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INSIGHTS

The Role of Giant Armadillos (*Priodontes maximus*) as Physical Ecosystem Engineers

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ABSTRACT

Through their excavations, giant armadillos (*Priodontes maximus*) alter their physical surroundings and create new habitats, which influence resources for at least 24 other species of vertebrates in the Brazilian Pantanal. The role of this poorly known species as an ecosystem engineer may be of high value to the community of vertebrates.

Key words: armadillo; burrow; Dasypodidae; ecosystem engineer; Pantanal; South America; Xenarthra.

An ecosystem engineer is an organism whose presence or activity alters its physical surroundings or changes the flow of resources, thereby creating or modifying habitats and influencing all associated species (Jones *et al.* 1994, 1997). Autogenic engineers change the environment via their own physical structures, whereas allogenic engineers change the environment by transforming living or non-living materials from one physical state to another, primarily by mechanical means (Jones *et al.* 1994). The most famous example of an allogenic physical ecosystem engineer is the beaver (*Castor canadensis*). Beavers physically modulate water flow and create ponds and wetlands by cutting trees and damming streams (Naiman *et al.* 1988, Wright *et al.* 2002). Burrowing species may have the same fundamental effects, albeit at more modest temporal and spatial scales.

Armadillos (Dasypodidae) are the most widespread group of living Xenarthrans and are primarily specialized diggers. They exhibit several adaptations to digging including large claws, tibia and fibula fused proximally and distally, large tuberosities for strong muscular insertions, and long lever arms for the line of action of the principal muscles (Vizcaíno & Milne 2002). The giant armadillo (*Priodontes maximus*) averages 150 cm in length (including the tail) and can weigh up to 50 kgs, and has large scimitar-shaped fore claws, the third of which is greatly enlarged and can reach over 15 cm (Silveira *et al.* 2009). Giant armadillos build large, deep burrows and we describe their role as allogenic physical ecosystem engineers.

This study took place in a 250-km^2 area in central Pantanal (S 19.16.60, O 55.42.60) between July 2010 and September 2012. The Pantanal is the world′s largest freshwater wetland and subject to a predictable monomodal flood pulse. Giant Armadillo excavations were intensively searched throughout the study area. Three types of excavations were identified based on characteristics and use: feeding excavations, resting holes, and burrows. Each of these was referenced by GPS, and height, width, and depth measured. An excavation was considered new when tracks, prints of tail, and fresh sand were encountered; or old when the front mound was flattened and entrance littered with leaves. Differences in excavation characteristics were analyzed using Kruskal–Wallis one-way analysis of variance with pairwise multiple comparisons. Four data loggers (HOBO Pendant Temperature logger) were set inside the giant armadillo burrows, and one within a forested area, inside a solar radiation shield. Readings were taken simultaneously every 20 min by all data loggers and compared using Mann–Whitney Tests.

Fifteen Reconyx HC-500 cameras were positioned in front of old burrows, new burrows, and new resting holes. Cameras were left on average for 40 days, totaling an effort of 3141 camera trap nights involving 70 giant armadillo burrows/holes. Recorded observations of animals were considered independent from earlier ones only if the same individual appeared after an interval of 10 min had elapsed. Results were divided into four categories: (1) animal traveled or passed in front of the burrow; (2) the animal interacted (observed, smelled) the burrow or sand mound for less than 5 sec; (3) the animal interacted with the burrow or sand mound (foraged in the sand mound, wallowed or rested on the sand mound, searched the entrance of the burrow for prey, entered the entrance of the burrow, but remained visible to the camera) for over 5 sec; and (4) entered inside the burrow and disappeared. Categories (3) and (4) were considered to characterize use. Frequency of behaviors from each category (1–4) at each excavation (old burrows, new burrows, new resting holes) per 24-h periods was compared using Kruskal–Wallis one-way analysis of variance with pairwise multiple comparisons.

A total of 490 excavations were measured including: 297 feeding excavations, 106 resting holes, and 87 burrows (Table S1). Although there was no significant difference between the height of these excavations (H = 1.025; df = 2; $P = 0.599$), there was a significant difference between the width (H = 22.471; df = 2; $P < 0.01$). The width of feeding excavations differed from resting holes and burrows using a pairwise multiple comparison procedure with Dunn's method (I < 0.05). The sand

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mound in front of a burrow was much larger and higher than that of a resting hole. Giant armadillos will use a resting hole for just one night, but may return and re-use a burrow. Although mean temperature inside and outside the burrows appear similar, they were significantly different ($P < 0.001$), and temperatures inside the burrows fluctuated much less than outside (Table S2; Fig. S1).

A total of 57 species were photographed by the camera traps, although the actual number of species visiting burrows was much higher as small rodents were grouped, and many species of birds and domestic animals were not included in the analysis. Of these 57 species, 24 species were considered to use either the sand mound or the burrow itself (Table 1 and S3) and 3853 sequences of pictures were taken describing their behavior. The difference in the frequency of non-interactive behaviors (Categories 1 and 2) was not significant between the three excavations ($H = 1.649$; $df = 2$; $P = 0.438$) and totaled 1740 sequences. There was a significant difference ($H = 11.743$; $df = 2$; $P = 0.003$), however, between excavations and interactive behaviors (categories 3 and 4) for which 2113 sequences were photographed (Figs. S2–S15). Both Category 3 ($H = 9.703$; $df = 2$; $P = 0.008$) and Category 4 ($H = 11.417$; $df = 2$; $P = 0.003$) were significantly different among the three excavations. A pairwise multiple comparison procedure with Dunn's method showed that the significant difference for both Categories 3 and 4 was between new and old burrows ($P < 0.05$). More interactive behaviors occurred in new burrows than older ones.

The different species interacted with the excavations in different ways (Table 1 and S3; Figs. S2–S15). The sand mound in front of the burrow was used by *Tayassu pecari*, *Sus scrofa,* and *Pecari tajacu* to wallow, rest, and cool down. This usually occurred when the mound of sand was fresh and still humid. *Myrmecophaga tridactyla* was also photographed taking sand baths in the sand mound. *Tapirus terrestris* and *Puma concolor* were photographed using the sand mound as a resting spot. Many species searched for their prey either in the sand mound (*Cyanocorax sp*, *Ameiva sp.*, *Tupinambis teguixin*, small rodents, *Nasua nasua*, *Cerdocyon thous*, *Crax fasciolata*) or at the entrance of the burrow (*Cariama cristata*, small rodents, *Tupinambis teguixin*, *Procyon cancrivorus*, *Cerdocyon thous*, *Leopardus pardalis*, *Eira barbara*, *Puma concolor*). Sixteen species used the burrow itself as a refuge against predators or temperatures (both high and low) or to seek resources. All the other species of armadillos present in the study area (*Cabassous unicinctus*, *Dasypus novemcinctus*, *Euphractus sexcintus*) were registered spending

TABLE 1. *Proportion and behavior of species photographed in front of giant armadillo resting holes and burrows. Travel describes when animal traveled or passed in front of the burrow/hole; Interact < 5 sec describes when the animal interacted (observed, smelled) the burrow/hole or sand mound for less than 5 sec; Interact > 5 sec describes when the animal interacted with the burrow/hole or sand mound (foraged in the sand mound, wallowed or rested on the sand mound, searched the entrance of the burrow/hole for prey, entered the entrance of the burrow/hole) for over 5 sec; In Burrow describes when the species entered inside the burrow/hole and disappeared from the camera.*

Species		*N*	Travel (%)	Inspect <5 sec (%)	Inspect >5 sec (%)	In Burrow (%)
Southern naked tail armadillo	*Cabassous unicinctus*	3	0	0	0	100
Southern tamandua	*Tamandua tetradactyla*	477	5	19	30	46
Tortoise	*Chelonoidis carbonaria*	16	0	23	15	46
Nine banded armadillo	*Dasypus novemcinctus*	129	13	23	27	36
Tegu	*Tupinambis teguixin*	67	9	24	34	33
Collared peccary	*Pecari tajacu*	74	12	5	54	28
Agouti	*Dasyprocta azarae*	316	16	20	36	28
Tayra	*Eira barbara*	82	26	19	34	27
Ocelot	*Leopardus pardalis*	78	21	13	45	22
Six banded armadillo	*Euphractus sexcintus*	267	21	26	31	22
Seriema	*Cariama cristata*	139	21	5	55	19
Small rodents	*Unidentified (<5 spp)*	1284	18	33	35	13
Racoon	*Procyon cancrivorus*	13	0	15	77	8
Jay	*Cyanocorax sp.*	15	7	13	73	7
Coati	*Nasua nasua*	210	37	19	39	6
Lizard	*Ameiva sp.*	173	43	35	17	5
Crab eating fox	*Cerdocyon thous*	93	13	22	61	4
Lowland tapir	*Tapirus terrestris*	45	44	13	42	0
Bare-faced Curassow	*Crax fasciolata*	30	47	3	50	0
Feral pig	*Sus scrofa*	200	53	10	38	0
White-lipped peccary	*Tayassu pecari*	123	54	12	34	0
Bush dog	*Speothos venaticus*	1	0	0	100	0
Puma	*Puma concolor*	10	84	0	16	0
Giant Anteater	*Myrmecophaga tridactyla*	18	67	6	28	0

prolonged periods in the giant armadillo burrows. The Xenarthra that was most often documented using giant armadillo burrows, however, was the scansorial Southern tamandua (*Tamandua tetradactyla)*, which spent long periods of time in the burrow and was also observed feeding in the burrow on termites or ants. Carnivores such as *Leopardus pardalis* and *Eira barbara* were also observed resting in burrows for prolonged periods, as were reptiles such as *Ameiva sp*., *Tupinambis teguixin,* and *Chelonoidis carbonaria*. Collared peccary (*Pecari tajacu*) were also photographed entering the burrow, and up to two animals entered inside the burrow together. These observations indicate that through their excavations, giant armadillos alter their physical surroundings and create new habitats, which influence resources for at least 24 other vertebrate species in the Pantanal. They can therefore be considered as allogenic physical ecosystem engineers.

Jones *et al.* (1994) list six criteria that scale the impact of ecosystem engineers, most of which apply to giant armadillos. They are highly fossorial spending almost 75 percent of their time belowground in burrows of their own construction (A.L.J. Desbiez & D. Kluyber, unpubl. data). Although densities of giant armadillos are low (Noss *et al.* 2005, Silveira *et al.* 2009), they change holes/burrows very frequently, and will dig on average a new burrow or resting hole every 2 days (A.L.J. Desbiez & D. Kluyber, unpubl. data). Although, the frequency of use of older burrows is significantly lower than fresh burrows, new burrows are regularly constructed and made available. Nevertheless, despite the wide use of the burrows by other species, none of these species appears to entirely depend on the burrows.

In the Pantanal, due to annual inundation and sandy soils, there are few opportunities to seek shelter in holes or burrows. The giant armadillo is the only species capable of digging large and deep burrows, and their excavations provide shelter from predators and can also act as a thermal refuge since temperatures inside the burrows fluctuate less than aboveground temperatures. Excavations and their associated sand mounds also appear to provide new food resources for opportunists within the ecological community. This includes predators feeding on invertebrates and vertebrates that use the excavations or sand mounds. Burrows might also serve as collection areas for seeds and organic debris, whereas burrow tunnels and mounds are likely to affect water infiltration, soil nutrients distributions and, potentially, the diversity of plants and soil biota (Whitford & Kay 1999).

Finally, we propose that the frequency of burrow use by a diversity of mammals coupled with favorable microclimatic conditions within burrows could potentially favor survival and proliferation of fungi, bacteria, ticks, fleas, other parasites, protozoa, and viruses, and thus serve as transmission nodes of pests and pathogens among wild and domestic animals.

Giant armadillos are currently classified as 'Vulnerable' (A2 cd) by the IUCN/SSC Red List of Threatened Species and listed on Appendix I of CITES. In Brazil, the species is classified as 'Critically Endangered' in many State lists, and the species has practically disappeared from the Atlantic forest (Srbek-Arujo *et al.* 2009). Main threats include habitat loss and hunting, and in the Pantanal, some ranch workers kill them on sight as they are believed to bring bad luck (A.L.J. Desbiez & D. Kluyber, unpubl. data). The decline of this species might have wider consequences for the structuring of microhabitats and the availability of food resources in the landscapes in which they occur.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Measurements of three types of giant armadillo excavations.*

TABLE S2. *Temperatures measured by data loggers placed inside two burrows and outside in the forest capturing both colder and hotter seasons in the Pantanal.*

TABLE S3. *Frequency of species behaviors per 24-h periods for each excavation.*

FIGURE S1. Example of variations in temperatures from data logger readings outside a burrow and inside a burrow during the cold season.

FIGURES S2–S15. Photographs of different species interacting with the excavations.

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