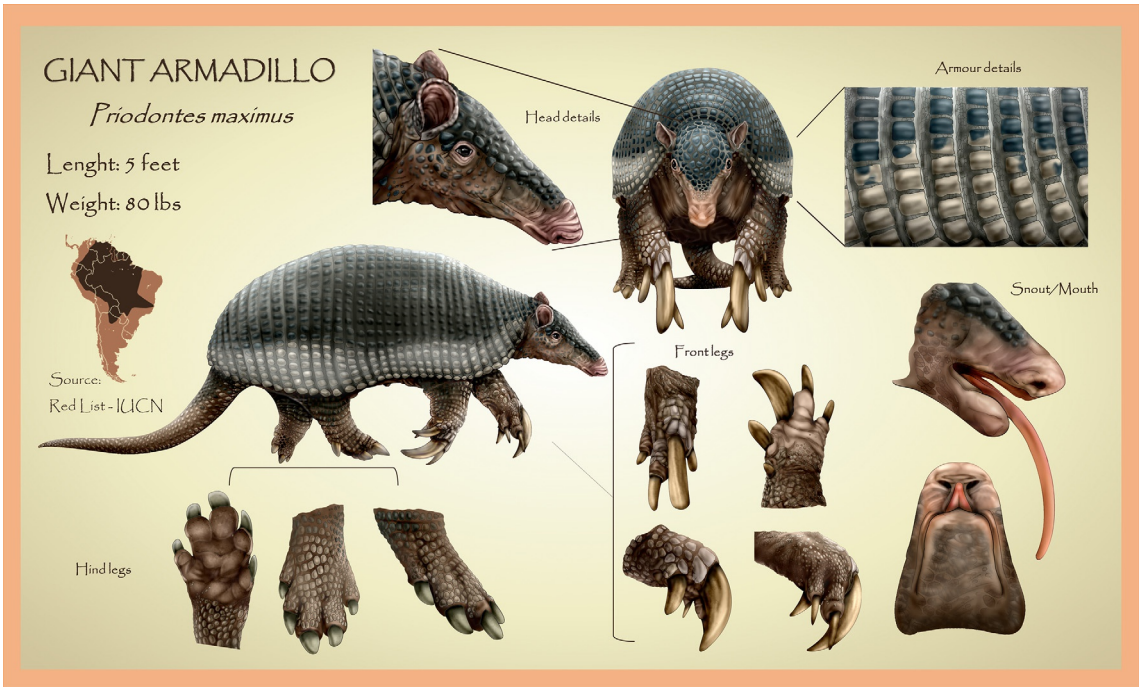

Fig. 2 Detailing of the external morphology of giant armadillos *Priodontes maximus*. Credit: Pedro Busana.

are independent from their mother but do not present signs of sexual activity (penis length, vulva, and teats size) have a wide body mass range (18–30.4 kg) and morphometric variation due to the long developmental process (up to 7 years) between weaning and sexual maturity (Desbiez et al., 2019).

Giant armadillos have a dark gray carapace that extends halfway down its sides with 11–13 flexible plates (Fig. 2). The armor is marked laterally on its edge by a distinctive lighter band surrounding the entire carapace. Legs, tail, and head are also covered with tough pentagonal scales while underneath the carapace, the bare skin is pinkish, wrinkly, and unprotected. Giant armadillos are practically hairless, with just a few hairs protruding between the scales. One of the most striking features of this species are the large scimitar-shaped fore claws, the third of which is greatly enlarged and can reach over 14 cm. Giant armadillos can be individually distinguished through light band width and shape, tail, and hind limb markings, and cephalic and flank scale patterns (Massocato and Desbiez, 2019). This is particularly useful for camera trap studies.

Although giant armadillos are famous for having the greatest number of teeth of any terrestrial mammal, their teeth are small, lack enamel, and play little role in grasping or chewing their food. Instead, they use their long and vermiform tongue to seek the small insects mainly termites and ants that they feed upon.

Distribution

Giant armadillos range over much of South America from Colombia and Venezuela, south to Paraguay and Northern Argentina (Fig. 3). They are present in 11 different countries (Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, and Venezuela). Although widespread, giant armadillos are rare over their entire distribution range. They are probably extinct in Uruguay. They occupy a diversity of habitats ranging from tropical forests to open savannas (Anacleto et al., 2014).

Feeding

Giant armadillos feed mainly on termites and ants but may be more opportunistic than previously thought. Several authors report the consumption of fruits, caiman eggs, bee larvae and other invertebrates, through direct observations as well as analysis of stomach or fecal contents. Because of their low-calorie diet, giant armadillos also present low body temperatures (34 °C) and low metabolic rates, for what would be expected for a placental mammal of its body mass. Giant armadillo morphology is well adapted to digging and opening hard termite mounds. Their powerful front claws break the hardest of soils while their back paws act as shovels (Fig. 4). Their armor, cephalic scales, and the scales covering them also protect them from roots, abrasive soil, and insect bites.

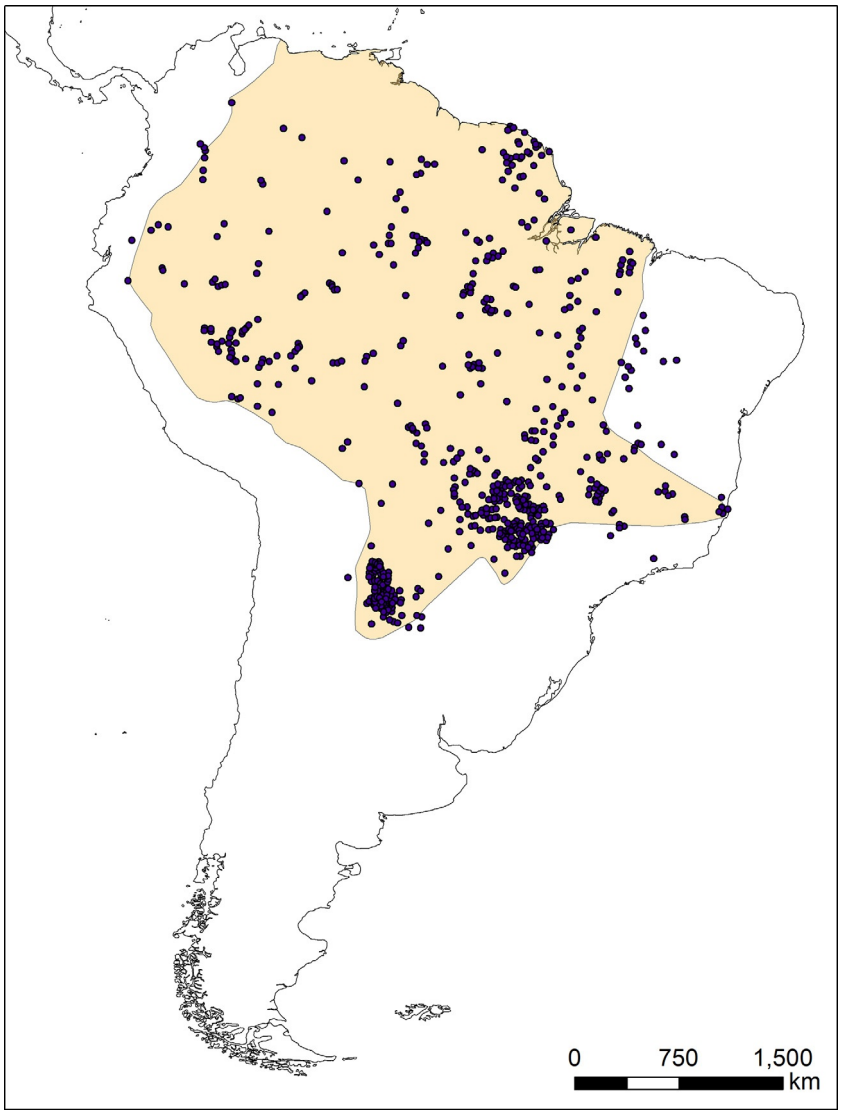

Fig. 3 Occurrence records of giant armadillos *Priodontes maximus* throughout its distribution in South America. The shaded polygon represents the species distribution according to IUCN. Credit: Giant Armadillo Conservation Program.

Fig. 4 A giant armadillo *Priodontes maximus* stands on its hind feet in a typical vigilance pose allowing the visualization of its long scimitar front claws. These strong claws are key for their fossorial behavior, enabling them to dig deep burrows for shelter and termite and ant mounds for feeding. Credit: Kevin Schafer.

Ecology

Although the species may be found across a relatively widespread area in central and northern South America (Fig. 3), it is not as common as the range maps imply. The species is cryptic, nocturnal, solitary, and occurs at low densities. They are also challenging to study and for this reason most information comes from only a few locations.

Population density estimates from camera traps range from 1.27–7.69 individuals/100 km^2. Variation could be due to the study areas and habitats but is most likely due to sampling methodologies of field studies and analysis as well as low sample size. Nevertheless, giant armadillos are naturally rare, occupy large home ranges, and occur at low densities.

Giant armadillos are notoriously difficult to capture and study. Results characterizing the spatial use of giant armadillos vary due to tracking methodologies, low sample size, and different analyses. Home range information reported in the literature ranges from 300 to 1500 ha. In the Brazilian Pantanal, Desbiez et al. (2020a) conducted the most complete spatial study available for the species. They gathered 12,168 telemetry locations from 23 individuals indicating a median adult home-range area of 2518 ha and median adult daily displacement of 1651 m. Home-range area scales positively with daily displacement and daily displacement scales positively with body mass. Median home-range overlap between pairs of individuals was low (4%) and adult females presented exclusive home ranges among themselves. However, males exhibited exploratory behaviors. Camera traps have detected adult males 15 and 20 km away from their home ranges, possibly to search for receptive females. Individuals of both sexes showed movement patterns indicative of site fidelity.

Most reports or studies on habitat use of giant armadillos are based mainly on the presence of their characteristic excavations or on few individuals captured. Giant armadillos are reported to occur in humid to dry lowland forests, open habitats, closed savannas, and forests. However, recently Desbiez et al. (2020b) published a detailed study that shows that giant armadillos select different landscape features according to sex, life stage, and behavioral state. Overall, forests are fundamental for the species survival, especially during early life stages. Younger individuals selected forests with dense vegetation and less predation risk for activity and rest. Females, which are exclusively responsible for parental care, presented stronger selection of forests and closed savannas during rest. Closed savannas, with high food availability, were selected for activity irrespective of sex or age. Floodable areas were selected only by adult males. These open areas are used mostly to return more quickly to their burrows at the end of the night. This study indicated that females select habitats in a way to balance offspring safety and food availability, while males are risk takers and explore the space widely.

There is almost no information of giant armadillo longevity. However, recently, two long-term camera trap initiatives in the Brazilian Pantanal and the Chaco alluvial plains in Bolivia documented adult females in the same area after intervals of 10 and 15 years. This indicates a potential lifespan of at least 18 years for wild giant armadillos and long-term site fidelity. Furthermore, in captivity a giant armadillo was documented to live 16 years (Carter et al., 2016). Luba et al. (2020), estimated that giant armadillos reproduce and live for over 20 years.

Fig. 5 Cross-sectional view of a giant armadillo *Priodontes maximus* digging a typical burrow under a vegetation patch. Giant armadillos dig burrows that can be up to 5 m deep and are usually over 40 cm wide and 30 cm high. Credit: Pedro Busana.

Giant armadillos dig large characteristic excavations for shelter and feeding (Fig. 5), much larger than those of any other armadillo species. Burrows can be up to 5 m deep and are usually over 40 cm wide and 30 cm high. Feeding excavations may appear similar to burrows but are much shallower. Giant armadillos can return to the same burrow or dig a new burrow, in which they will spend the day. In the Pantanal, it was observed that giant armadillos, on average, dig a new burrow every two to 3 days. Therefore, there are many giant armadillo burrows in an individual's home range. These burrows are important resources for other species. Throughout their distribution, authors studying the species in the Argentinean Chaco, forests of Peru, llanos of Colombia, the Brazilian Pantanal, Cerrado and Atlantic forest have described the role of giant armadillos as ecosystem engineers (Desbiez and Kluyber, 2013).

Giant armadillo burrows, and the associated sand mound at its entrance, provide and create new habitats and influence resource availabilities for over 70 vertebrate species throughout their distribution (Fontes et al., 2020). Burrows of giant armadillos also collect seeds and organic debris, their tunnels and mounds affect water infiltration and soil aeration, distribution of soil nutrients, the diversity of local plants and the soil biota (Desbiez and Kluyber, 2013). Therefore, the extinction of giant armadillos and the loss of these important burrow microhabitats may have cascading effects on communities and ecosystems.

The only natural predators for adult giant armadillos are the big cats, such as Jaguar (*Panthera onca*) and Puma (*Puma concolor*) however, younger juveniles could potentially be predated by Ocelot (*Leopardus pardalis*). Giant armadillos tend to flee when sensing danger and can rapidly crash through vegetation to their nearest burrow or dig a new one in a matter of minutes. They do not use their claws for defense, as the giant anteater *Myrmecophaga tridactyla* does, for example.

Behavior

Giant armadillos are strictly solitary. In the Brazilian Pantanal, little overlap was observed between home ranges. On rare occasions, camera traps may detect pairs, however, this is usually a mother and her offspring, which can be large and even appear to be almost adult size. Offspring have been detected in its mother's territory for up to 3 years of age. Also, during reproduction, male giant armadillos have been detected following a female and even sharing a burrow (Desbiez et al., 2020c).

Giant armadillos are strictly nocturnal. They generally leave their burrows in the first hours after sunset and return from their foraging activities between midnight and 4 AM. The longest activity duration recorded was close to 10 h, but generally, the species is active above ground only between 4 and 6 h per day. They spend 75–80% of their time underground. Accelerometer sensors showed that giant armadillos are not active and do not feed while underground. For this reason, giant armadillos are classified as fossorial.

Giant armadillos appear to communicate using olfactory clues. Giant armadillos urinate and defecate when digging or when excavating a burrow. Camera traps regularly detect individuals from neighboring areas (usually males) smelling the sand mound at the entrance of the burrow to seek clues about its occupant. Giant armadillos have rarely been seen occupying and using a burrow dug by another individual.

Like other xenarthran species, giant armadillo behavior is influenced by environmental temperatures. In the Pantanal, individuals leave their burrows for shorter periods (~2 h) during cold winter nights. More study is needed on this.

Reproduction

During a long-term in situ study in the Brazilian Pantanal using both morphometric characteristics (e.g., body, penis, and testes dimensions through ultrasound), and data on sperm production (assessed by electroejaculation), Luba et al. (2020) estimated that male giant armadillos reach sexual maturity at 6.5–8 years of age. Field observations from the same study suggested female sexual immaturity lasts until ~7 years of age.

Reproductive information is rare (Aya-Cuero et al., 2015; Desbiez et al., 2020c). Giant armadillos have an interbirth rate of 3 years (Desbiez et al., 2020c), and give birth to a single pup (Aya-Cuero et al., 2015) after a 5-month gestation period. Females are exclusively responsible for parental care. Parental care for the single pup is long. The single offspring is completely dependent on its mother's milk until 6–8 months, weaned at 11–12 months, dependent on its mother's burrows until 18 months old, and remains in her territory until ~ 3 years of age (Fig. 6). Due to their late sexual maturity, single pups, and long interbirth rates, the population growth rate of giant armadillos is very low, and the species can therefore easily be locally extirpated by anthropogenic threats.

Health

Research on wild giant armadillo health is still very scarce. In the Brazilian Pantanal, a long-term health project has been ongoing since 2011 (Kluyber et al., 2021). The use of giant armadillo burrows by several vertebrate species and the constant mild

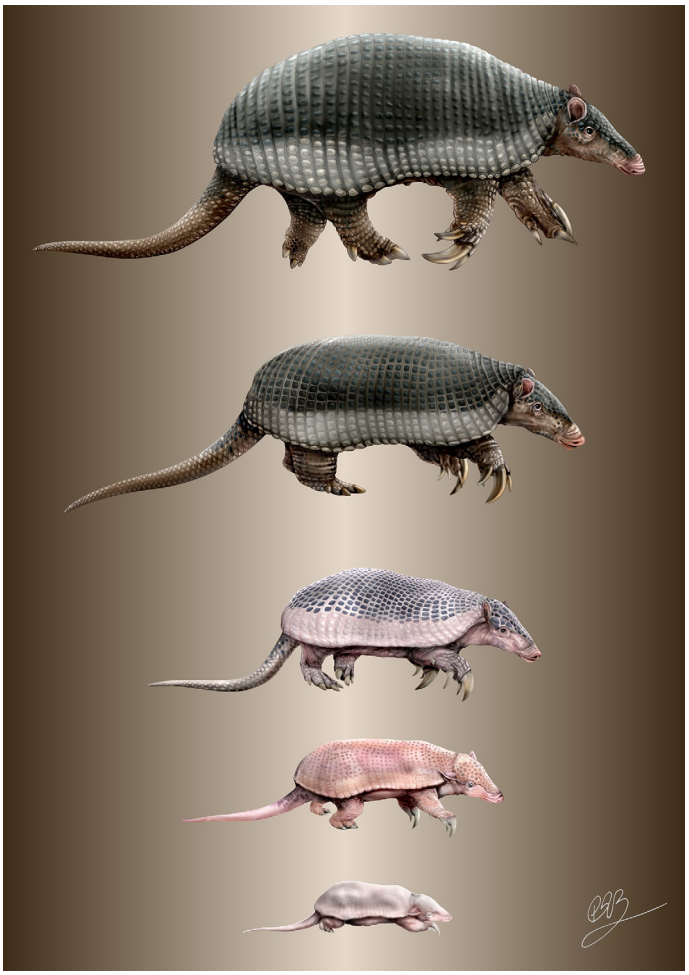

Fig. 6 External morphology of giant armadillos *Priodontes maximus* according to age. With less than 20 days old, almost all scales are light-colored (bottom); between 25 and 50 days old, darker scales on the cephalic shield and carapace are pale ("faded") but distinguishable and eyes are still closed; after 50 days, the darker scales of the carapace become easily distinguishable, and eyes are open. Giant armadillos take several years to reach adult size, and only reach sexual maturity between 6.5 and 8 years of age. Credit: Pedro Busana.

temperatures inside the burrows (24–26 °C), may contribute to the maintenance and proliferation of parasites and their vectors (Desbiez and Kluyber, 2013).

Salmonella serotypes *Carrau*, *Newport*, and *Escherichia coli* were isolated from rectal swabs samples of wild giant armadillos captured in the Brazilian Pantanal wetland. Antibiogram analyses revealed these bacteria were resistant to ß-lactam antibiotics. In the same area, *Malassezia furfur* dermatophytes were isolated from the carapace, abdominal and ventral skin, but not from ear canal samples. Soil samples from burrows identified the presence of *Microsporum gypseum* (SD Coutinho, UNIP, personal communication).

In the same study area, analysis of feces samples revealed endoparasites from the families *Strongylida* and *Eimeridae* spp. Ectoparasites (ticks) of the species *Amblyomma pseudoconcolor*, *A. sculptum*, *A. parvum*, *A. cajennense*, and *A. humerale* were identified in wild individuals from four different states in Brazil. Mite infestations of the species *Dasyponyssus neivai* have been recorded in wild individuals from the Pantanal (*Mesostigmata*: *Dasyponyssidae*). *Tunga* spp. and fly larvae of *Cochliomyia hominivorax* are commonly found in wild individuals.

In the Pantanal, studies reported wild individuals exposed to *Toxoplasma gondii*, *Trypanosoma cruzi* and *T. rangeli*. Wild individuals tested negative for *Leishmania* spp., *Mycobacterium leprae* and *Brucella abortus* (PCR and serodiagnostic) but presented antibodies anti-*Leptospira* (*Pomona*–and *Cynopteri*). A recent study detected a new hemoplasma species. Giant armadillos tested negative for viruses like Morbilivirus and Parvovirus. However, recent studies, using conventional PCR, detected a novel herpesvirus (*Cingulatid gammaherpesvirus*). In the Brazilian Cerrado savanna, molecular analysis (PCR) of two road-killed individuals tested negative for *Paracoccidioides brasiliensis* (F Antunes and E Bagagli, UNESP, unpublished data).

Human care

A search of the Species 360 (accessed 14 November 2021) international database on animals in captivity reveals that, currently, there are no registered giant armadillos held in captivity. However, unregistered individuals exist in some South American Zoos or private collections. The first record of the species in captivity dates to 1934 and the last animal held in captivity died in 1988. No known records exist of the species breeding in captivity. One female was received with its eyes still closed and was subsequently hand-raised in the Brasília Zoo, but died at 7 years of age. Although most records indicate that the species does not survive very long once in captivity, there are several records of animals living for 14 to 16 years. Eighteen (10 M, 3 F, 5 unsexed) giant armadillos are registered in Species 360. Zoological institutions recorded to have kept the species in the past include Lincoln Park Zoological gardens, Fort Worth Zoological Park, Smithsonian National Zoological Park, Oklahoma City Zoological Park, Philadelphia Zoo, Rotterdam Zoo, San Antonio Zoological Gardens and Aquarium, and Santa Cruz Museum of Natural History in the United States; and, Frankfurt Zoological gardens, Hannover Zoo, and Zoological Society of London in Europe.

Genetics

Giant armadillos have a diploid number (2n) of 50 chromosomes and a fundamental number (FN) of 76. Chromosomal numbers are lower in giant armadillos than in other species of armadillos: e.g., *Cabassous centralis* (2n = 62); *Dasypus hybridus* (2n = 64); *D. novemcinctus* (2n = 64); *D. septemcinctus* (2n = 64); *Euphractus sexcinctus* (2n = 58); *Chaetophractus villosus* (2n = 60); and *C. vellerosus* (2n = 62).

Phylogenetic analysis performed with mitochondrial genes, protein-coding nuclear genes and complete mitochondrial genes confirm the close genetic relatedness of giant armadillos and naked-tailed armadillos, genus *Cabassous*, which diverged about 25 million years ago.

In giant armadillos, the X chromosome is a medium-sized metacentric, and the Y chromosome is a small metacentric. Recently, is has been described an effective molecular method of sex identification for Xenarthra using a multiplex PCR for Zinc finger (ZF) and sex-determining region Y (SRY) gene. Like giant anteaters and six-banded armadillos, giant armadillos do not present polymorphisms between the sequences of ZFY and ZFX. However, this contrasts with other species of Xenarthra (e.g., *Dasypus novemcinctus*, *Cabassous unicinctus*, *Tamandua tetradactyla* and *Bradypus variegatus*). Molecular methods for sex identification are useful to study species without morphological sexual dimorphism or when diagnostic characteristics for sexing are lost (e.g., road-killed or poached individuals).

Only one population genetics study of giant armadillos exists. Rodrigues (2020) described 14 microsatellite loci to investigate the structure and genetic diversity of giant armadillos in populations that occupy areas of the Pantanal and Cerrado, in the Midwest of Brazil. They found a reduction in gene flow between the Pantanal and the Cerrado, probably due to the high degree of degradation and fragmentation of the Cerrado in the region. They also found genetic signs that these giant armadillo populations suffered a recent bottleneck and could be undergoing a process of genetic diversity loss. The average allelic richness of giant armadillos (AR = 3.46) was lower than that described for other xenarthrans that are not under extinction risk, such as *Chaetophractus vellerosus* (AR = 15) and *Dasypus novemcinctus* (AR = 12.6).

Threatened species that suffered a population decline have already lost part of its alleles. Hence, they tend to present a lower allelic richness, when compared to closely related species that are not under any threat of extinction. This research also encountered a low effective number of alleles in both studied populations, which indicates that the number of alleles that contributes to the

population genetic diversity is smaller than the total number of alleles encountered. This pattern is expected for highly threatened species and highlights the worrisome conservation status of giant armadillos in Midwestern Brazil. Nevertheless, moderate levels of mean heterozygosity were observed (Ho = 0.64; He = 0.63), which means that these populations still retain some level of genetic diversity, which is key for their adaptive and evolutionary potential. However, heterozygosity is lost more slowly than the other two diversity indices, and the long generation time and lifespan of giant armadillos could be acting as an intrinsic buffer against the loss of genetic diversity in these populations.

Giant armadillo genome size is 4.47 ± 0.34 SD pg (picograms) and has 4372 M base pairs. The complete mitochondrial genome is available from GenBank (NCBI, BioProject, accession number NC_028573). Genetic sequences are in GenBank for the following genes: TTN, RAG2, BRCA1, BRCA2, BCHE, APOB, ADORA3, RUNX2, ADRA2B, VWF, ZFY, ZFX, glycoprotein B, DNA polymerase.

Conservation

Despite being present in different habitats throughout South America, the population growth rate of giant armadillos is very low, and the species can easily be locally extirpated. The giant armadillo is classified as 'Vulnerable' (A2 cd) on the IUCN Red List of Threatened Species (Anacleto et al., 2014) and is also included in Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2021). According to Carter et al. (2016), national red lists classify giant armadillos as endangered in Colombia, Venezuela, Argentina, and Paraguay. It is considered vulnerable in Bolivia, Peru, Ecuador, and Brazil. In French Guiana, it is fully protected by law. Its main threats are habitat loss and fragmentation, road collisions, hunting, and suspected illegal trafficking (Anacleto et al., 2014).

Habitat loss

Habitat loss is one the biggest threats to giant armadillo persistence. In fact, their classification on the IUCN Red List is inferred based on the loss of habitat the species is experiencing throughout its range. Estimates for population declines based on habitat are of at least 30% in the past 21 years. Deforestation also often provides more access to hunters.

The extent of occurrence of giant armadillo distribution can provide an erroneous impression of the species conservation status, as the species has gone locally extinct in many areas within its distribution (e.g., in most Atlantic Forest remnants). Recently, fragments of the Cerrado and the Atlantic Forest in 344 watersheds of Mato Grosso do Sul state (259,641 km^2; Brazil) were explored and surveyed for evidence of giant armadillos. They confirmed the presence of the species in 164 watersheds, and its absence in 180 of them. They used these presence points to model the current potential distribution of the species using Maxent. Only 25% of the evaluated region was predicted to be suitable for giant armadillos. This highlights the incongruence between the polygons commonly used to portray the species distribution and the suitable area for the species. Furthermore, one of the most important explanatory variables for the species distribution was land cover and giant armadillo's presence probability was highest in forest formations. Nevertheless, only 0.15% of the areas suitable to giant armadillos in the region are strictly protected. In addition, over 25% of the suitable forest and savanna areas in the region have been lost in the last 33 years (1985–2018). This results in a severe fragmentation of the suitable areas left for the giant armadillos, with most suitable habitat patches (forest and savanna) surrounded by an agricultural matrix. Only four suitable patches larger than 100 km^2 remain in the region and are very distant from each other. There are only 69 patches larger than $\geq$25 km^2, which is the average area required for a single giant armadillo. Therefore, giant armadillos are likely to need to occupy several fragments to meet their resource requirements in this highly fragmented landscape. This means high exposure to the other threats listed below. In addition, this could also mean that the giant armadillo individuals recorded in this fragmented landscape could be part of declining or functionally extinct populations. This situation highlights the threat of habitat loss to giant armadillos not only in the state of Mato Grosso do Sul, but throughout its distribution.

Hunting

Armadillos, particularly nine-banded armadillos, are a preferred hunting target throughout South America. Due to the large size of adult giant armadillos, although rare, they are sought out by local communities throughout their distribution, particularly by subsistence hunters in the Amazon (Carter et al., 2016). The fresh sand at the entrance or within the mouth of the burrow can easily reveal if an armadillo is present in a burrow or not. In the Atlantic forest, in the Sooretama complex, giant armadillos are now considered functionally extinct due to hunting pressure (Fig. 7; Fontes et al., 2020). Due to their low population densities and low population growth rates, giant armadillos cannot be sustainably hunted. Hunting is a major threat to this species.

Roadkill

Giant armadillo carcasses are usually rare in road survey reports. However, 24 records of giant armadillo roadkill were reported on Brazilian highways between 2007 and 2020 in the Cerrado, Pantanal and Amazon biomes. This illustrates that highways are a threat to this species. There are several reasons why road killed giant armadillos are rarely reported including: (1) the species' low densities; (2) that they go extinct rapidly due to low population growth rates and therefore there will be few animals living near roads; (3) drivers sighting a giant armadillo carcass have been observed to stop to collect their claws and dispose of the carcass, reducing their detection by surveyors.

Fig. 7 Hunting evidence. A researcher from the Giant Armadillo Conservation Program stands by a giant armadillo burrow recently dug by poachers to enable its capture at Sooretama Biological Reserve, Espírito Santo, Brazil.

Fire

Fires are a threat to giant armadillos with deaths reported in several studies (Desbiez et al., 2020b; Silveira et al., 2009). Fires, particularly out of control fires, may burn accumulated biomass on top of burrows increasing heat, causing smoke inhalation, and burning the animal when it leaves its burrow.

Challenges in co-existence between humans and giant armadillos

Giant armadillos are sometimes killed by beekeepers as a retaliation for destroying beehive boxes. Giant armadillos have learned to stand up using their tail as a tripod to knock over hives to consume bee larvae in the frames. This issue has been reported throughout the Brazilian Cerrado, but also in the llanos of Colombia and the Argentinean Chaco. One giant armadillo can destroy a beekeeper's livelihood in a matter of weeks. To prevent this, beekeepers sometimes apply lethal poison on the fallen beehive which will kill the giant armadillo. This solves the problem as giant armadillos are solitary and occur at such low densities that the damage is usually done by a single individual. The poison will also kill *Eira barbara*, *Myrmecophaga tridactyla*, *Tamandua tetradactyla* and other species that also come to feed on the fallen hive. However, there are several techniques and methods to mitigate this threat, most involving alternative methods of installation and management of beehive boxes. The Armadillos & Honey Project in Mato Grosso do Sul, Brazil is focused on finding strategies that promote the co-existence between beekeepers and giant armadillos. The project has initiated a certification protocol to reward and open new markets to beekeepers that implement mitigation measures that prevent giant armadillo attacks allowing beekeepers to co-exist peacefully with giant armadillos.

Another reported conflict with people is due to superstitions rather than economic reasons. In some areas throughout their range, giant armadillos are believed to bring bad luck and even death to family members and therefore should be killed on site. Beliefs vary, but overall, it is believed that if you see a giant armadillo you, or those close to you, will suffer a negative consequence, which ranges from bad luck to death.

Illegal armadillo trade

In the past, giant armadillo parts were widely used by indigenous communities to carry and keep food (e.g., carapace) or for decorative purposes (e.g., claws). Due to the species rareness today, it is not known if there is still an illegal trade of giant armadillo parts. However, Anacleto et al. (2014) reported that the illegal capture of giant armadillos for clandestine sale to wealthy animal collectors may be a threat for the species.

Poisoning

Although not quantified, it is highly probable that pesticides represent a threat to giant armadillo health, reproduction, and general fitness. Cash crops such as soy, corn, cotton, and eucalyptus, which generally require heavy use of pesticides, have replaced giant armadillo habitat throughout their range particularly in the Brazilian Cerrado, and have been reported to affect the health of other mammal species in the region.

Conservation initiatives

There has been an increasing number of conservation initiatives for giant armadillos in recent years. The IUCN SSC Anteater, Sloth, and Armadillo specialist group (ASASG) brings together all armadillo specialists from around the world. The ASASG works on behalf of xenarthrans by supporting field research, conservation measures and educational programs in their range countries. In addition, the ASASG provides technical support to rehabilitation centers and zoological institutions that care about and care for xenarthrans. Founded in 2010, the Giant Armadillo Conservation Program is the longest running initiative dedicated exclusively to this species. It acts mainly in Brazil (Pantanal, Cerrado and Atlantic forest), but also in Argentina. Other initiatives such as: Projeto Tatu-Canastra Uberaba (Minas Gerais, Brazil), Cunaguaro Biodiversidad y Cultura (Colombia), and Armadillos de los Llanos Orientales (Fundacion Omacha, Colombia) also focus on local giant armadillo conservation. The Brazilian government launched an action plan for giant armadillos and other species of Xenarthra that brings together many armadillo specialists. More information on these initiatives can be found at:

- The IUCN SSC Anteater, Sloth and armadillo specialist group (ASASG, https://www.xenarthrans.org/)
- Brazilian National Action Plan for Giant Anteaters, Giant Armadillos and three banded armadillos https://sites.google.com/view/nucleo-pan-cpb/PANTATA
- The Giant Armadillo Conservation Program https://www.giantarmadillo.org/
- Projeto Tatu-Canastra Uberaba https://projetotatucanastra.com.br/
- Fundacion Omacha https://omacha.org/
- Cunaguaro Biodiversidad y Cultura http://www.cunaguaro.org/

Acknowledgment

We are thankful to the donors of the Giant Armadillo Conservation Program that allowed the 10-year study of giant armadillos in the wild. We also thank Danilo Kluyber and Nayra Rodrigues for their contributions to this chapter.

References

Anacleto TCS, Miranda F, Medri IM, et al. (2014) *Priodontes maximus*. IUCN 2014. The Red List of Threatened Species. Version 2014.3. Available from www.iucnredlist.org. [10 August 2021].

Aya-Cuero C, Superina M, and Rodríguez-Bolaños A (2015) Primeiros registros de crias de ocarro (*Priodontes maximus* Kerr, 1792) em Colombia. *Edentata* 16: 57–64.

Carter TS, Superina M, and Leslie DM (2016) *Priodontes maximus* (Cingulata: Chlamyphoridae). *Mammalian Species* 48: 21–34.

Desbiez ALJ and Kluyber D (2013) The role of giant armadillos (*Priodontes maximus*) as physical ecosystem engineers. *Biotropica* 45: 537–540.

Desbiez ALJ, Massocato GF, Kluyber D, Luba CN, and Attias N (2019) How giant are giant armadillos? The morphometry of giant armadillos (*Priodontes maximus* Kerr, 1792) in the Pantanal of Brazil. *Mammalian Biology* 95: 9–14.

Desbiez ALJ, Kluyber D, Massocato GF, Oliveira-Santos LGR, and Attias N (2020a) Spatial ecology of the giant armadillo *Priodontes maximus* in Midwestern Brazil. *Journal of Mammalogy* 101(1): 151–163.

Desbiez ALJ, Kluyber D, Massocato GF, Oliveira-Santos LGR, and Attias N (2020b) Life stage, sex, and behavior shape habitat selection and influence conservation strategies for a threatened fossorial mammal. *Hystrix* 31(2): 123–129.

Desbiez ALJ, Massocato GF, and Kluyber D (2020c) Insights in giant armadillo (*Priodontes maximus* Kerr, 1792) reproduction. *Mammalia* 84(3): 283–293.

Eisenberg JF and Redford KH (1999) *Mammals of the Neotropics: The Central Neotropics. Ecuador, Peru, Bolívia, Brazil*. Chicago: The University of Chicago Press.

Fontes BL, Desbiez ALJ, Massocato GF, et al. (2020) The local extinction of one of the greatest terrestrial ecosystem engineers, the giant armadillo (*Priodontes maximus*) in one of its last refuges in the Atlantic Forest will be felt by a large vertebrate community. *Global Ecology and Conservation* 24: e01357.

Kluyber D, Desbiez ALJ, Attias N, et al. (2021) Zoonotic parasites infecting free-living armadillos from Brazil. *Transboundary and Emerging Diseases* 68: 1639–1651.

Luba CN, Kluyber D, Massocato GF, et al. (2020) Size matters: Penis size, sexual maturity and their consequences for giant armadillo conservation planning. *Mammalian Biology* 100: 621–630.

Massocato GF and Desbiez ALJ (2019) Guidelines to identify individual giant armadillos, *Priodontes maximus* (Kerr, 1792), through camera traps. *Edentata* 20: 1–16.

Rodrigues NT (2020) *Diversidade genética e estruturação populacional do tatu-canastra (*Priodontes maximus*) em uma área do Centro-Oeste do Brasil*. Master's thesis São Carlos, São Paulo, Brazil: Centro de Ciências Biológicas e da Saúde: Federal University of São Carlos. 55 pp.

Silveira L, Jácomo ATA, Furtado MM, et al. (2009) Ecology of the giant armadillo (*Priodontes maximus*) in the grasslands of Central Brazil. *Edentata* 8–10: 25–34.

Further reading

Arteaga MC, Piñero D, Eguiarte LE, et al. (2012) Genetic structure and diversity of the nine-banded armadillo in Mexico. *Journal of Mammalogy* 93: 547–559.

Aya-Cuero C, Rodríguez-Bolaños A, and Superina M (2017) Population density, activity patterns, and ecological importance of giant armadillo (*Priodontes maximus*) in Colombia. *Journal of Mammalogy* 98: 770–778.

Banhos A, Fontes BL, Yogui DR, et al. (2020) Highways are a threat for giant armadillos that underpasses can mitigate. *Biotropica* 52: 421–426.

Barragán-Ruiz CE, Paviotti-Fischer E, Rodriguez-Castro KG, Desbiez AL, and Galetti PM Jr. (2021) Molecular sexing of Xenarthra: A tool for genetic and ecological studies. *Conservation Genetics Resources* 13(1): 41–45.

CITES (2021) Convention on international trade in endangered species of wild fauna and flora. Appendices I, II and III. Available at https://www.cites.org/eng/app/appendices.php. [08 July 2021].

Delsuc F, Stanhope MJ, and Douzery EJP (2003) Molecular systematics of armadillos (Xenarthra, Dasypodidae): Contribution of maximum likelihood and Bayesian analyses of mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 28(2): 261–275.

Desbiez ALJ, Oliveira B, and Catapani ML (2020) Bee careful! Conflict between beekeepers and giant armadillos (*Priodontes maximus*) and potential ways to coexist. *Edentata* 21: 1–12.

Desbiez ALJ, Massocato GF, Attias N, and Cove M (2020) Comparing density estimates from a short-term camera trap survey with a long-term telemetry study for a rare, wide-ranging nocturnal species with fossorial habits. *Mastozoologia Neotropical* 27(2): 241–246.

Desbiez ALJ, Massocato GF, Kluyber D, and Attias N (2021) Methods for the characterization of activity patterns of elusive species: The giant armadillo in the Brazilian Pantanal. *Journal of Zoology*. https://doi.org/10.1111/jzo.12921.

Desbiez ALJ, Larsen D, Massocato GF, et al. (2021) *First Estimates of Potential Lifespan of Giant Armadillo (*Priodontes maximus*) in the Wild*. Edentata. In press.

Di Blanco YE, Desbiez ALJ, di Francescantonio D, and Di Bitetti MS (2020) Excavations of giant armadillos alter environmental conditions and provide new resources for a range of animals. *Journal of Zoology* 311: 227–238.

Emmons LH and Feer F (1997) *Neotropical Rainforest Mammals: A Field Guide*. The Chicago, Illinois: University of Chicago Press.

Ferraz KMPMB, Oliveira B, Attias N, and Desbiez ALJ (2021) Species distribution models reveals only highly fragmented suitable patches for giant armadillos in the Brazilian Cerrado. *Perspectives in Ecology and Conservation* 19: 43–52.

Frankham R, Ballou JD, and Briscoe DA (2008) *Fundamentos de genética da conservação*. Ribeirão Preto: Sociedade Brasileira de Genética.

Hailer F, Helander B, Folkestad AO, et al. (2006) Bottlenecked but long-lived: High genetic diversity retained in white-tailed eagles upon recovery from population decline. *Biology Letters* 2: 316–319.

Kluyber D, Lopez RPG, Lima CFM, et al. (2020) Anesthesia and surgery protocols for intra-abdominal transmitter placement in four species of wild armadillo. *Journal of Zoo and Wildlife Medicine* 51: 514–526.

Nardelli M, Ibánez EA, Dobler D, et al. (2016) Genetic structuring in a relictual population of screaming hairy armadillo (*Chaetophractus vellerosus*) in Argentina revealed by a set of novel microsatellite loci. *Genetica* 14(4): 469–476.

Noss AJ, Peña R, and Rumiz DI (2004) Camera trapping *Priodontes maximus* in the dry forests of Santa Cruz, Bolivia. *Endangered Species Update* 21: 43–52.

Nowak RM (1999) *Walker's Mammals of the World*. Baltimore: Johns Hopkins University Press.

Prince MR and Hadfield MG (2014) Population genetics and the effects of a severe bottleneck in an ex-situ population of critically endangered Hawaiian tree snails. *PLoS One* 9(12): e114377.

Quiroga VA, Di Blanco YE, Noss A, Paviolo AJ, and Di Bitetti MS (2017) The giant armadillo (Priodontes maximus) in the argentine Chaco. *Mastozoologia Neotropical* 24: 163–175.

Smith P (2007) Giant armadillo *Priodontes maximus* (Kerr, 1792). Mammals of Paraguay N° 6. In: *FAUNA Paraguay: Handbook of the mammals of Paraguay*, Available at http://www.faunaparaguay.com/priodontesmaximus.html. [08 Jun 2021].

Srbek-Araujo AC, Scoss LM, Hirsch A, and Chiarello AG (2009) Records of the giant-armadillo *Priodontes maximus* (Cingulata: Dasypodidae) in the Atlantic Forest: Are Minas Gerais and Espírito Santo the last strongholds of the species? *Zoologia* 26: 461–468.