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RESEARCH ARTICLE

Behavioral Responses of Three Armadillo Species (Mammalia: Xenarthra) to an Environmental Enrichment Program in Villavicencio, Colombia

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Enrichment is a powerful tool to improve the welfare of animals under human care. Stress-related health and behavioral problems, as well as reproductive failure, are frequent in armadillos (Xenarthra, Cingulata, Dasypodidae) under human care, which hinders the development of successful ex situ conservation programs. Nevertheless, scientific studies on the effect of enrichment programs on armadillos are virtually non-existent. The objective of this study was to assess the impact of an enrichment program on the behavior of armadillos under human care. The behavior of 12 individuals of three species (*Dasypus novemcinctus*, *D. sabanicola*, and *Cabassous unicinctus*) maintained at Finca El Turpial, Villavicencio, Colombia, was recorded using scan sampling during three daily time blocks of 2 hr each before (4 weeks) and after (4 weeks) implementing an enrichment program. Enrichment did not stimulate the armadillos to change or extend their activity period. In general, activity levels were low during the entire study, and virtually no activity was recorded in the morning in any species, neither without nor with enrichment. The latter did, however, improve welfare by reducing abnormal and increasing natural foraging behaviors. All species were attracted by artificial termite mounds. *Dasypus* spp. showed special interest in cardboard boxes with food, while *Cabassous* was mainly attracted to hollow plastic balls filled with food. Our results suggest that separate enrichment programs need to be developed for different armadillo species, and that they should be applied during the time of day at which they are most active. Zoo Biol. 35:304–312, 2016.

Keywords: behavior; ex situ conservation; stereotypies; welfare

INTRODUCTION

Environmental enrichment has been widely recognized as a powerful tool to improve the welfare of zoo-housed animals [Shepherdson et al., 1998; Mason et al., 2007; Maple and Perdue, 2013]. Research on animal welfare and environmental enrichment has been biased toward charismatic species, especially primates [Azevedo et al., 2007; Goulart et al., 2009; Melfi, 2009]. Many other species would, however, greatly benefit from environmental enrichment, as the welfare of animals maintained in controlled conditions is key to reduce stress and its biological costs [Moberg, 2000], including abnormal behaviors such as stereotypies [Castillo-Guevara et al., 2012] and reduced reproductive success [Carlstead and Shepherdson, 1994].

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Armadillos (Xenarthra, Cingulata, Dasypodidae) are currently represented by 20 species, six of which occur in Colombia [Gardner, 2008; Abba et al., 2015]. Scientific information on their biology and, especially, their behavior is scarce and mainly focuses on one species, the nine-banded armadillo *Dasypus novemcinctus* [Superina et al., 2014b].

Armadillos are intensely hunted and used as a protein source in most of their range, including in Colombia. As a consequence, they are often confiscated by the authorities and handed over to zoological institutions or breeding facilities. Their maintenance is challenging, and institutions often do not have appropriate enclosures and experience in the husbandry of these semifossorial animals [Superina, 2000; Superina et al., 2008]. Scientific research that would help improve their conditions is scarce, as less than 2% of scientific publications on armadillos is based on studies performed in zoological institutions [Superina et al., 2014b]. Consequently, stress-related health problems [Resoagli et al., 1985], agonistic behavior between conspecifics [Roberts et al., 1982], stereotypical behavior [Superina, 2000], and reproductive failure [Rideout et al., 1985] are frequent. The latter is especially worrisome, as it hinders the development of successful ex situ conservation programs.

Although some zoos carry out enrichment programs for their armadillos [Superina, 2000], their effect on the behavior and welfare has only been scientifically evaluated in a single study dealing with three-banded armadillos *Tolypeutes matacus* [Howell-Stephens, 2012]. The aim of the present study was to assess the behavioral changes of armadillos of the species *Dasypus sabanicola*, *D. novemcinctus*, and *Cabassous unicinctus* maintained in controlled conditions and subjected to an environmental enrichment program in a breeding facility in Villavicencio, Colombia. The results will help improve the welfare of armadillos under human care.

MATERIALS AND METHODS

Study Animals

The study was carried out within the natural range of the three studied armadillo species in Finca El Turpial, a breeding facility near Villavicencio, Meta, Colombia (04°09′N, 73°38′W). Twelve adult armadillos of three species were used: three nine-banded armadillos *D. novemcinctus* (two males, one female), seven northern long-nosed armadillos *D. sabanicola* (two males, five females), and two naked-tailed armadillos *C. unicinctus* (one male and one female). The latter species can be easily distinguished from *Dasypus* by its flattened carapace with a clear border and its "naked" tail lacking scutes and scales [Wetzel, 1985; Trujillo and Superina, 2013]. *D. sabanicola* is smaller than *D. novemcinctus* (mean body mass 1.5 kg and mean head-body length 29 cm vs. 3–8 kg and 36–57 cm, respectively), its carapace has a more uniform color and its rostrum, tail, and ears are proportionally shorter [Mondolfi, 1967; Wetzel, 1985; Trujillo and Superina, 2013].

All animals were wild-born and had been confiscated by law enforcement agencies, except for the male *C. unicinctus* that was born in the breeding facility. Their exact age and origin were unknown due to the lack of individual records. Although we are aware that the sample sizes of two species are low, we decided to include them in the study because the results may provide preliminary information on interspecific differences in the response to environmental enrichment. Furthermore, it was not possible to obtain additional individuals of these species because they are rarely kept under human care in Colombia. Animals were individually numbered on their carapace with white nail polish for the duration of the study.

All animals were kept together in a single enclosure of $5 \times 5 \times 2.5$ m with concrete floor and metal roofing. We deliberately did not separate species or genders prior to initiating our observations because the animals had been living in this enclosure for several months and we wanted to investigate whether this type of management was suitable for armadillos. The enclosure's perimeter consisted of a smooth concrete wall of 1.25 m height and mesh fence from the wall to the roofing, and a door made of metal. The enclosure was equipped with three wooden nesting boxes of $100 \times 30 \times 30$ cm; a water pool ($51 \times 35 \times 13$ cm); a latrine filled with sand; and a central, open wooden box ($140 \times 140 \times 38$ cm) permanently filled with wood shavings to dig and hide, accessible by means of four ramps made of wooden planks of 90×10 cm. The floor was covered with a thin layer of wood shavings, which the animals gathered and transported into the nesting boxes. The weekly cleaning routine, which was always performed on Sunday to reduce the possibilities of interfering with the study, consisted of removing all wood shavings from the floor and the nesting boxes and covering the floor again with wood shavings. The sand in the latrine was replaced in intervals of 7 or 14 days. The animals were fed once daily, around 7 PM, with dry dog food soaked in water. They had free access to water, which was replaced every day at feeding time.

Behavioral Observations

We used scan-sampling [Lehner, 1998] to record the behavior of armadillos during a total of 8 weeks. We divided the observation period in two phases, one before (4 weeks) and the second after implementing the enrichment plan (4 weeks). We performed behavioral observations during three daily time blocks of 2 hr each, 5 days a week (Monday–Friday).

A preliminary study [Cortés Duarte et al., 2015] revealed that activity levels of the armadillos at Finca El Turpial were highest between 6:30 and 8:30 PM. Animals were also active, but to a lesser degree, between midnight and 2:00 AM. Only few animals were active in the morning, around 10:00 AM. Hence, we registered their behavior from 6:30 to 8:30 PM (*evening*) and from 00:00 to 2:00 AM (*night*). We also included an observation period from 9:30 to 11:30 AM

(*morning*) because we wanted to test whether we could stimulate the armadillos to become more active during their usual resting period through environmental enrichment.

Every 3 min, we scanned the enclosure from left to right and noted whether the individuals were active or inactive in the order they were sighted. For active animals, we coded their behavior based on the categories and events described in the ethogram developed by Cortés Duarte et al., [2015]. Briefly, the categories used were feeding (four events), locomotion (five), exploration (eight), resting (one), social interaction (seven), excretion (one), burrow or nest construction (four), stereotypies (seven), and others (seven events). We interrupted observations for 5 min every 45 min to avoid observer fatigue. Hence, we obtained 38 data points per individual, and a total of 456 data points for all animals, during each 2-hr observation period.

Observations were performed by the naked eye by a single observer (ACD) located outside the enclosure to avoid interference with natural behavior [Lehner, 1998]. Coded behaviors [Cortés Duarte et al., 2015] were recorded per armadillo and sample point in a spreadsheet.

Enrichment

We developed an enrichment plan based on previously published recommendations [Superina, 2000; Superina et al., 2008] as well as our observations of the enclosure type and the behavior of our study animals (Table 1). Each enrichment type was applied once per week in the second phase of the study, always on the same day of the week. In week 1 of Phase 2, enrichment items were offered at 9:30 AM and removed from the enclosure at 6 PM, that is, 30 min before the next observation period; in week 2, they were offered at 6:30 PM and removed at 11:30 PM; in week 3, they were left in the enclosure from 0:00 AM until 6:00 AM; and in week 4, they were placed in the enclosure at 9:30 AM and removed at 2:00 AM the next day. In other words, in the first 3 weeks the animals had access to the enrichment items during one time block, while they did so during three observation periods in the 4th week. With the latter, we wanted to test whether the animals could be stimulated to be active during several observation periods if they had access to the same enrichment items during the entire day.

Data Analysis

To test whether the cleaning regime influenced the behavior of our study animals, we compared the number of sample points corresponding to active animals per day of the week during Phase 1 by means of an Analysis of Variance. We ran a non-parametric paired Wilcoxon test to compare activity levels before and after implementing the enrichment plan. For this, we quantified the number of sample points per species and time block in which the animals were active or inactive in each phase.

To determine which behavioral states were modified by enrichment, we ran a principal component analysis using the mean number of sample points per species and phase for each behavioral category. We then performed non-parametric paired Wilcoxon tests to further examine the behavioral categories that were most influenced by enrichment, and compared the sum of sample points for these behaviors for both phases by time block and per species.

During the initial screening of data, we observed that the categories and events most influenced by the implementation of enrichment were "abnormal behavior" (which included scratching on walls, hyperactivity, extreme passiveness, and suspending from mesh fencing) and "feeding behavior with use of claws." We therefore decided to analyze them in more detail and ran a non-parametric paired Wilcoxon test to assess how the environmental enrichment program influenced the appearance of these behaviors.

TABLE 1. Enrichment types offered during Phase 2

Enrichment type	Description	Quantity offered	Day of the week	Behavior*
Rotten logs	Natural logs containing insects collected near Finca El Turpial and placed on the enclosure's concrete floor.	2 or 3	Monday	AL04
Dry banana leaves	Dry banana leaves collected in Finca El Turpial and placed on the enclosure's concrete floor.	2 or 3	Tuesday	C04
Plastic balls	Hollow plastic balls of 8 cm diameter with a 2 cm hole, filled with sugar-free fruit pulp (first week: strawberry, second to fourth week: mango) or dog food soaked in water.	12 (6 with fruit pulp, 6 with dog food)	Wednesday	E08
Artificial termite mounds	Termite mounds were built with commercially available clay and dried during 4 days. They were filled with compost and earthworms on Wednesday night and covered with a lid made of clay. An orifice of 4–5 cm in the upper part of the termite mound allowed the armadillos to sniff the content of the artificial mound.	1	Thursday	AL04
Cardboard boxes with food	Cardboard boxes of 35 × 35 × 20 cm, half filled with either dog food or compost and earthworms and sealed with transparent tape. Several orifices of 1 cm diameter on the sides of the boxes allowed the armadillos to sniff the content.	3 boxes with 1 kg of dog food or compost with earthworms	Friday	AL04

*Specific behaviors exhibited in response to the enrichment items offered. AL04, Use of claws to access food item; C04, Gather material and introduce it into sleeping box; E08, Examine objects by licking.

We also assessed whether there were differences in the level of acceptance of the enrichment items. For this, we first identified which behaviors were exhibited by the armadillos in response to enrichment (Table 1) and quantified the number of sample points corresponding to these behaviors per species. For instance, we calculated the sum of sample points at which the armadillos examined the objects by licking every Wednesday of Phase 2. We graphically verified whether the number of sample points of behaviors related to enrichment were stable over time. Finally, we compared the sum of sample points of these behaviors over the entire Phase 2 by means of a Kruskal–Wallis test and evaluated by means of Mann–Whitney tests whether there were significant differences among types of enrichment.

We performed statistical analyses for *D. novemcinctus* and *D. sabanicola* with SPSS 22.0 (SPSS Inc., Chicago, IL). The low sample size of *C. unicinctus* precluded statistical analyses for this species, but we nevertheless included it in the principal component analysis. Results are considered statistically significant at $P < 0.05$.

RESULTS

Activity Patterns

We collected a total of 54,720 data points during 240 hr of observation. Activity levels during Phase 1 did not vary significantly over the course of the week ($P > 0.05$), indicating that the cleaning routine on Sundays did not modify the animals' behavior.

In general, both *Dasypus* species were more active than *Cabassous* (Fig. 1). *D. novemcinctus* did not show any difference in activity levels without or with enrichment (2,054 vs. 2,012 data points in Phase 1 and 2, respectively; $P = 1.0$). In *D. sabanicola* the activity decreased significantly (4,032 vs. 3,542; $P = 0.028$) with enrichment, especially at night (1,081 vs. 766; $P = 0.018$) (Fig. 1). The main activity period of *C. unicinctus* shifted from evening to night after implementing the enrichment plan (Fig. 1). Virtually no activity was recorded in the morning in any of the three species, neither without nor with enrichment (32 vs. 55 data points for all species).

Enrichment Items

In general, the armadillos approached the enrichment items, inspected them by sniffing, and started digging and tearing them apart with their front claws to extract the hidden food.

We observed, however, interspecific differences in the acceptance of enrichment items (Fig. 2). All species were attracted by the artificial termite mounds offered on Thursdays; they immediately attacked them and would not recede until they were completely destroyed. *Dasypus* showed special interest in the cardboard boxes with food offered on Fridays, but virtually ignored the plastic balls filled with any kind of fruit pulp or dog food. In contrast to this, both individuals of *C. unicinctus* were mainly attracted

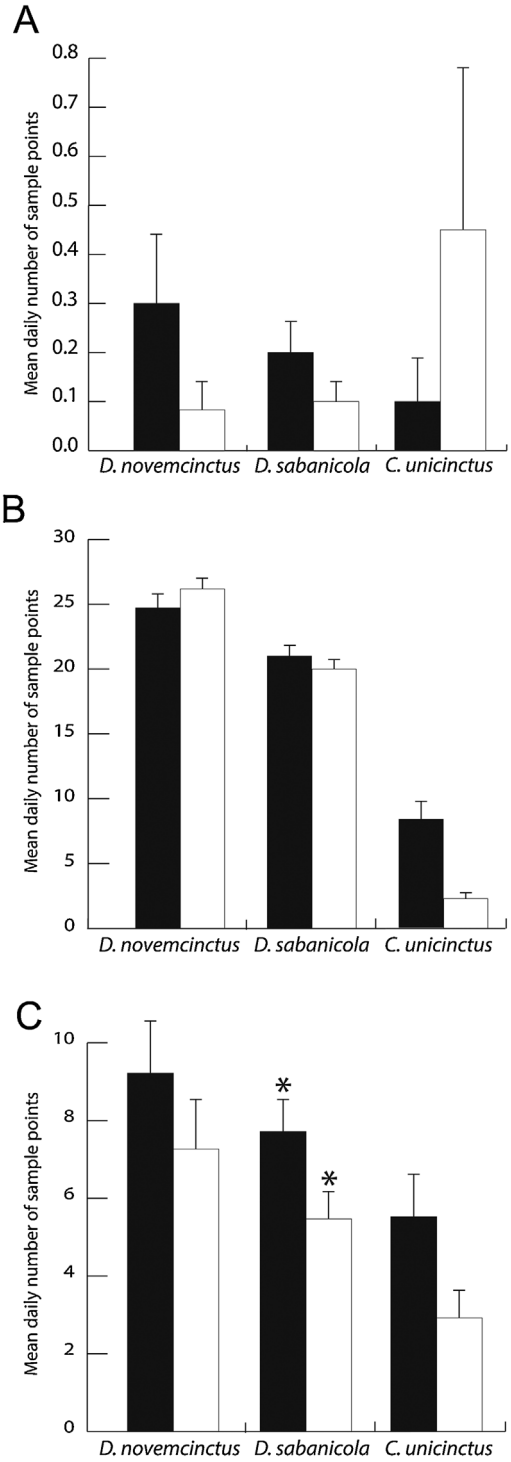

Fig. 1. Activity levels in the morning (**A**), evening (**B**), and at night (**C**) of three armadillo species before (black bars) and after (white bars) implementing an enrichment plan at the breeding facility El Turpial, Villavicencio, Colombia. Values represent the mean daily number of sample points during which the armadillos were active; error bars indicate Standard Error of the Mean. Note the different scales used in the three graphs. Maximum number of sample points was 38. Asterisks mark significant differences ($P < 0.05$); no statistical analyses were made for *C. unicinctus*.

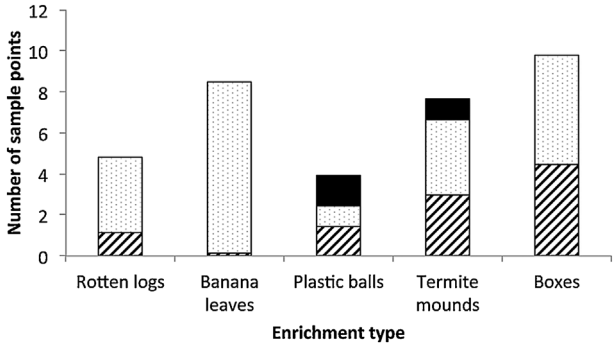

Fig. 2. Mean number of sample points per enrichment type over a 4-week observation period in three armadillo species kept in the breeding facility El Turpial, Villavicencio, Colombia. Hatched, *D. sabanicola*; dotted, *D. novemcinctus*; black, *C. unicinctus*.

to the plastic balls. They readily inspected the balls filled with mango pulp or dog food (but not strawberry pulp, which was rejected by all armadillos), and extracted them with their tongue. This species did not, however, interact with rotten logs, banana leaves, or the cardboard boxes filled with food.

Differences in the reaction to enrichment items were statistically significant in *D. sabanicola* ($P = 0.019$), which showed significantly more interest in termite mounds than in banana leaves ($P = 0.004$). Although this species used both the dry leaves and parts of the cardboard boxes as bedding material, it did so significantly more often with the latter ($P = 0.004$). For this, the animals would tear them apart with their front claws, gather them under their body, hop backwards, and introduce them into the sleeping boxes. Finally, in *D. sabanicola* there was also a significant difference ($P = 0.049$) in the acceptance of cardboard boxes over the plastic balls filled with fruit pulp. There were no

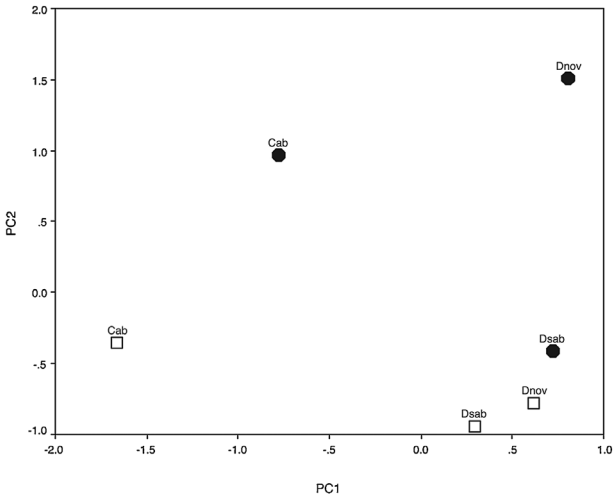

Fig. 3. Principal component analysis of the mean number of sample points per species and study phase (circles: without enrichment; squares: with enrichment) for each behavioral category recorded for three armadillo species in a breeding facility (El Turpial) in Villavicencio, Colombia. Dsab, *D. sabanicola*; Dnov, *D. novemcinctus*; Cab, *C. unicinctus*.

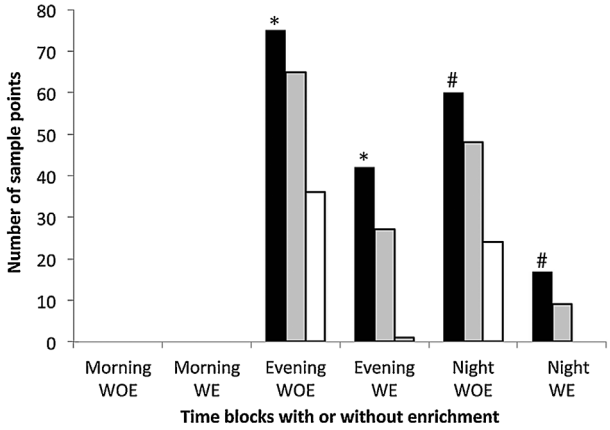

Fig. 4. Total number of sample points for the category "abnormal behaviors" in three armadillo species without enrichment (WOE) and with enrichment (WE). Black bars, *D. sabanicola*; gray bars, *D. novemcinctus*; white bars, *C. unicinctus*. Statistically significant differences ($P < 0.05$) are marked with symbols.

statistically significant differences among types of enrichment in *D. novemcinctus* ($P > 0.05$ in all cases).

Activity levels were similar during all 4 weeks of Phase 2, that is, exposure to enrichment over an extended period of time during the last week did not lead to prolonged activity. Similarly, the number of sample points of behaviors related to enrichment varied between study weeks, but there was no obvious trend such as a steady decrease that would indicate habituation (data not shown).

Principal Component Analysis

Principal component 1 (PC1) accounted for 66.8% and PC2 for 18.4% of the total variance. PC1 had high scores for behaviors of the category "exploration" (PC1 value 0.970) and negative scores for those of the category "rest" (−0.982). PC2 mainly represented abnormal behaviors (0.888).

The first two PCs are plotted in Figure 3. *Dasypus* species showed high positive values for PC1 for both study phases (without and with enrichment), while they were negative in *C. unicinctus*. In other words, *C. unicinctus* spent more time resting and less time exploring than *Dasypus*. In all three species, values for PC1 were lower with than without enrichment, indicating that the frequency of exploratory behaviors decreased and resting increased after implementing the enrichment program.

D. novemcinctus and *C. unicinctus* had positive values for PC2 without, but negative ones with enrichment (Fig. 3). Values were negative during both phases in *D. sabanicola*, but higher without than with enrichment. Consequently, the enrichment program led to a reduction of abnormal behaviors in all three species.

Abnormal Behaviors

None of the three armadillo species exhibited abnormal behaviors in the morning because they were sleeping

during virtually the entire observation period of both study phases (Fig. 4).

The environmental enrichment program significantly reduced the frequency of abnormal behaviors. It led to the complete disappearance of stereotypic behavior and coprophagy in all three species, and to a reduction of extreme passiveness, scratching walls, and suspending themselves from mesh fencing.

In *D. sabanicola*, the appearance of abnormal behaviors was significantly lower in Phase 2 in the evening (60 vs. 17 sample points in Phase 1 and 2, respectively; $P = 0.027$) and at night (75 vs. 42; $P = 0.046$; Fig. 4). Similarly, abnormal behaviors were less frequent in *D. novemcinctus* exposed to an enrichment program (evening: 48 vs. 9; night: 65 vs. 27 sample points in Phase 1 and 2, respectively; Fig. 4). In this species, the differences were not statistically significant ($P > 0.05$ in both cases), possibly due to the low sample size. The enrichment program also led to a notable reduction of abnormal behaviors in *C. unicinctus* (evening: 24 vs. 0; night: 36 vs. 1 sample points in Phase 1 and 2, respectively; Fig. 4).

Behaviors That Were Only Exhibited With Enrichment

Three behaviors were only observed during the second phase of the study; they were seen in all three species. Two of them were exploratory behaviors and involved intense sniffing or licking an item, respectively. In the third one, which was by far the most frequent new behavior (sum of all armadillos: 99 data points during Phase 2), the armadillos used their front claws prior to ingesting their food (behavior AL04; Cortés Duarte et al. [2015]). For instance, they would scratch and tear apart the rotten logs to reach hidden insects or rip open the artificial termite mound to feed on the earthworms.

The behavior AL04 significantly increased in its frequency after implementing the enrichment plan, both in the evening ($P = 0.01$) and at night ($P = 0.008$). There was no difference in the morning because the animals were resting at that time during both phases. The difference in behavior AL04 without or with enrichment was not significant in *D. novemcinctus*, probably due to the low sample size. However, it increased significantly in *D. sabanicola* in the evening ($P = 0.027$) and showed a tendency to increase at night ($P = 0.063$).

Additional Observations

C. unicinctus spent considerably more time sleeping than the other study species. *D. sabanicola* often exhibited aggressive behavior toward the resting naked-tailed armadillos.

A few reproductive events, including several mounting attempts, were observed during the study period; most of them involved *D. sabanicola*. One *D. sabanicola*, of which gestation had remained undetected, gave birth inside a nesting box. Males of *D. novemcinctus* attacked and killed one of the newborn *D. sabanicola*, while the others could be rescued by the observer.

DISCUSSION

None of the three armadillo species studied here showed high activity levels, neither before nor after implementing an environmental enrichment program. Although enrichment did not stimulate them to increase their activity period, it enhanced the quality of the time they were active, thus improving their welfare [Mason et al., 2007]. The latter was evidenced by a considerable reduction in abnormal behaviors, such as scratching on walls, suspending themselves from mesh fencing, or the extreme passiveness observed at the beginning of the study. This reduction was statistically significant in *D. sabanicola*, but not in *D. novemcinctus*, possibly due to the low number of individuals of this species included in our study. In *C. unicinctus*, the abnormal behaviors virtually disappeared with the implementation of the enrichment program.

Enrichment also allowed the armadillos to exhibit behaviors that are common in nature, but had not been observed during the first phase of the study. These new behaviors were related to foraging and included intense sniffing or licking an item, as well as the use of their claws to gain access to the food. The performance of natural behaviors in animals under human care is of fundamental importance because it increases the chances of successful reproduction [Carlstead and Shepherdson, 1994], which in turn allows captive populations to be self-sustainable [Mason et al., 2007]. In addition, they are an important pre-requisite for releasing captive individuals into free-ranging wild habitats [Kleiman, 1989], which is relevant in the case of armadillos that are confiscated by environmental authorities and released into the wild after a quarantine and/or rehabilitation period [Superina et al., 2014a].

On the other hand, the reduction of abnormal and the promotion of natural behaviors are essential to ensure animal welfare, but also to enhance the educational value of a species. McPhee and Carlstead [2010] suggested that visitors who observe captive animals behaving naturally are more likely to perceive them as "happy" and to comprehend their biological significance and need for conservation. In this context, the importance of enrichment programs for armadillos cannot be overstated given that several armadillo species are threatened by extinction [IUCN, 2014], they often exhibit stereotypies, and frequently remain unnoticed by zoo visitors [Superina, 2000].

Superina [2000] proposed to use behavioral enrichment to modify the activity period of armadillos under human care and, thus, increase the chances that zoo visitors can observe species with predominantly crepuscular or nocturnal habits during opening hours. In accordance with Cortés Duarte et al. [2015] who observed only few active animals in the morning, all three evaluated species were less

active during the first observation period of the day. This was expected because *D. novemcinctus*, *D. sabanicola*, and *C. unicinctus* have been reported to have crepuscular or nocturnal habits [McBee and Baker, 1982; Meritt, 1985; Trujillo and Superina, 2013] although the latter species seems to be diurnal in part of its range [Bonato et al., 2008]. Our observations suggest, however, that providing enrichment during their normal resting times does not stimulate them to change their activity period.

Contrary to our expectations, the armadillos were resting more frequently when exposed to the enrichment program although the latter was also implemented during the natural activity period of the animals. We can only speculate about the reason for this unexpected result. Individuals under human care tend to sleep more than their wild conspecifics because they do not need to spend time and energy searching for food or being alert to avoid predators [Rattenborg et al., 2008], which may explain the low activity levels observed here even with enrichment. It does not explain, though, why the animals reduced their activity in the presence of enrichment. It is possible that external factors unrelated to the enrichment influenced the behavior of our study animals. Ambient temperature, humidity, and rainfall were not significantly different between study phases (data not shown), and the general husbandry practices at the breeding facility remained unchanged during the entire study period. Both *Dasypus* species gathered fragments of dry banana leaves and cardboard boxes and introduced them into the nesting box by hopping backwards, a behavior that has previously been described in wild armadillos [Eisenberg, 1961; Taulman, 1994]. Due to their osseous carapace, armadillos have a high minimal thermal conductance [McNab, 1985] and quickly lose body heat in cold environments or, in this case, to a cold concrete floor. Filling the burrow or nesting box with insulating material helps the animals maintain a constant temperature inside their burrow [Gómez-Montoya, 2014]. Furthermore, Johansen [1961] described that sustained cold exposure can lead to increased activity levels in nine-banded armadillos. Similarly, a pichi (*Zaedyus pichiy*) kept in a concrete enclosure devoid of nesting material or a substrate to dig ran around incessantly during periods of low ambient temperature, probably to avoid hypothermia through heat production related to exercise [Superina, unpublished data]. Hence, we hypothesize that by offering the armadillos increased nesting material, we indirectly provided them a more comfortable environment with higher temperatures inside their burrows due to the reduced heat loss to the concrete floor, thus diminishing the need to move as a means to produce muscular heat and maintain their body temperature at an adequate level.

C. unicinctus showed more interest in the plastic balls filled with food than in the artificial termite mounds and other enrichment items containing invertebrates. This result was unexpected, as *Cabassous* is largely, if not exclusively, myrmecophagous [Redford, 1985] and often digs its burrows under termite nests [Carter and Encarnação, 1983]. Because *Dasypus* species are classified as generalist insectivores that ingest a wide variety of food items, including fruit [Redford, 1985; Whitaker et al., 2012], we expected them to show more interest in the plastic balls filled with fruit pulp than the specialist insectivore *Cabassous*. Instead, both *D. novemcinctus* and *D. sabanicola* rarely inspected the plastic balls—neither those with fruit pulp nor with dog food—and preferred termite mounds, rotten logs, and cardboard boxes. This preference for enrichment items with invertebrates is consistent with published analyses of the diet of wild individuals. According to Barreto et al. [1985] and Pacheco and Naranjo [1978], *D. sabanicola* feeds almost exclusively on insects. The proportion of insects in the diet of *D. novemcinctus* can vary depending on location and season, ranging from 29.0% to 97.3% while plant matter may represent from 70.6% to 0.0% of stomach contents [reviewed in McDonough and Loughry, 2008].

Although we used unsweetened fruit pulp, both types (mango and strawberry) naturally contain sugar (mango: 13.7%; strawberry: 4.9%; The National Agricultural Library [2015]). It is possible that the pulp did not attract them because experiments suggest that *D. novemcinctus* is indifferent to solutions described by man as "sweet" (saccharin and sucrose) and avoids maltose [Maller and Kare, 1967].

No information is available about the sense of taste of *Cabassous*, but we cannot exclude the possibility that interspecific differences in the sense of taste exist or that the naked-tailed armadillos were more attracted by the sweet fruit pulp than by insects due to individual preferences. A similar observation was made by Superina [2011] in a pink fairy armadillo (*Chlamyphorus truncatus*) maintained in controlled conditions. The animal refused to ingest insects although the species is classified as a generalist insectivore [Redford, 1985]. Another pink fairy armadillo, in turn, only ate *Tenebrio* larvae [Superina, unpublished data], while it did not accept the mixture described by Superina [2011].

Nevertheless, it is not clear why *Dasypus* individuals were not stimulated by the plastic balls filled with dog food, either, although all study animals were habituated to the latter. As it was difficult for the animals to extract the pellets from the plastic balls, it is possible that the *Dasypus* armadillos simply lost interest in them after a few failed attempts to reach the food.

Finally, it is possible that the differences in overall activity levels, as well as the varying reactions to different enrichment items, are related to age, origin, or prior experiences of the armadillos. Although no data are available about the influence of age on the behavior of armadillos, declines in activity levels of old individuals have been described in many other taxa [Sallis, 2000]. Unfortunately, we do not know the exact age of our study animals due to the lack of individual records and because it is not possible to accurately determine the age of an armadillo once it is fully grown [Loughry and McDonough, 2013]. Similarly, we have no information about the exact origin of our study animals or

how long they have been living under human care prior to this study. It is therefore difficult to assess whether their behavioral differences could be related to their background or other factors that have shaped their personality or caused temperament differences. For instance, an armadillo that has been recently captured in the wild is expected to respond differently to external stimuli than a hand-reared conspecific or one that has been under human care for a prolonged period because the development of mental processes may differ in captivity as a result of lower environmental complexity [Carlstead, 1996].

Although wild individuals have solitary habits except during the breeding season [Loughry and McDonough, 2013], all armadillos, irrespective of their species, gender or reproductive status, are kept together in the same enclosure at the breeding facility Finca El Turpial. Ignoring their social organization and spatial needs, as well as the lack of sufficient places to which subordinate individuals can retreat, can lead to increased stress levels and agonistic behavior in animals maintained in controlled conditions [Morgan and Tromborg, 2007], including armadillos [Roberts et al., 1982; Superina, 2000]. Indeed, we repeatedly observed aggressive behavior, especially from *D. sabanicola* toward *C. unicinctus*. In addition, keeping such a large group of individuals in the same enclosure precludes an effective reproductive and genetic management, although the latter are key elements of ex situ breeding programs [de Boer, 1994]. The lack of reproductive management at Finca El Turpial resulted in an unexpected parturition of a female *D. sabanicola*. The sire of this litter was unknown because several males were kept in the same enclosure and mating had occurred prior to the initiation of this study. Parturition was followed by an infanticide caused by males of *D. novemcinctus*. Armadillo dams are highly sensitive to external disturbances, and in some species neonate mortality can be up to 100% in the presence of males [Superina et al., 2008]. To our knowledge, this is the first report of an armadillo infanticide caused by another armadillo species.

CONCLUSIONS

1. Although enrichment did not increase the armadillos' activity period, it did improve their welfare by reducing the occurrence of abnormal behaviors and promoting natural exploratory behaviors.
2. Offering enrichment during natural resting periods did not stimulate armadillos to become more active. Because activity periods may vary among species, location, and even individuals, the activity period of all animals should be determined, for example, by means of an ad libitum sampling, and the enrichment program applied during the time of day at which they are most active.
3. Due to interspecific differences in the acceptance of varying items, it may be necessary to develop a separate enrichment program for different armadillo species. Artificial termite mounds are recommended for all armadillos, and cardboard boxes with food and rotten logs for most. Species that use nesting material inside their burrows, such as *Dasypus*, will gather dry (banana) leaves, shreds of cardboard, wood shavings, and similar materials and introduce them into their boxes. *Cabassous* can be stimulated with hollow plastic balls filled with food.
4. *C. unicinctus* spent considerably more time resting than *Dasypus*, and the latter repeatedly attacked the sleeping naked-tailed armadillos. As a consequence, we recommend keeping these species in separate enclosures to avoid agonistic behavior.

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