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CONSERVATION PERSPECTIVES FOR A HIGHLY DISPARATE LINEAGE OF MAMMALS: THE XENARTHRA

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ABSTRACT. The Xenarthra, which are endemic to the Americas, consist of two distinct clades, the Pilosa (anteaters and sloths) and the Cingulata (armadillos). The association between xenarthrans and humans dates back to ancient times. Although these associations do not appear to have negatively impacted all wild populations, hunting probably contributed to the extinction of some xenarthrans in archaeological-geological times and, more recently, to the depletion or extinction of local populations. Undoubtedly, human activities are increasingly impacting the wild populations of many xenarthran species. According to the last assessment for the IUCN Red List of Threatened Species, 15 of the 30 species of Xenarthra are classified as Least Concern, five as Data Deficient, five as Near Threatened, and five are included in a threatened category, with one (*Bradypus pygmaeus*) being considered Critically Endangered, and four (*Myrmecophaga tridactyla*, *Bradypus torquatus*, *Priodontes maximus*, and *Tolypeutes tricinctus*) designated as Vulnerable. Here, we discuss the current taxonomic challenges of working with xenarthrans and the impacts of those challenges on the conservation of these animals. We evaluate the main threats affecting the Xenarthra now and in the future, we identify some successful conservation initiatives, and we highlight the importance of initiatives by individual experts. Our goals are to summarize the current status of xenarthrans and to facilitate the development and implementation of conservation strategies for these animals.

RESUMEN. Estrategias de conservación para un linaje divergente de mamíferos: los Xenarthra. Los xenartros son un grupo de mamíferos endémicos de América que contiene dos clados distintos, Pilosa (hormigueros y perezosos) y Cingulata (armadillos). La asociación entre los xenartros y el hombre se remonta a tiempos remotos. Si bien algunas asociaciones pueden no haber representado un impacto negativo significativo en las poblaciones silvestres, la caza probablemente contribuyó a la extinción de xenartros en tiempos arqueológicos-geológicos y, más recientemente, a la degradación de sus poblaciones, llegando a registrarse numerosas extinciones locales. Sin lugar a duda, las actividades humanas están impactando cada vez más las poblaciones silvestres de los xenartros. Según la última evaluación global de los xenartros para la Lista Roja de Especies Amenazadas de la UICN, 15 de las 30 especies están clasificadas como Preocupación Menor (LC), cinco como Datos Insuficientes (DD), cinco como Casi Amenazadas (NT) y cinco están incluidas en una categoría amenazada, una de ellas en Peligro Crítico (CR; *Bradypus pygmaeus*) y cuatro Vulnerables (VU; *Myrmecophaga tridactyla*, *Bradypus torquatus*, *Priodontes maximus* y *Tolypeutes tricinctus*). En el presente trabajo discutimos los desafíos taxonómicos que estamos afrontando y su impacto en la conservación, evaluamos las principales amenazas que están sufriendo las especies y su perspectiva a futuro, enumeramos algunas iniciativas de conservación exitosas y destacamos la importancia de las iniciativas de expertos individuales. Con esta revisión pretendemos plantear las perspectivas

relacionadas con la evaluación del estado de conservación de los xenartros como así también con el desarrollo y la implementación de estrategias de conservación.

RESUMO. Perspectivas de conservação para uma linhagem altamente díspar de mamíferos: os Xenarthra.

Os Xenarthra, endêmicos das Américas, consistem em dois clados distintos, Pilosa (tamanduás e preguiças) e Cingulata (tatus). A associação entre xenartros e humanos remonta aos tempos antigos. Embora essas associações não pareçam ter impactado negativamente todas as populações selvagens, a caça provavelmente contribuiu para a extinção de alguns xenartros nos tempos arqueológico-geológicos e, mais recentemente, para o esgotamento ou extinção das populações locais. Sem dúvida, as atividades humanas estão impactando cada vez mais as populações selvagens de muitas espécies de xenartros. De acordo com a última avaliação da Lista Vermelha de Espécies Ameaçadas da IUCN, 15 das 30 espécies de Xenarthra são classificadas como Menos Preocupantes (LC), 5 como Deficientes em Dados (DD), 5 como Quase Ameaçadas (NT) e 5 são incluídas em uma categoria ameaçada, com uma (*Bradypus pygmaeus*) sendo considerado Criticamente em Perigo (CR) e quatro (*Myrmecophaga tridactyla*, *Bradypus torquatus*, *Priodontes maximus* e *Tolypeutes tricinctus*) designados como Vulneráveis (VU). Aqui, discutimos os desafios taxonômicos atuais do trabalho com xenartros e os impactos desses desafios na conservação desses animais. Avaliamos as principais ameaças que afetam os Xenarthra agora e no futuro, identificamos algumas iniciativas de conservação bem-sucedidas e destacamos a importância das iniciativas de especialistas individuais. Nossos objetivos são resumir o status atual dos xenartros e facilitar o desenvolvimento e a implementação de estratégias de conservação para esses animais.

Key words: Cingulata, Pilosa, taxonomy, threatened species.

Palabras clave: Cingulata, especies amenazadas, Pilosa, taxonomía.

Palavras chave: Cingulata, espécies ameaçadas, Pilosa, taxonomia.

INTRODUCTION

The superorder Xenarthra is a monophyletic lineage of mammals that is endemic to the Americas (Simpson 1980). The Xenarthra consists of two distinct clades, the Pilosa (anteaters and sloths) and the Cingulata (armadillos). Xenarthrans are considered to be one of the four primary lineages of placental mammals (Springer et al. 2005; Murphy et al. 2007; O’Leary et al. 2013), with molecular data indicating that the Xenarthra arose around 100 million years ago (Delsuc et al. 2004). Although at first sight the Pilosa and Cingulata appear to be morphologically very different, they share a range of synapomorphies, including additional intervertebral articulations, a reduction or loss of premaxillary teeth, and ossified sternal ribs (Gaudin & McDonald 2008). They also share several physiological peculiarities, such as low basal metabolic rates as well as low and variable body temperatures (McNab 1985).

The most outstanding character of armadillos (Dasypodidae and Chlamyphoridae) is their dorsal body armor. It consists of numerous osseous dermal scutes that are arranged in a regular pattern and covered by keratinous epidermal scales. The dermal scutes are generally organized into fixed scapular and pelvic shields that are separated by a variable number of flexible bands. The head is protected by a cephalic shield. In most species—except those of the genus *Cabassous*—the tail is also covered by scutes (Gardner 2008). Living armadillos range from 100 g (*Chlamyphorus truncatus*) to 20–60 kg (*Priodontes maximus*) (Superina & Abba 2018) and can be found from the southern US to the southern tip of South America (Fig. 1). All armadillos are semi-fossorial and use burrows for resting, protection, and thermoregulation (Superina & Abba 2018).

The anteaters (Myrmecophagidae and Cyclopedidae) share several intriguing characteristics, such as a complete absence of teeth and a very

long tongue that they use to capture ants, termites, and other insects. Living anteaters can be as small as 200-300 g (*Cyclopes* spp.) or as large as 20-45 kg (*Myrmecophaga tridactyla*). The general habits of anteaters vary from completely arboreal (*Cyclopes* spp.) to semi-arboreal or scansorial (*Tamandua* spp.) to cursorial or terrestrial (*M. tridactyla*) (Bertassoni 2018; Miranda 2018). They occur from southern Mexico to northern Argentina and Uruguay (Fig. 1).

All extant sloths (Bradypodidae and Megalonychidae) are strictly arboreal, with the smallest species weighing about 2.5 kg and the largest up to 11 kg. Their global range is restricted to forested areas from Honduras to central Bolivia and Brazil (Fig. 1). Sloths have long, coarse hair with longitudinal grooves (*Choloepus* spp.) or transverse cracks (*Bradypus* spp.) that promote the growth of algae (Suutari et al. 2010). A mutualistic relationship has been identified between sloths, algae, and moths living in the sloth fur (Pauli et al. 2014). Sloths are herbivores; while *Bradypus* is strictly folivorous, *Choloepus* is a generalist that also eats fruit, flower buds, young stems, and some animal material (Moraes-Barros 2018; Pauli 2018).

The association between xenarthrans and humans dates back to ancient times. For example, armadillos have been consumed as a protein source for centuries (Superina & Abba 2018) and anteaters appear in popular folklore and mythology (Bertassoni 2018). While these historical associations may not always have resulted in significant negative impacts on wild populations, hunting has likely contributed to the extinction of some xenarthrans over archaeological-geological time scales (Cione et al. 2003) and, more recently, to declines in extant populations (e.g., Peres & Nascimento 2006). There is no doubt that human activities are increasingly affecting the Xenarthra both directly and indirectly, with local extinctions already documented (e.g., Miranda et al. 2014a). Here, we discuss the challenges and possibilities associated with assessing the conservation status of each member of the Xenarthra as well as developing and implementing conservation strategies for these animals.

CONSERVATION STATUS OF THE XENARTHRA

The Xenarthra are almost exclusive to the Neotropics. At least one species occurs in each of the 21 primary countries of Central and South America (excluding islands). A single species, the nine-banded armadillo (*Dasypus novemcinctus*), can also be found in southern North America (Gardner 2008). According to the latest global assessment of the Xenarthra for the IUCN Red List of Threatened Species, 15 out of 30 species are listed as Least Concern, five as Data Deficient, five as Near Threatened, and five are included in a threatened category, with one being considered Critically Endangered and four being considered Vulnerable (Table 1, IUCN 2018). Thus, while half of extant xenarthrans are not thought to be facing significant conservation threats, others are clearly at risk due primarily to the effects of human activity.

Within Central and South America, numerous countries have compiled national lists of threatened species, at least some of which include xenarthrans. Comparing these more localized lists is difficult, in large part because data are often incomplete. For example, it is frequently unclear if species that fail to make national lists do so because they are considered to be of Least Concern or because they have not been assessed. Further, the methods used to compile different national lists as well as the definitions used to categorize taxa vary by country and thus likely reflect different suites of factors that were used to assess conservation status (e.g., extinction risk, conservation priorities, rarity, cultural significance; Miller et al. 2007). Collectively, these uncertainties preclude a meaningful, comprehensive assessment of the national and global conservation status of Xenarthra species.

Due to these challenges, we limited our analyses to species assigned to a threatened category (Vulnerable, Endangered, Critically Endangered, threatened, fully protected by national law) at either the national or global level. We calculated the percentage of all countries in

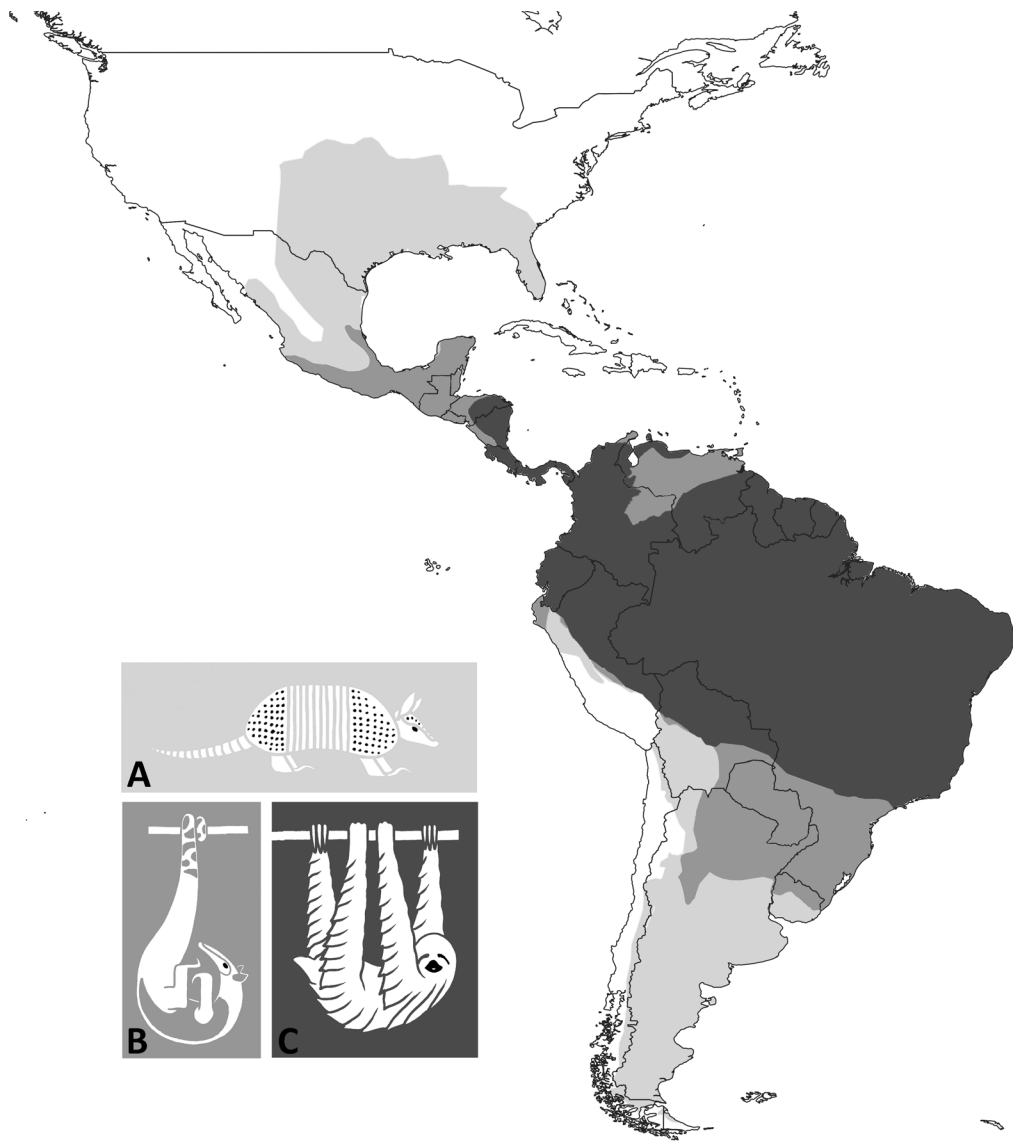


Fig. 1. Global distribution of (A) armadillos (Dasypodidae and Chlamyphoridae; light grey), (B) anteaters (Myrmecophagidae and Cyclopedidae; intermediate grey), and (C) sloths (Bradypodidae and Megalonychidae; dark grey). Note that armadillos are present throughout the range of anteaters and sloths and that anteaters occur throughout the entire distribution of sloths.

which the species occurs and is currently listed as threatened. Our analysis revealed that species that are considered threatened at a global level are also considered threatened in all countries in which they occur (**Table 1**). For example, the giant armadillo (*P. maximus*) is listed as Vulnerable in nine out of 11 (81.8%) countries

in which it is found (the two non-listed countries do not maintain threatened species lists) and is regionally extinct in Uruguay. Similarly, the giant anteater (*M. tridactyla*), which occurs in 17 countries, is listed as threatened in 13 (76.5%), and is regionally extinct in El Salvador and Belize.

Table 1

Currently recognized species of Xenarthra, their global conservation status (IUCN Red List of Threatened Species), number of countries in which they occur, and the percentage of countries that present local threats (number of countries in which a species is listed as threatened/total of countries of occurrence, multiplied by 100). Conservation categories listed are: LC, Least Concern; VU, Vulnerable; CR, Critically Endangered; NT, Near Threatened; DD, Data Deficient.

Species	Global status	Countries of occurrence	% of local threat
<i>Cyclopes didactylus</i>	LC	16	25
<i>Tamandua mexicana</i>	LC	12	42
<i>Tamandua tetradactyla</i>	LC	12	17
<i>Myrmecophaga tridactyla</i>	VU	17	76
<i>Bradypus variegatus</i>	LC	10	0
<i>Bradypus pygmaeus</i>	CR	1	100
<i>Bradypus torquatus</i>	VU	1	100
<i>Bradypus tridactylus</i>	LC	5	0
<i>Choloepus hoffmanni</i>	LC	9	11
<i>Choloepus didactylus</i>	LC	8	0
<i>Priodontes maximus</i>	VU	11	82
<i>Cabassous centralis</i>	DD	11	27
<i>Cabassous chacoensis</i>	NT	2	0
<i>Cabassous unicinctus</i>	LC	10	10
<i>Cabassous tatouay</i>	LC	4	50
<i>Euphractus sexcinctus</i>	LC	6	0
<i>Zaedyus pichiy</i>	NT	2	0
<i>Tolypeutes matacus</i>	NT	4	25
<i>Tolypeutes tricinctus</i>	VU	1	100
<i>Dasypus septemcinctus</i>	LC	2	0
<i>Dasypus mazzai</i>	DD	1	0
<i>Dasypus kappleri</i>	LC	9	0
<i>Dasypus hybridus</i>	NT	4	0
<i>Dasypus pilosus</i>	DD	1	100
<i>Dasypus novemcinctus</i>	LC	20	10
<i>Dasypus sabanicola</i>	NT	2	0
<i>Chlamyphorus truncatus</i>	DD	1	0
<i>Calyptophractus retusus</i>	DD	3	0
<i>Chaetophractus villosus</i>	LC	4	0
<i>Chaetophractus vellerosus</i> *	LC	5	40

* Assessed as *Chaetophractus nationi* in Peru and Chile. Both *C. vellerosus* and *C. nationi* are included in the Red List of Bolivia (as NT and EN, respectively, Aguirre et al. 2009); only the status of *C. vellerosus* has been considered for this analysis.

Source: Meerman (2005); Rodríguez-Mahecha et al. (2006); Mejía Ordoñez & House R. (2007); Autoridad Nacional del Ambiente de la República de Panamá (2008); Aguirre et al. (2009); Departamento de Vida Silvestre CONAP (2009); Tirira (2011); Catzefflis & de Thoisy (2012); Superina et al. (2012a, 2012b); Soutullo et al. (2013); Ministerio de Agricultura y Riego (2014); Instituto Chico Mendes de Conservação da Biodiversidade (2015); Rodríguez et al. (2015); Ministerio del Medio Ambiente (2016); Saldívar et al. (2017); Áreas Protegidas y Parques Nacionales de Costa Rica (2018); Medina-Fitoria (2018)

One outcome of this analysis was the discovery that of the 15 species of xenarthrans that are globally listed as being of Least Concern, eight (53.3%) are threatened in at least one country in which they occur and, in the case of the northern tamandua (*Tamandua mexicana*), in as many as 42% of the relevant countries. The percentage of xenarthran species designated as being of Least Concern by the IUCN Red List but that are nationally threatened is much higher compared to that for other clades of mammals in Brazil, Colombia, China, and the Philippines, which averaged only 2% of species that were threatened nationally but not globally (Brito et al. 2010). The reasons for this disparity should be assessed, as they may indicate a need for re-categorization of some species at the global level. Similarly, the status of two endemic species—*Dasypus pilosus* and *Tolypeutes tricinctus*—needs to be re-examined, as their assigned category at the national level does not coincide with that of the IUCN Red List. In some cases, differences between the global and national assessments may reflect taxonomic issues, which we discuss below.

TAXONOMIC CHALLENGES

Over the past 30 years, biologists have increasingly recognized that taxonomy and conservation go hand-in-hand (Mace 2004). Multiple publications have argued that we cannot conserve organisms that we cannot identify and that our attempts to understand the consequences of environmental change and habitat degradation are compromised if we cannot recognize and describe the individual components of natural systems (Mace 2004; Morrison III et al. 2009). Indeed, taxonomists and conservationists need to work together to develop explicit rules to delimit the taxonomic units treated as species for the purpose of conservation planning and assessment (Mace 2004).

At first glance, extant xenarthrans seem to represent a relatively small group of mammals with a stable taxonomy. According to recent revisions (Gardner 2005a, 2005b, 2008), only 31 species of extant Xenarthra were described between 1758 and 2001, with four of these

species (*Dasypus sabanicola* Mondolfi, 1968, *Cabassous chacoensis* Wetzel, 1980, *Dasypus yepesi* Vizcaíno, 1995, and *Bradypus pygmaeus* Anderson and Handley, 2001) discovered between 1968 and 2001. All 31 species were described based on morphological or morphometric analyses, or a combination of both.

The advent of new morphometric and, in particular, molecular techniques has rocked the stability of xenarthran taxonomy, resulting in important changes—a process that has only just begun and will certainly lead to additional taxonomic changes in the near future. The last three years alone have produced three new species descriptions of silky anteaters (*Cyclopes*), six revalidations (four *Cyclopes* and two *Dasypus* species), and one synonymization of hairy armadillos (*Chaetophractus*), increasing the number of extant xenarthran species to thirty-nine. Additional new species and three more synonymizations within the Dasypodidae, as well as three generic rearrangements (*D. kappleri*, *D. pilosus* and *Bradypus torquatus*), have been proposed but require confirmation before they can be implemented (see below). In short, xenarthran taxonomy is now experiencing an unprecedented level of activity.

Description of new species. The most significant of these recent changes have occurred within the genus *Cyclopes* and have led to an important increase in the number of known xenarthran species. This genus of small-bodied anteaters was thought to be monotypic, but a 10-year-long investigation by Miranda et al. (2018) provided morphological, morphometric, and molecular evidence of the validity of four previous species designations: *C. didactylus* (Linnaeus, 1758); *C. ida* Thomas, 1900; *C. catellus* Thomas, 1928; and *C. dorsalis* (Gray, 1865). In addition, this revision included descriptions of three new species of silky anteaters: *C. rufus* Miranda et al., 2018; *C. thomasi* Miranda et al., 2018; and *C. xinguensis* Miranda et al., 2018. Currently, *C. didactylus* is identified on the IUCN Red List as being of Least Concern, due primarily to its wide geographic distribution and presumably large total number of individuals (Miranda et al. 2014b). Each of the seven recently recognized species of *Cyclopes* will need to be assessed for the

IUCN Red List, and it is probable that at least some will be included in a threatened category due to their more restricted distributions as well as associated local conservation threats (F. Miranda, pers. comm.). Making these assessments, however, will be challenging. For example, the exact distributional range limits of the seven newly recognized species are not well established, nothing is known regarding the population status of each, and little is known about potential ecological differences that might impact conservation efforts (Miranda et al. 2018). Realistic assessments of the conservation status of each species will require additional fieldwork, an undertaking that is particularly difficult for such small, inconspicuous animals that are restricted to the forest canopy.

Similar challenges surround the two taxonomic revalidations that have occurred within the Dasypodidae. Based on integrative morphological and morphometric analyses, Feijó & Cordeiro-Estrela (2016) and Feijó et al. (2018) proposed the elevation of two subspecies of *D. kappleri* to species level, thus recognizing *D. kappleri* Krauss, 1862, *D. pastasae* (Thomas, 1901), and *D. beniensis* Lönnberg, 1942. This new taxonomy has not yet been widely adopted (McDonough & Loughry 2018), primarily because its confirmation via molecular data has occurred only very recently (Feijó et al. 2019). As with *Cyclopes*, assessing the conservation status of these three new species of greater long-nosed armadillos will be difficult due to the lack of basic information on their exact ranges and potential threats.

"Future" new species. The widespread *D. novemcinctus* may in fact constitute a species complex. Phylogeographic and molecular analyses have identified several lineages of *D. novemcinctus* that may constitute previously unrecognized species (Arteaga et al. 2019; Feijó et al. 2019). For example, one lineage of this species in French Guiana has been revealed to be different at the molecular (Huchon et al. 1999; Gibb et al. 2016) as well as at the anatomical and morphological levels (Billet et al. 2017; Hautier et al. 2017). Although splitting of this species would not affect the conservation status of *D. novemcinctus* (Least Concern), it would likely add at least one additional species

to the already relatively long list of armadillo species categorized as Data Deficient.

Among sloths, Plese et al. (2016) identified three distinct geographical groups of *Choloepus hoffmanni* in Colombia that differ with regard to some external diagnostic characters. Analyses are underway to determine whether these morphological differences may warrant a distinct taxonomic arrangement. As with *Cyclopes* and *D. kappleri*, splitting *Ch. hoffmanni* into several species would require new Red List assessments, both at the national and global levels. Information on the ecologies, exact geographic distributions, and conservation threats to these species are lacking and difficult to obtain and thus it is likely that taxonomic reassessment would be followed by confusion regarding appropriate conservation efforts.

Synonymizations. Another taxonomic change with important conservation implications is the synonymization of *Chaetophractus nationi* with *Chaetophractus vellerosus* (Abba et al. 2015a). While *Cha. nationi* was previously listed as Vulnerable on the IUCN Red List, *Cha. vellerosus* was considered to be of Least Concern (Abba & Superina 2010). The synonymized species is now listed as of Least Concern (IUCN SSC Anteater, Sloth and Armadillo Specialist Group 2017), a designation that may serve to mask conservation challenges to populations previously recognized as *Cha. nationi*. At the national level, *Cha. nationi* is listed as Endangered in Peru (Ministerio de Agricultura y Riego 2014) and as Vulnerable in Chile (Ministerio del Medio Ambiente 2016), indicating concerns about these animals. Assuming that local threats and population assessments have not changed, it seems reasonable that the status of animals in Peru and Chile should remain the same after the synonymization, particularly given that *Cha. vellerosus* does not occur in those countries. The situation in Bolivia also argues for the importance of national Red List assessments. Both high-elevation northern populations (formerly *Cha. nationi*) as well as southern populations (*Cha. vellerosus*) are declining in Bolivia but the global listing of *Cha. vellerosus* does not reflect these more local conservation concerns. These animals need to be included in a threatened category at the national level

in order to receive protection through effective conservation measures (Abba et al. 2015a); if this is not done, the high-altitude populations may well become extinct in the near future.

Additional, proposed synonymizations. The long-nosed armadillos (Dasypodidae) are currently undergoing a thorough taxonomic revision. As part of this effort, Gibb et al. (2016), Feijó et al. (2018) and Feijó et al. (2019) have suggested that *Dasypus hybridus* (currently Near Threatened, Abba & Gonzalez 2014) is a synonym for *D. septemcinctus* (Least Concern, Anacleto et al. 2014), as had been proposed previously by Frechkop & Yepes (1949) but rejected by both Hamlett (1939) and Wetzel (1985). While this synonymization is still being debated (see Abba et al. 2018), if accepted it would result in a long-nosed armadillo species with a wide geographic range that would likely be categorized as being of Least Concern.

A particularly surprising potential taxonomic change is the proposed synonymization of *Dasypus mazzai* and *D. sabanicola*. The taxonomic status of *D. mazzai* has long been uncertain. Originally described by Yepes (1933), this small long-nosed armadillo was re-examined by Vizcaíno (1995), who identified its holotype as a juvenile *D. novemcinctus* and other specimens as *D. novemcinctus*, *D. hybridus* or *D. septemcinctus*. All remaining, unclassified individuals were assigned to a new species named *D. yepesi*. Recent morphological (Feijó & Cordeiro-Estrela 2014; Feijó et al. 2018) and molecular (Abba et al. 2018) analyses appeared to have resolved the status of this group, concluding that the correct name for this long-nosed armadillo is *D. mazzai* Yepes, 1933. Studies by Gibb et al. (2016), however, have revealed that the mitogenome of *D. mazzai* is very similar to that of *D. sabanicola* (98.7% identity), leading to the proposed synonymization of these species. *D. sabanicola* occurs in the Llanos of Venezuela and Colombia and is listed as Near Threatened, while the Data Deficient *D. mazzai* is known only from northern Argentina (Abba & Vizcaíno 2014; Superina et al. 2014c; Abba et al. 2018; McDonough & Loughry 2018). Additional analyses are needed to understand fully these molecular results. The

synonymization of *D. mazzai* and *D. sabanicola* would generate numerous questions, including inquiries regarding the taxonomic identity of small long-nosed armadillos occurring in the area between the known ranges of these two species. This taxonomic change would also have a significant impact on the global conservation status of these animals. The resulting synonymized species would have a large geographic distribution that could lead to its listing as being of Least Concern; this designation would potentially reduce the incentive to conduct the additional field studies required to understand fully the animals' ecology and conservation needs.

Proposed generic rearrangements. Forty years ago Wetzel & Mondolfi (1979) proposed that *Dasypus kappleri* should be placed in its own subgenus *Hyperoambon* due to its distinctive morphology. A recent molecular study identified *D. kappleri* as sister to all other long-nosed armadillo species, which may be consistent with placement in a distinct genus (Gibb et al. 2016). The recent study that split *D. kappleri* into three species (see above), however, supported Wetzel & Mondolfi's (1979) original idea of the subgenus *Hyperoambon* (Feijó et al. 2019). Similarly, Wetzel & Mondolfi (1979) placed *Dasypus pilosus* in the subgenus *Cryptophractus*. Castro et al. (2015) proposed to raise the latter to the genus level, which was contradicted by Gibb et al. (2016), while Feijó et al. (2019) suggested that the subgenus *Cryptophractus* should be resurrected. Clearly, more studies are needed to elucidate the correct taxonomic placement of the existing species of *Dasypus*.

Finally, *Bradypus torquatus*, one of the most threatened species of xenarthrans, is the sister to the other three species of *Bradypus* (Moraes-Barros et al. 2011; Gibb et al. 2016); its distinct morphology may argue for its placement in the separate genus *Scaeopus* (Barros et al. 2008). These proposed taxonomic changes to the Xenarthra may not affect the conservation status of the associated species, but they may increase the need for conservation efforts by revealing greater phylogenetic depth among currently recognized taxa.

THREATS AFFECTING WILD XENARTHROPOID POPULATIONS

Wild populations of xenarthrans are thought to be subject to a range of conservation challenges (Fig. 2), although few studies have evaluated the effects of these threats in detail. Species-specific conservation strategies, however, depend on clear identification of the type of threat, as well as the nature and extent of its impact on the taxa in question. As a result, much work is needed to be able to provide accurate assessments of the conservation challenges facing natural populations of xenarthrans. Below, we consider several threats currently faced by these animals.

Hunting by humans. The majority of species in both the Cingulata and Pilosa are affected by hunting and trapping (Fig. 2), although the reasons for these pressures differ among taxa. Virtually all armadillo species are used as a protein source (Kennerley et al. 2018). The impacts of subsistence hunting may be increasing in areas subject to forest fragmentation because the latter facilitates access to previously undisturbed areas and the associated populations of armadillos (Peres 2001). Hunting pressure on small-bodied armadillo species may also be increasing due to the reduction of alternative, larger-bodied game species (Peres 2000). Further, a shift from subsistence to commercial armadillo hunting has been observed in regions such as the Llanos of Colombia, where changes in the demography of human populations have created a market for xenarthran meat (Superina et al. 2014d). The impact of these changes in hunting pressures on wild armadillo populations needs to be carefully assessed, after which appropriate mitigation measures can be identified and implemented (see e.g. Superina et al. 2014d, 2019).

Although some species of Pilosa are used locally as a protein source, these animals are more frequently hunted for use in the pet trade. In some countries (e.g., Colombia), illegal trafficking of sloths has been identified as a significant threat to their conservation due to the large numbers of individuals that are extracted from

the wild, the extremely high mortality rates before these animals reach the pet market, and the low survival rates for sloths kept as pets (Ministerio de Ambiente, Vivienda y Desarrollo Territorial de Colombia 2008; Superina et al. 2019). Anteaters are also subject to this problem. For example, the commercial trade of tamanduas (mainly *Tamandua tetradactyla*) in the United States has undergone a sustained and worrisome increase (Gramieri 2015). Because reproductive rates for tamanduas in captivity are low (Superina et al. 2008), the majority of individuals entering the pet trade are captured in the wild. As with sloths, mortality rates are high during extraction from the wild, acclimation to captive conditions, importation into the United States, and following sale to people who are ill-prepared to care for this challenging species. Although the IUCN SSC Anteater, Sloth and Armadillo Specialist Group (ASASG) and the Pangolin, Aardvark, and Xenarthra Taxon Advisory Group (PAX TAG) of the Association of Zoos and Aquariums (AZA) have initiated a joint campaign to reduce the tamandua trade (IUCN SSC Anteater, Sloth and Armadillo Specialist Group 2014), implementation of additional measures, such as legal protection of the affected species within their geographic ranges and inclusion in CITES, should be considered as part of efforts to halt the use of xenarthrans as pets.

Changes in land use. Changes in how habitats are used also affect a significant number of the Xenarthra (Fig. 2). Response to such changes (e.g., modifications of agricultural practices) may differ markedly among xenarthrans (e.g., Abba et al. 2007; Abba et al. 2015b; Abba et al. 2016). For example, while some armadillos (e.g., *Euphractus sexcinctus*, *ChaetophRACTUS villosus*) seem to tolerate at least some degree of habitat modification and appear to thrive in agricultural plantations (Anacleto et al. 2006; Abba et al. 2015b, 2016), others such as *P. maximus* are more restricted to pristine habitats (Carter et al. 2016). While two-toed sloths (*Ch. hoffmanni*) and, to a lesser degree, three-toed sloths (*B. variegatus*) use shade-grown cocoa plantations in Costa Rica, these

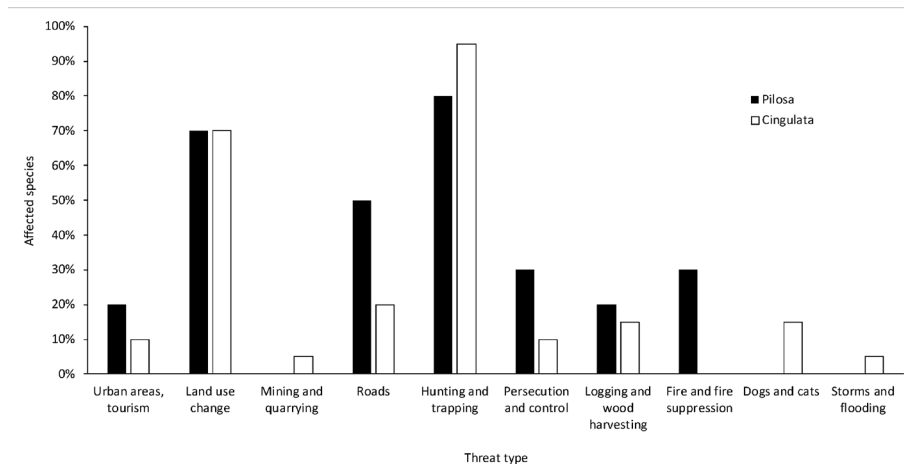


Fig. 2. Percentage of Pilosa (black bars) and Cingulata (white bars) affected by different types of environmental threats. Source: IUCN (2018).

animals strongly avoid monocultures (Mendoza et al. 2015), thereby demonstrating clear differences in the use of modified landscapes. Given the potential for different changes in land use to produce distinct impacts on these animals, additional studies are needed to explore the effects of specific habitat modifications and to identify practices that allow agro-industrial activities and xenarthrans to coexist.

Changes in land use may also have indirect effects on xenarthrans. For example, rather than impacting animals directly, the use of agrochemicals may reduce the availability of insects, which are the primary food resource for anteaters and most armadillos (Redford 1985; Trujillo & Superina 2013; Abba et al. 2016; Superina et al. 2019). At present, it is not known if agrochemicals have lethal consequences for xenarthrans due to either direct exposure or ingestion of contaminated insects (Braga et al. 2014). Further, it is not known whether the reduction of insects leads to the displacement of xenarthrans to undisturbed habitats. Herbst et al. (1989) determined that nine-banded armadillos have relatively low plasma cholinesterase activity, which may make them more sensitive to the organophosphates that are frequently used in herbicides or insecticides. As a result, it is important to perform environmental toxicology studies of

armadillos (Loughry & McDonough 2013). If these animals are particularly sensitive to organophosphates, land use changes that involve increased application of agrochemicals may have especially negative consequences for at least some xenarthrans.

Vehicular traffic. Collisions with vehicles are a significant cause of mortality for several species of Xenarthra (**Fig. 2**). Dead tamanduas are often found on roadsides and armadillos are among the most frequently reported mammalian victims of vehicular traffic (e.g., Weiss & Vianna 2012; Monge-Nájera 2018). Collisions with vehicles have been recognized as a threat to the persistence of several xenarthrans (Ribeiro et al. 2017; Hannibal et al. 2018), including the giant anteater (*M. tridactyla*), which is currently listed as Vulnerable. Several studies have reported on the incidence of vehicle-induced mortality of giant anteaters; these analyses have tended to focus on Brazil (e.g., Freitas et al. 2015; Pinto et al. 2018). For example, based on his observations of 91 dead individuals on 420 km of a state road in Mato Grosso do Sul between April 1996 and November 1997, Fischer (1997) estimated roadkill rates of giant anteaters to be as high as 0.19 individuals/km/year. In part, this may reflect cultural traditions in some regions of Brazil, where it is considered a bad omen if

a giant anteater crosses in front of a truck and the only way to break this curse is to kill the animal (Bertassoni 2012). In areas with low road density, habitat fragmentation appears to have a greater impact on giant anteater populations than mortality due to vehicle collisions (Pinto et al. 2018). This relationship changes, however, in areas with high road density, such as in central-southern parts of Brazil (Pinto et al. 2018). Considering that transportation infrastructure is expected to increase in many parts of the range of the giant anteater, vehicle collisions will likely represent an increasing threat in the future. Methods for mitigating this impact need to be sought and could include changes to infrastructure such as the construction of wildlife crossings.

Pathogen exposure. Diseases are not explicitly identified in **Fig. 2** as a threat to xenarthrans, due primarily to the scarcity of data regarding the disease ecology of these animals and, especially, the potential impacts of pathogens on the persistence of these taxa. Pathogens that may interfere with reproduction and population dynamics have been identified in free-ranging giant anteaters (Miranda et al. 2015) and similar threats may affect other xenarthran species. For example, a bacterial skin infection known as “pichi plague” has been reported as the cause of local extinctions of pichis (*Zaedyus pichiy*) in Mendoza Province, Argentina (Superina et al. 2009). Outbreaks of this disease, caused by opportunistic bacteria, appear to be associated with extreme precipitation events, designated as “storms and flooding” in **Fig. 2**. Climate change scenarios predict a persistent increase in summer rainfall in the Monte desert of central Argentina (Labraga & Villalba 2009), where the pichi plague has been recorded. It thus seems likely that the incidence of this disease and the associated local extinctions will increase in the future. This example is important because it reveals that the more researchers look, the more they are likely to find unusual or unexpected threats to the persistence of xenarthrans. This example also reveals an important gap in our knowledge of the Xenarthra: the role of changing environmental conditions in shaping the conservation threats faced by members

of this clade. This topic may be particularly important for this lineage of mammals given their relatively poor thermoregulatory abilities and often relatively specialized ecologies.

PAST AND PRESENT CONSERVATION STRATEGIES

Conservation strategies for xenarthrans are rare, due primarily to the limited number of researchers working on these animals and to the historically low priority given to protecting members of this clade. This lack of attention is in some ways surprising: given their peculiar anatomy and physiology as well as their basal position in the evolution of placental mammals, it would seem reasonable to expect these animals to be of considerable interest to the scientific community. Instead, the Xenarthra have long been neglected by researchers. One notable exception is the nine-banded armadillo (*D. novemcinctus*), which has been studied extensively as part of its central role in research on leprosy (17% of all publications on armadillos are related to leprosy research; Superina et al. 2014b). Despite this effort, gaps persist in our knowledge of this species. Most field studies have been conducted in the southern United States, which is thought to represent a relatively recent range expansion for *D. novemcinctus* (Audubon & Bachman 1854). As a result, it is not known whether data from US populations are representative of those in the tropics or the southern hemisphere (McDonough & Loughry 2008). Because not many researchers are focused on the Xenarthra, basic information on their biology is slow to accumulate, which presents significant challenges when attempting to assess their conservation needs.

The history of the conservation biology of xenarthrans is reflected in the key publications on the biology of these animals. One such resource is Montgomery (1985). Based on a symposium held at the 1979 annual meeting of the American Society of Mammalogists but including additional data collected from 1979 to 1985, this publication reflects the extent of our knowledge of the Xenarthra at that time. Surprisingly, Montgomery (1985) does not contain a single chapter addressing conserva-

tion issues. Moreover, the terms “conservation” and “threat” (in relation to conservation issues) do not appear anywhere in this seminal work on the Xenarthra.

The subsequent publication by Vizcaíno & Loughry (2008), affectionately known as the X-Book, was intended as an update to Montgomery (1985). One of five sections of this more recent volume is dedicated to conservation, and this topic is also addressed in other chapters. Hence, conservation was recognized as an important topic by 2008, raising the question as to what happened between the publication of Montgomery (1985) and Vizcaíno & Loughry (2008) to focus attention on the conservation of xenarthrans. In part, this shift reflects increasing overall awareness of conservation, including recognition of Conservation Biology as a scientific discipline (Soulé 1985) that gave rise to new lines of inquiry directed at preservation of biodiversity and implementation of conservation plans. In parallel, the Edentate Specialist Group was established by the IUCN in 1980 to initiate conservation efforts focused on this subset of mammals (IUCN 1982). In 2009, this unit was renamed the IUCN SSC Anteater, Sloth and Armadillo Specialist Group (ASASG), with the goal of making its purpose more comprehensible to the general public. One outcome of the formation of this IUCN group was the creation in 1994 of a newsletter named *Edentata*, which was soon recognized as an important forum for publishing conservation-related information on xenarthrans. *Edentata* is now a peer-reviewed journal and is the only periodical dedicated to publishing information on the ecology, distribution, and conservation of xenarthrans. The importance of *Edentata* as a means of disseminating information relevant to the conservation of xenarthrans is reflected in the statistic that 21 (25.9%) of 81 scientific articles on giant anteaters published between 1957 and 2011 appeared in this outlet (Diniz & Brito 2012). Similarly, 20% of all available publications on armadillo conservation have appeared in *Edentata* (Superina et al. 2014b).

A second informative metric is the number of members of the ASASG, which has varied over time but has always been low compared

to other IUCN specialist groups. As of 2019, the ASASG includes 25 members from 12 countries, three of which occur outside the native ranges of xenarthrans. Hence, only nine (40.9%) of 22 the countries where xenarthrans are endemic are represented in the Specialist Group. Although the ASASG aims to have at least one member per country where xenarthrans occur, at present this is not possible due to the absence of research or conservation efforts targeted on xenarthrans in several critical countries. Clearly there is a need to increase the number of researchers dedicated to xenarthrans, particularly in underrepresented countries. However, as noted by Superina et al. (2019), the absence of researchers or university lecturers working with xenarthrans means that students are not being encouraged to work with these animals and thus, at present, there is no means by which to train a next generation of conservation professionals that includes local xenarthran specialists. One way to break this cycle is for current specialists to visit other countries, to give talks to students, and to offer them the mentorship (and, if possible, funding) needed to undertake studies of xenarthrans. This strategy has been successfully employed in Colombia (Superina et al. 2019) and in Chile, where it has led to the formation of Armadillos de Chile. It is also being applied in Brazil through the actions of the Instituto Tamanduá. To facilitate this process, the ASASG offers training courses on xenarthran biology aimed at providing biologists and veterinarians with the basic tools required to study armadillos, sloths, and anteaters; eventually, courses will be held in all countries where xenarthrans occur, including countries that do not currently participate in the ASASG.

Despite low numbers of xenarthran experts, successful conservation strategies are being developed and employed. Examples of such programs that are being led by ASASG members and/or that are supported by ASASG include the following:

- 1) The Instituto de Pesquisa e Conservação de Tamanduás no Brasil (<http://www.tamandua.org>) was initiated in 2005 by Flávia Miranda and quickly became the leading organization for the study and conservation of *Myrmecophaga*,

Tamandua, and *Cyclopes*. Instituto Tamandua is located primarily in Brazil, where it has been spearheading efforts to assess the national conservation status of xenarthrans, to develop action plans, and to implement conservation strategies for these taxa. It also works with other xenarthran taxa and provides technical assistance to colleagues in other countries.

2) The Colombian NGO Fundación AIUNAU (<http://www.aiunau.org>, formerly UNAUI) began working with sloths in 1996. Best known for its extensive experience in sloth rehabilitation, this organization is led by Tinka Plese, who is an authority on the conservation of *Bradypus* and *Choloepus*. Similar to Instituto Tamandua, the scope of this effort has expanded to include other xenarthran species and has led to the development of the Colombian National Action Plan for Xenarthra (Ministerio de Ambiente y Desarrollo Sostenible 2016).

3) The Conservation and Management Program for the Armadillos of the Llanos of Colombia is dedicated to the five species of armadillos found in the Orinoco region of this country. Founded in 2012, this multi-institutional initiative combines research, policy formulation, and enforcement with practical interventions and education (Superina et al. 2019). It was instrumental in developing the first joint action plan between two environmental authorities in Colombia, thereby allowing implementation of the same conservation strategies throughout the entire Orinoco region of this country (Superina et al. 2014d). More importantly, the program has raised awareness of armadillos and established them as ambassador species in the Orinoco.

4) The Associação Caatinga in Brazil has played a critical role in the conservation of *T. tricinatus* by declaring this charismatic, endangered armadillo the mascot of the 2014 FIFA World Cup. Although FIFA did not provide financial support for conservation of these animals (Melo et al. 2014), *T. tricinatus* received international attention, which led to the development of a Brazilian action plan for protecting this species (ICMBio 2014). In the short period since its inception, this conservation program has achieved promising results, including the creation of a Conservation Unit

that will help protect the wild populations of these animals (Superina et al. 2014d).

These successful initiatives could be replicated in other countries to raise awareness and to increase protection of xenarthrans. The advantage of such local or national strategies is that they can address the specific threats facing animals in a given area and they can accommodate local legislation, practices, and cultural idiosyncrasies. Promoting such local efforts, however, does not negate the need for more global action plans for widely distributed species and, ideally, conservation efforts would proceed at both levels simultaneously. For example, local efforts should be paired with international collaborations to halt the illegal trafficking of xenarthrans for the pet trade or to protect specialized habitats that cross national boundaries. One badly needed example of the latter is a joint action plan between Colombia and Venezuela aimed at protecting the northern long-nosed armadillo (*D. sabanicola*), which is endemic to the Orinoco Llanos that form much of the boundary between these two countries.

THE IMPORTANCE OF INDIVIDUAL EXPERT INITIATIVES

As is true for most mammals, efforts to conserve the Xenarthra are crucially dependent on the work of passionate individuals who advocate for specific taxa. Pioneers such as Gustavo Fonseca (e.g., Aguiar & Fonseca 2008), Dennis Meritt Jr. (e.g., Meritt 1973), and Virgilio Roig (e.g., Roig 1995) have paved the way for xenarthran conservation throughout South America.

Understanding the evolutionary origins of the Xenarthra is central to understanding their taxonomic diversity and to defining conservation priorities. Studies by Sergio Vizcaíno (Vizcaíno & Bargo 2014) on extinct xenarthrans have contributed substantially to placing current conservation concerns in the context of historical loss of diversity in this lineage. Now that molecular genetic data are essential for resolving taxonomic issues, studies by Frederic Delsuc (e.g., Delsuc & Douzery 2008), Nadia Moraes-Barros (Moraes-Barros et al. 2011), and María Clara Arteaga (Arteaga et

al. 2012) have provided critical methods and data regarding the exact organismal units that must be considered when making conservation decisions.

Basic data on the biology are fundamental to assessing a taxon's conservation status and developing appropriate conservation plans, and both the Cingulata and the Pilosa have passionate advocates who have worked tirelessly towards better understanding of and protection for their study species. The work of Jim Loughry and Colleen McDonough on *D. novemcinctus* (e.g., McDonough et al. 2007; Loughry & McDonough 2013; Loughry et al. 2013) exemplifies such contributions. Similarly, the work of Teresa Cristina Anacleto on the ecology of armadillos in Brazil (Anacleto et al. 2006; Anacleto 2007) has provided a critical foundation for efforts to conserve these animals. Although studies of armadillos had been conducted in Argentina before we began our careers about 20 years ago, our enthusiasm for these animals has enhanced research and conservation efforts for these animals and, more generally, all xenarthrans (Superina & Boily 2007; Superina et al. 2009; Abba et al. 2012; Abba et al. 2017). We have now extended efforts in Argentina to other countries such as Chile (Armadillos de Chile, <http://www.armadilloschile.cl/>) and Colombia (Superina et al. 2019), pushing for greater attention on armadillo conservation at the international scale. Concomitantly, Erika Cuéllar and Andrew Noss have been fundamental in promoting armadillo research and conservation in Bolivia (Cuéllar 2008; Noss et al. 2008).

The Pilosa also have received increased attention over the past decades. *Bradypus torquatus* has been the focus of work by Adriano Chiarello (Hirsch & Chiarello 2011), while Bryson Voirin and Diorene Smith have engaged in sustained efforts to study and protect *B. pygmaeus* (Voirin 2015; IUCN SSC Anteater, Sloth and Armadillo Specialist Group 2016). One of the champions for conservation of anteaters is Flávia Miranda, who is the leading force behind Instituto Tamanduá (e.g., Miranda 2012). Currently, new advocates for xenarthran conservation are emerging in Suriname (Monique Pool; Pool et al. 2016) and Paraguay (Paul Smith; Smith 2012; Smith & Ríos 2018). Thus, the past 25

years have seen tremendous growth in concerns about and efforts to protect these fascinating animals.

Article 9c of the Convention on Biological Diversity (CBD) states that Contracting Parties shall "Adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions." Growing human pressures on wild xenarthran populations, including illegal pet trafficking (Moreno & Plese 2006; Gramieri 2015), have led to a sustained increase in the number of injured or confiscated individuals that must be rescued and rehabilitated. The maintenance of xenarthrans under human care is challenging (Superina et al. 2008) but the ex situ community also includes tireless defenders of the Xenarthra. The ex situ conservation approach is exemplified by the work of Tinka Plese, who founded the sloth rehabilitation NGO Fundación AIUNAU in Colombia 20 years ago (e.g., Plese & Moreno 2005; Ministerio de Ambiente, Vivienda y Desarrollo Territorial de Colombia 2008) and who remains a leading force for the conservation of *Bradypus* and *Choloepus*. In addition to a number of the individuals mentioned above, Roberto Aguilar, John Gramieri, Ilona Schappert, Jutta Heuer, and Lizette Bermúdez have each contributed significantly to advancing knowledge of the care of captive xenarthrans, thus improving the success of efforts to rehabilitate and, ideally, release rescued animals (e.g., Meritt 1976; Superina et al. 2008; Bermúdez Larrazábal 2011; Miranda 2012; Superina et al. 2014a). The international conservation community increasingly recognizes the importance of ex situ techniques for ensuring the long-term persistence of species (Pritchard & Harrop 2010). Studbooks, Population Management Plans (PMPs), and Species Survival Plans (SSPs) are already in place for some xenarthran species (see the Pangolin, Aardvark and Xenarthra Taxon Advisory Group's website <http://www.paxtag.org> for an overview of SSPs and PMPs held at the Association of Zoos and Aquariums), and similar resources have been developed by the European Association of Zoos and Aquaria. One of the challenges for the future will be to assess the feasibility of ex situ conservation

breeding and reintroduction programs for threatened Xenarthra.

CONCLUSIONS

Although long neglected by the scientific community, the Xenarthra have over the last few decades gained relevance as research subjects. Xenarthrans are experiencing a period of significant taxonomic change, with important implications for conservation. Concomitantly, the nature and severity of threats are changing, all of which suggests that conservation is more important than ever. While there are multiple successful local or individual-driven conservation initiatives, a necessary next step is to replicate them in other countries and to coordinate international efforts to ensure the long-term conservation of these fascinating animals. Raising awareness and capacity building will be key in this process. Many challenges have yet to be resolved, but we are convinced that the “X-community” is on the right track.

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