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Beyond natural history: some thoughts about research priorities in the study of xenarthrans

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Abstract Based on a review of the existing literature on xenarthrans, we argue that there are few obvious examples of publications that could be considered "classics", *i.e.*, those with far-reaching and long-lasting impacts. Why not? Xenarthrans are exceptional mammals, but they are notoriously difficult to study in the wild. Perhaps for this reason, among others, much of the research on xenarthrans has been primarily descriptive. Clearly, this is a necessary first step when so little is known about so many species. However, if we are to increase general awareness of xenarthrans and their biology, we need to move beyond a focus on the intrinsically interesting properties of particular species to how those properties can be exploited to address fundamental questions in ecology, evolution, and other disciplines, ideally with findings that will have implications for the study of non-xenarthrans as well. In this essay we try to identify specific areas that appear promising for such an approach. For field studies, the single most pressing need is for more long-term studies of populations of known individuals. Difficulties in maintaining xenarthrans in captivity may make laboratory-based investigations more challenging, but even here multiple opportunities exist. The end result of this exercise is not to issue some rigid manifesto regarding research on xenarthrans, but rather to initiate a discussion within the scientific community on priorities for future work.

Keywords: conservation, ecology, mammalogy, physiology, research priorities, Xenarthra

Más allá de la historia natural: algunas reflexiones sobre las prioridades de investigación en el estudio de los xenartros

Resumen Basado en una revisión de la literatura existente sobre los xenartros, argumentamos que existen pocos ejemplos claros de publicaciones que podrían considerarse "clásicos", o sea, que tengan un impacto duradero y de amplio alcance. ¿Por qué no? Los xenartros son mamíferos excepcionales, pero son notoriamente difíciles de estudiar en estado silvestre. Tal vez por esta razón, entre otros, gran parte de la investigación sobre xenartros haya sido principalmente descriptiva. Está claro que es un primer paso necesario cuando se sabe tan poco sobre tantas especies. Sin embargo, si queremos incrementar el conocimiento general sobre los xenartros y su biología, debemos ir más allá de un enfoque en las propiedades intrínsecamente interesantes de determinadas especies, para mostrar cómo estas propiedades pueden ser explotadas para abarcar preguntas fundamentales en ecología, evolución y otras disciplinas, idealmente mediante hallazgos que también tendrán implicancias para el estudio de no-xenartros. En este ensayo intentamos identificar áreas específicas que parecen prometedoras para este tipo de abordaje. Respecto a los estudios a campo, la necesidad más urgente es la realización de una mayor cantidad de investigaciones a largo plazo de poblaciones de individuos conocidos. Los estudios que requieran mantener xenartros en laboratorios pueden ser más desafiantes debido a las dificultades de mantener estos animales en cautiverio, pero aún aquí existen diversas posibilidades. No deseamos emitir ningún manifiesto rígido sobre la investigación de los xenartros como resultado final de este ejercicio, sino impulsar una discusión entre los integrantes de la comunidad científica sobre las prioridades para futuros estudios.

Palabras clave: conservación, ecología, fisiología, mastozoología, prioridades de investigación, Xenarthra

Introduction

It is a common practice in many disciplines to occasionally produce historical retrospectives that review major contributions to the field. For example, the journal *Animal Behaviour* is currently celebrating 60 years of publication with anniversary essays that highlight seminal papers from past issues (*e.g.*, Bee *et al*., 2013; Dobson, 2013). Likewise, in the fields of animal behavior and ecology, volumes have been produced that reprint papers (from multiple sources) that are considered classics (Real & Brown, 1991; Houck & Drickamer, 1996). We begin this essay by posing the following questions: Would it be possible to do something similar for the study of xenarthrans? Are there papers that should be considered classics in our field?

Such questions may seem unfair because Xenarthra is a taxon whereas animal behavior and ecology are disciplines that encompass studies of multiple species. Thus, it may not be valid to evaluate publications about xenarthrans in the same way as those categorized by topic. There is some merit to this argument but, even so, just among mammals it is still relatively easy to think of classic papers that are taxon-specific, and compilations of these have been produced (*e.g.*, Jones *et al*., 1976). However, one rarely sees papers about xenarthrans included in such volumes. So, to slightly rephrase the questions above, suppose one was to put together a book containing classic papers in mammalogy. What, if any, papers about xenarthrans should be included?

Why does asking such a question matter? We argue that the answer can tell us much about the state of research in a particular field. For example, a lack of classic papers might indicate an inability to address fundamental problems in exciting, innovative ways. Conversely, assuming publication classics exist, this is often not just because of the specific findings they present, but because these papers have far-reaching consequences in shaping the future directions of research in the field. Thus, asking about classic papers in the study of xenarthrans may tell us something about the current state of our field, where it is going, and, perhaps, where it should be going.

What constitutes a classic?

Obviously, in order to identify important papers one must review the existing body of literature about xenarthrans. Recently, Superina *et al*. (2014) have done just that for armadillos. Their analyses revealed that, not surprisingly, of >3,000 papers published over 400 years, 1,337 of these focused on nine-banded armadillos (*Dasypus novemcinctus*), which in turn was largely due to the explosion of interest in these animals as a model for leprosy studies, beginning in the 1970s. A more limited analysis by Diniz & Brito (2012) found 81 papers published between 1957 and 2011 about the giant anteater (*Myrmecophaga tridactyla*). Although papers on sloths and other species of anteaters have not been analyzed, it seems clear that publications about those species have been less common than ones covering armadillos. Thus, based on sheer numbers, one might expect that some of the most seminal papers about xenarthrans would have to do with nine-banded armadillos and leprosy.

A common alternative approach to identifying important publications nowadays is to use various databases that locate papers that have been cited most often, or that have some form of high impact score (*e.g.*, Thomson Reuters, 2013). In a preliminary exploration of this approach, we queried the Scopus database to identify the 20 most frequently cited publications that used the terms Xenarthra, Folivora, Myrmecophagidae, or Dasypodidae. The number of citations for papers returned from the Xenarthra search ranged from 77–769. Most of the top papers in this search dealt with genomic analyses about the origins of placental mammals (*e.g.*, in first place was the paper by Murphy *et al*., 2001). Consequently, many of these highly cited papers were not really about xenarthrans, but just included DNA from one or more species in the analyses. The paper by Murphy *et al*. (2001) was also the most cited using the Myrmecophagidae (range of citations: 16–769) and Dasypodidae (range: 30–769) search terms. In second place (for both terms), with 133 citations, was the paper by Delsuc *et al*. (2002). Delsuc also had the most cited paper using the Folivora search term (53 citations for Delsuc *et al*., 2001). However, this search could only identify a total of 7 publications (range of citations: 1–53). Based on these data, one might conclude that the highest profile papers about xenarthrans are those concerned with molecular analyses of mammalian evolution.

Of course, any attempt to single out certain papers as more important than others is bound to generate controversy because such an exercise may not be entirely legitimate (*e.g.*, Alberts, 2013), and will be highly dependent on the metric used, as well as the search terms employed. For example, our results might have been very different if we had used Phyllophaga or Tardigrada instead of Folivora in searching for papers about sloths (see Fariña & Vizcaíno, 2003; Shockey, 2008). Similarly, the history of science is filled with many instances where papers of lasting importance were underappreciated originally and not among those most heavily cited when first published.

Despite the various shortcomings of our crude overview of the literature on xenarthrans, we feel it is fair to conclude that coverage of the group as a whole has been exceedingly uneven, with just a few species garnering most of the attention while many others have been largely ignored. Furthermore, few papers have resonated with the larger scientific

community in the sense that they have become citation classics. So, to answer the question posed at the outset, we would argue that there are few papers that would qualify as classics in the study of xenarthrans. This is not to say that none exist, and certainly some of the older literature merits consideration for such status even if it is not cited commonly today (*e.g.*, Cuvier, 1798; Owen, 1842; Ameghino, 1889; Newman, 1913). Nonetheless, we feel that studies of xenarthrans have more often languished in obscurity, with the majority of publications largely relegated to a small audience of like-minded researchers studying the same or similar animals.

Current trends in research and publication

In reviewing the body of literature on armadillos, Superina *et al*. (2014) categorized each paper based on subject matter. Reflecting the tremendous interest in leprosy in nine-banded armadillos, health topics ranked first (1100 of 3117 total papers, with 541 of these specifically devoted to studies of leprosy). Most other categories, such as ecology, evolution, conservation, and so on, were less well-represented, and often consisted of primarily descriptive accounts. The emphasis on leprosy also accounted for the fact that >60% of all studies were laboratory-based, although some other anatomical and physiological studies contributed to this category as well (Superina *et al*., 2014). In contrast, field studies were relatively scarce, probably because of the many problems associated with studying armadillos in the wild. For giant anteaters the situation was a bit different, with ecological studies predominating (25/81 publications), and the majority of studies conducted in the field (48/81; see Diniz & Brito, 2012). However, these field studies were limited to a small number of sites, leading to concerns about how representative findings might be for the species as a whole (Diniz & Brito, 2012; the same issue applies for other xenarthrans, such as *D. novemcinctus*, see Loughry & McDonough, 2013).

Based on the foregoing, two reasons why there may not be many classic papers in the study of xenarthrans are: (1) few species have been studied extensively; and (2) even the few that are better known have been the subject of just a handful of detailed field studies. The situation is a bit different with regard to leprosy and other health-related studies, but even here, it seems that, for example with leprosy, many papers were published and widely cited within the small community of those studying leprosy, but fewer, if any, papers proposed using leprosy in nine-banded armadillos as a model system for understanding fundamental questions about wildlife diseases. Perhaps for this reason, one sees little mention of these papers in general treatments of wildlife disease (*e.g.*, Hudson *et al*., 2001; Collinge & Ray, 2006; Ostfeld *et al*., 2008).

Xenarthrans are undeniably unique animals (Gaudin & McDonald, 2008; Vizcaíno & Loughry, 2008). However, their uniqueness may actually be a detriment when it comes to generating widely cited publications. To us, there seem to be two aspects to this problem. First, because they are so unique, it often seems difficult to relate findings about xenarthrans to other species. For example, it is hard to envision how field studies of sloths would have much direct relevance for individuals studying other species of mammals such as primates, bats or rodents. Second, the uniqueness of xenarthrans is often used as sufficient justification to study them. As one arbitrary example, silky anteaters (*Cyclopes didactylus*) are clearly very interesting animals. Therefore, any information about silky anteaters is by definition interesting in its own right, regardless of whether it provides any insights into other species, or allows for any tests of basic theoretical concepts. Similarly, a strong case can be made that conservation studies of xenarthrans are a critical priority (Diniz & Brito, 2012; Superina *et al*., 2014), and there is definitely a need for applied research that leads to development of species-specific management plans. Nonetheless, it seems likely that there are deeper issues in conservation science that research on xenarthrans could help address. What we advocate here is that researchers try to think more about how to accommodate the twin goals of providing information about a particular species, coupled with consideration of how such data provide insight into fundamental, theoretical concerns.

We claim no superiority with regard to such issues. Indeed, much of our work with nine-banded armadillos was motivated by the fact that little was known about their ecology or behavior in the wild. Therefore, even simple descriptive studies were valuable contributions (review in Loughry & McDonough, 2013). Nevertheless, as our work has continued, we have come to recognize that we must move beyond basic accounts of natural history to address broader, more conceptual issues. To illustrate the point, consider the recent paper by Jarvis *et al*. (2013) that documents concentrations of various metal toxicants in the liver tissues of nine-banded armadillos collected at several sites in the southeastern United States. To our knowledge, this is one of very few toxicology studies in xenarthrans, and certainly the first paper to look at metal accumulation in armadillos, so for those reasons the information is valuable. Even so, because the study was retrospective, exploiting tissues collected for other reasons, the paper is almost entirely descriptive, with no data about the functional consequences of different metal concentrations, nor how these levels compare with those present in other mammals found at the same sites. Of course, no study is perfect, and the paper by Jarvis *et al*. (2013) may set the stage for future analyses of the issues just mentioned. Our main point is

that a better approach would have been to have such issues in mind at the outset.

We do not intend to be too negative or critical here because there are a number of instances where research on xenarthrans has moved beyond purely descriptive accounts. One obvious example is work on fossil xenarthrans, which has been critical in the development of evolutionary thinking ever since Darwin (Brinkman, 2010), and has contributed much to our understanding of major historical processes such as the Great American Interchange (Marshall, 1988). Likewise, there are a number of individuals examining extant xenarthrans with theoretically-driven research programs. For example, studies of functional morphology (*e.g.*, Vizcaíno *et al.*, 1999; Vizcaíno, 2009; Nyakatura, 2012) have generated testable hypotheses that apply to many species, not just xenarthrans. Similarly, genomic comparisons (review in Delsuc & Douzery, 2008; see also Delsuc *et al.*, 2012) have provided insights not just for specialists interested in the details of xenarthran systematics, but have had broader implications for the evolution of mammals, and for theories to explain patterns of evolutionary change. A few final examples include the use of various models to predict species distributions (*e.g.*, Anacleto *et al.*, 2006; Phillips *et al.*, 2006; Abba *et al.*, 2011b) and patterns of biodiversity (Silva *et al.*, 2012), the coupling of niche models with genetic data to test hypotheses about gene flow (Arteaga *et al.*, 2011), and the use of population biology models to test ideas about how features of populations are impacted by, among other things, the costs of reproduction, range expansion, and habitat alterations (Loughry *et al.*, 2013a, b). Thus, the situation is not so grim, and there is reason to believe the study of xenarthrans is moving in a positive, productive direction.

Future Directions

What is needed to keep things moving? In our opinion, for field studies of xenarthrans, the single most important task is to develop more long-term studies of populations of known (*i.e.*, marked) individuals. Such data are essential in order to address virtually any important question in ecology or evolution (Clutton-Brock & Sheldon, 2010; Hoogland, 2013). Although technically more challenging, the addition of more experimental components to field studies is also needed. Natural "experiments", coupled with other forms of variation over time, space, and among individuals can provide much important information, but usually experimental manipulations are required to fully exclude alternative explanations. For example, it is difficult to imagine how we will ever understand much about sexual selection or chemical communication in xenarthrans without employing some form of experimental approach.

Part of the reason for advocating field experiments as opposed to laboratory tests has to do with the paucity of xenarthrans held in captivity, and the many problems associated with maintaining them in a laboratory environment (Superina *et al.*, 2008). Nonetheless, some species, such as pichis (*Zaedyus pichiy*) and two-toed sloths (*Choloepus* spp.) seem more able to handle the stresses associated with captivity, and may make good choices for laboratory studies (see *e.g.*, Gilmore *et al.*, 2008; Superina & Jahn, 2009, 2013). Although techniques exist for conducting certain types of physiological studies in the wild, it seems probable that most future work on xenarthran physiology will require use of captive animals in the lab. For example, because of their low metabolic rate, documenting the costs of reproduction for female xenarthrans is particularly interesting. To take one extreme case, female *Dasypus hybridus* not only have a low metabolic rate, but they are among the smaller of the *Dasypus* species, and yet they have the largest litter size of any xenarthran (Abba *et al.*, 2011a). Thus, a fascinating question is how female *D. hybridus* manage to meet what appear to be extremely high costs associated with reproduction. Given that most armadillos, including *D. hybridus*, give birth and nurse infants underground in burrows, coupled with the enormous difficulties associated with observing animals underground in the wild, laboratory investigations would appear to be the only viable means of obtaining data on maternal investment in young. Likewise, many other studies of physiology, biomechanics, and so on, will have to be conducted in the laboratory. Consequently, researchers will need to be creative in finding ways to complete these experiments while maintaining healthy populations of captive animals.

Conclusion

We are not the first to discuss research priorities in the study of xenarthrans (for recent examples, see Meritt, 2006; Vizcaíno & Loughry, 2008; Diniz & Brito, 2012; Loughry & McDonough, 2013; Superina *et al.*, 2014). There is certainly merit in all of these previous suggestions, and we hope the ideas provided here are not construed as an attempt to make a definitive statement about what needs to be done. Indeed, it is difficult to write about research priorities without it coming across as hubris, setting oneself up as the final arbiter of what is important and what is not. Fortunately, the future direction of research on xenarthrans will be dictated by the predilections of those involved. Our goal here is to persuade researchers to consider ways in which to broaden their studies to address fundamental questions that apply to many species, including non-xenarthrans. We are confident that there are plenty of talented people out there capable of doing so. And perhaps with a little luck such an approach will lead to the publication of

papers that will one day merit inclusion in a volume of collected classics. Such an outcome would be the ideal legacy for this essay.

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