



Original Investigation

Climate fluctuations as a cause of rarity in fairy armadillos

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ABSTRACT

Despite having a moderately large distributional area, both the pink fairy armadillo (*Chlamyphorus truncatus*) and particularly the Chacoan fairy armadillo (*Calyptophractus retusus*), which are among the least known xenarthrans, appear to be rare or patchily distributed. Although low density in species with large range sizes has been associated with large body size, this is not the case for fairy armadillos. We propose that past climate variations may have caused their current low densities, and evaluate retractions and expansions of suitable areas of fairy armadillos by extrapolating the consensus of habitat suitability models fitted with current climatic conditions to past conditions. We found great variation in suitable area along time in both species, with a drastic reduction in the Last Interglacial (LIG) period when compared with current situation. Both the variations and the reduction during LIG were more pronounced in *Calyptophractus* than in *Chlamyphorus*. We postulate that past extreme reductions in suitable areas could cause a delay in the recovery of the populations, resulting in low densities despite climatic conditions during more benign times allowing a more widespread distribution.

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Introduction

The pink fairy armadillo (*Chlamyphorus truncatus*) and the Chacoan fairy armadillo (*Calyptophractus retusus*; Mammalia: Cingulata: Dasypodidae: Chlamyphorinae) are among the least known xenarthrans (Superina et al., 2014a,b), in part due to their small size (up to 100 g) and subterranean lifestyle, for which they are highly adapted (Gardner, 2008; Wetzel, 1985). Consequently, field research on these cryptic mammals is difficult and information on their ecology is scarce, with aspects as basic as their distributional range being incompletely known (Superina et al., 2014a). It is thus not surprising that both species are currently listed as Data Deficient in the IUCN Red List of Threatened Species (Abba and Superina, 2010).

The current known distributions of the two fairy armadillo species are allopatric (Delsuc et al. 2012). The occurrence records of *Chlamyphorus* extend over 350,000 km² in central Argentina, and are concentrated in the Monte and Espinal ecoregions (sensu Burkart et al., 1999). The scarce presence localities of *Calyptophractus* are distributed over 258,000 km² in the Gran Chaco region,

a tropical area encompassing northern Argentina, south-eastern Bolivia and western Paraguay (Fig. 1; Abba and Superina, 2010; Abba et al., 2012; Gardner, 2008). Despite their moderately large distributional area, fairy armadillos, and particularly *Calyptophractus*, are rare and patchily distributed (Abba and Superina, 2010). These low densities are also shared by some other insectivorous subterranean mammals living in arid sandy zones, such as the Australian notoryctids (Benshemesh and Burbidge, 2008; Dickman et al., 2008) and some golden moles (e.g., Jackson and Robertson, 2011). They cannot be attributed to the elusiveness of such species alone given that other insectivorous, strictly subterranean mammals, such as moles and most golden moles, are observed far more frequently (e.g., Bronner, 2008; Goszczynski, 1983; Nevo, 1979).

Although some factors, such as habitat loss and hunting by domestic dogs and cats (*Chlamyphorus*) or persecution and death due to local traditional beliefs (*Calyptophractus*), could have deleterious effects on some populations (Aguar and da Fonseca, 2008; Roig, 1995; Superina, 2006), there is no doubt that fairy armadillos are naturally rare (Chébez, 2008; Cuellar et al., 2014; Superina et al., 2014b). Natural factors associated with limited distribution or density include species traits such as low growth rates, long generation time, small litter size, large area requirements, high specialization and large body size, as well as ecosystem traits such as low carrying capacity or scarcity of suitable habitats (Flather and Sieg, 2007). This last factor seems to be an important constraint, as some

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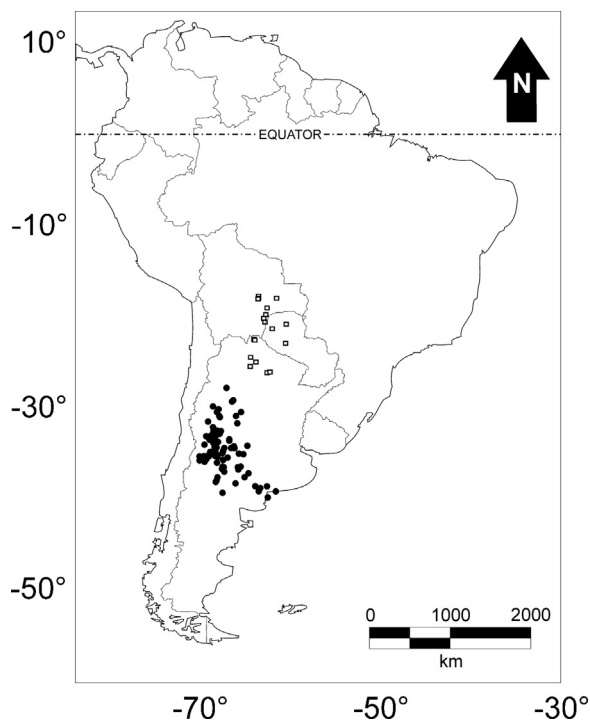


Fig. 1. Distribution of presence localities of *Chlamyphorus* (dark circles) and *Calyptophractus* (open squares). Geographic projection: Aitoff.

evidence suggests that species with very limited distributional ranges would be survivors of past climatic changes that currently persist only in those small areas where climates resemble conditions that were more widespread in the past (Ohlemüller et al., 2008). Rarity is, however, not determined solely by range size but also by population density (Flather and Sieg, 2007; Rabinowitz, 1981; Rabinowitz et al., 1986), and many species (such as fairy armadillos) can be regarded as “rare” for their low densities despite showing broad distributional areas. We postulate that low density in these species could be the consequence of extreme variations in range size and habitat suitability, caused in turn by extreme variations in past climates. In other words, after having suffered a drastic decrease in suitable areas as a consequence of a past climate change, species with high specialization and low dispersal capability (and possibly low productivity), such as fairy armadillos, could take an exceedingly long time to recolonize all suitable habitats once the climate becomes benign again.

We modeled the habitat suitability for fairy armadillos under current climate conditions and extrapolated these models to the projected past conditions (Last Interglacial, Last Glacial Maximum and Mid Holocene) to evaluate retractions and expansions of suitable areas according to changes in climate. Species typical of arid environments, such as the fairy armadillos, would have been more common and widespread when aridity predominated, while they would have rarefied with increasing humidity. The scarce information about the climate in the Last Interglacial period (LIG; ~140,000–120,000 yBP) in South America indicates warmer and more humid conditions than at present (Hammen, 1974). In the plains of southern South America the climate turned cold and dry during the Last Glacial Maximum (LGM; ~21,000 yBP), warming and wetting again at the end of this period and reaching higher values of temperature and precipitations than at present in the Mid Holocene (MH), around 8000–6000 yBP (Iriando and García, 1993). In southern tropical areas, however, the aridity and temperature increased from LGM to MH, with rains increasing to current levels during the Late Holocene (Burbridge et al., 2004; Mayle and

Beerling, 2004; Mayle et al., 2004). Thus, compared to the current distribution and assuming niche conservatism (*sensu* Wiens and Graham, 2005), for *Chlamyphorus* we expect an expansion of suitable areas in the LGM and a retraction in LIG and MH. This prediction follows the “zig-zag” hypothesis raised by Cione et al. (2003), which for the plains of southern South America postulates an expansion of open areas at the expense of forests during the cold and dry periods, and the inverse situation during warm and humid periods. On the other hand, for *Calyptophractus* we expect an expansion of suitable habitats from the LIG until the MH, followed by a retraction until today.

Material and methods

Occurrence records

Occurrence records of fairy armadillos were obtained from museum collections, localities cited in the bibliography, field observations, and personal reports from other researchers (see Supplementary Material 1). Three occurrence points for *Chlamyphorus* and one for *Calyptophractus* from newspaper reports with photographs and data about the locality of observation were also included. Records were filtered according to the date of collection (or observation); only records after 1950 were considered, given that the bioclimatic variables used for modeling (see below) represent the climate in the 1950–2000 period (Hijmans et al., 2005). The spatial error associated with the geographic location of the remnant localities was lower than the spatial resolution used for modeling (5 arc-minutes; see below) in all cases. Finally, all duplicate presence points (i.e., those records falling in cells already occupied by a previous record) were deleted.

Modeling techniques

Projecting habitat suitability models to the past requires dealing with the uncertainty associated mainly to the use of different modeling techniques and atmospheric General Circulation Models (GCM; Buisson et al., 2010; Diniz-Filho et al., 2009). To overcome this, Araújo and New (2007) proposed the use of ensembles of model forecasts, where models of the same species are developed with diverse techniques and considered together (e.g. Araújo et al., 2006, 2011; Prasad et al., 2006; Rodríguez-Soto et al., 2011). We used a consensus of three methods: Maximum Entropy (Maxent), Bayesian Classification and Mahalanobis Distance. These methods are known as “presence-only” methods because they do not require information about areas not occupied by the entity being modeled. However, strictly speaking only the Mahalanobis Distance is a presence-only method given that the other ones rely on differences in environmental conditions between the occurrence points and a sample of points taken at random from the study area. Further information on modeling techniques is provided in Supplementary Material 2.

Environmental variables and modeling procedures

Models were first fitted using the 19 bioclimatic variables from the WorldClim database (Hijmans et al., 2005), downloaded at a resolution of 5 arc-minutes for continental South America, plus three topographic variables: an elevation layer of South America, obtained at a resolution of 30 arc-seconds from the SRTM database (<http://srtm.usgs.gov>), and slope and aspect, derived from the elevation layer with the SURFACE module of Idrisi v17 Selva (Eastman, 2012). Given that fairy armadillos are associated to sandy soils (Aguilar and da Fonseca, 2008), a categorical layer describing the percentage of sand at 0–20 cm depth was obtained at a resolution of 5 arc-minutes from the ISRIC-WISE database (Batjes, 2006; <http://>

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