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Crowned solitary eagle (*Buteogallus coronatus*) as accumulator of armadillo osteoderms in the archaeological record? An actualistic taphonomic study for central Argentina



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ABSTRACT

To distinguish whether the presence of osteoderms of armadillos (Xenarthra, Dasypodidae) in the zooarchaeological and paleontological record can be assigned to anthropic action or predators is an interesting topic. The Crowned solitary eagle (*Buteogallus coronatus*, Accipitriformes, Accipitridae) is among the predators that usually consume armadillos. It is one of the largest South American birds of prey, inhabiting southern Brazil to northern Patagonia in Argentina. Prey remains of the armadillos *Zaedyus pichi*, *Chaetophractus villosus* and *C. vellerosus* were collected in 13 breeding areas from two biogeographic regions including La Pampa and Mendoza provinces, central Argentina, during 2010–2012. The significant amount of carapaces, osteoderms, and cranial elements of armadillos accumulated in nests is a distinctive feature of the Crowned solitary eagle. These accumulations are taphonomically characterized by the presence of: 1) complete or almost complete flattened, depressed or book-shaped folded carapace; 2) scarce caudal armors and cephalic shields; 3) flexible bands, and scapular and pelvic shields well represented; 4) anterior region of scapular shields usually broken; 5) many isolated osteoderms broken, crenulated or with irregular borders; 6) posterior regions of skulls often with crenulated, broken or missing borders; 7) skulls with beak marks in the dorsal and posterior parts of the braincase, and in the palates; 8) some mandibles with the posterior part broken; 9) scarce, but well preserved limb bones; and 10) beak marks on scapulae and pelves. In addition, the information obtained from abandoned nests showed that these taphonomic features could have been altered by weathering. These observations can be used in subsequent studies of armadillo bone accumulations from open-air archaeological or paleontological sites from central Argentina, and other parts of America, inhabited by the Crowned solitary eagle, as well as in future revisions of samples.

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1. Introduction

Armadillos (Xenarthra, Dasypodidae) are mostly distributed in South America. They are semi-fossorial mammals that use burrows for shelter, nesting, parturition, hibernation or torpor (e.g.,

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Superina and Loughry, 2012; Superina et al., 2014). Their fossorial activities produce archaeological and sedimentological disturbances by moving and destroying lithic and bone materials while digging (Mello Araujo and Marcelino, 2003; Frontini and Escosteguy, 2012). Armadillos are the only mammals covered by a flexible carapace composed of numerous osteoderms or bony dermal scutes (~800) (Wetzel et al., 2007; Superina et al., 2014 and references therein). Therefore, the presence of only few individuals would be sufficient to produce an osteoderm accumulation.

Armadillos were first recorded in the Late Paleocene of Brazil (Krmptotic et al., 2009), and in the Early Eocene of Argentina (Ciancio and Carlini, 2008). They have been described as prey of different predators such as mammalian carnivores and birds of prey inhabiting different environments of South America (e.g., Montalvo et al., 2007; Ballejo et al., 2012; Frontini and Vecchi, 2014 and references therein). Hunter–gatherers have also hunted them since prehistory. For these reasons, exoskeletal (osteoderms) and endoskeletal bones of armadillos are frequently recorded in archaeological and paleontological sites of Argentina (e.g., Vizcaíno and Bargo, 1993; Vizcaíno et al., 1995; Ciancio and Carlini, 2008; del Papa, 2012; Loponte and Acosta, 2012; Otaola et al., 2012; Soibelzon et al., 2013; Frontini and Vecchi, 2014; Hammond et al., 2014; Fernández et al., in this volume).

The osteoderms recovered from archaeological sites have drawn the attention of zooarchaeologists, who treated them as a problem of taphonomic equifinality, using actualistic models (e.g., Frontini and Escosteguy, 2012; Frontini and Vecchi, 2014; Hammond et al., 2014; Muñoz, 2015). From a taphonomic point of view, it is crucial to distinguish if raptor birds, carnivore mammals, or humans accumulated the remains of armadillos, in order to evaluate natural action (death *in situ* and predation) vs. human subsistence (Binford, 1981; Andrews, 1990; Lyman, 1994). Cut marks, thermal alteration patterns, and skeletal anatomical representations are the main taphonomic evidence to infer that these animals could have been hunted and consumed by humans (e.g., Frontini and Vecchi, 2014 and references therein). Although several mammals and raptor birds consume armadillos (Massoia and Pardiñas, 1986; Hiraldo et al., 1995; Saggese and de Lucca, 2004; Trejo et al., 2006; Foster et al., 2010; Sarasola et al., 2010; Zanón et al., 2012), little is known about the taphonomic modifications of bones and osteoderms produced by them (Montalvo et al., 2007; Ballejo et al., 2012). Most actualistic studies of diurnal raptors (Falconiformes and Accipitriformes) were focused on small mammals and small birds (e.g., Mayhew, 1977; Hoffman, 1988; Andrews, 1990; Hockett, 1995; Bochenski et al., 1999; Gómez, 2007; Lloveras et al., 2008; Montalvo and Tallade, 2009, 2010; Souttou et al., 2012; Montalvo et al., 2014).

In this contribution, we present a taphonomic analysis of the modifications produced by the Crowned solitary eagle (*Buteogallus coronatus*, Accipitriformes, Accipitridae) during capture and handling on armadillos recovered from several accumulations of prey remains from central Argentina. In addition, we compared active and abandoned nests of the Crowned solitary eagle in order to evaluate the differential preservation in the accumulations. The taphonomic data presented here may be used as actualistic model for the zooarchaeological record.

2. Crowned solitary eagle (*Buteogallus coronatus*) as armadillo accumulator

The Crowned solitary eagle (*Buteogallus coronatus*) is among the largest South American birds of prey (~3 kg) (Fig. 1), inhabiting southern Brazil to northern Patagonia in Argentina (Fergusson-Lees and Christie, 2001; Sarasola et al., 2010). This species inhabits semi-open, arid and semi-arid areas, mainly in lowlands, but also at intermediate altitudes (Collar et al., 1992). Historically its distribution was wider, reaching central Patagonia (see Maceda, 2007; and references therein). The fragmentation and loss of habitat due to deforestation was proposed among the causes of low population numbers of this species (Collar et al., 1992; Maceda, 2007). For this reason, the Crowned solitary eagle is listed in the IUCN Red List of Threatened Species (2012), as well as in the Argentinean list of threatened birds (Chébez et al., 2008; López-Lanús et al., 2008). Studies on wild populations of this species are scarce. Many aspects

of its biology are still unknown, including habitat use and selection, and feeding ecology. This raptor is mostly solitary and crepuscular; its nests are a large platform of sticks placed on top of trees or occasionally in abandoned human constructions, such as metallic towers (Maceda, 2007). The hunting techniques of the Crowned solitary eagle include perching and waiting for prey, as well as performing circular low-altitude flights approximately 100 m above the ground (Pereyra Lobos et al., 2011). Knowledge about its food habits increased in the last 10 years, mainly in central Argentina (Maceda et al., 2003; Maceda, 2007; Chébez et al., 2008; Sarasola et al., 2010; Pereyra Lobos et al., 2011). In these works, the Pichi or Dwarf armadillo (*Zaedyus pichiy*) was the most important prey in terms of number and biomass, and a trophic selection was suggested for this prey. Armadillos represent about 50% of the Crowned solitary eagle diet [48.6% in Sarasola et al. (2010) and 57.9% in Pereyra Lobos et al. (2011)], while small mammals, reptiles, birds and fish constitute the remaining diet. The hunting activity pattern of the Crowned solitary eagle seems to be consistent with the daily activity patterns of its prey (M. Galmes unpubl. data).

The family Dasypodidae includes 21 living species of armadillos, distributed from the southern United States to the Strait of Magellan [Argentina and Chile; Wilson and Reeder (2005)]. Three species were identified in the samples analysed here. *Chaetophractus villosus* (Hairy armadillo) and *Chaetophractus vellerosus* (Screaming hairy armadillo) inhabit the Gran Chaco of Bolivia, Paraguay, Argentina and Chile. Both species extend south to Santa Cruz Province in Argentina and Magallanes in Chile. *Chaetophractus vellerosus* also inhabits central Argentina, and a small population was found in the coast of Buenos Aires Province (Abba and Superina, 2010). The third species recovered is *Zaedyus pichiy*, which ranges from central Argentina and eastern Chile south to the Strait of Magellan (Superina and Abba, 2014). *Chaetophractus vellerosus*, *C. villosus* and *Z. pichiy* are omnivorous and are threatened by human persecution (Abba and Superina, 2010; Abba et al., 2011; Superina and Abba, 2014).

There is scarce information about predators of *C. vellerosus*, which was reported only as prey of Crowned solitary eagles (Sarasola et al., 2010). *Chaetophractus villosus* was described as prey of crowned solitary eagles, but also of *Geranoaetus melanoleucus* (Black-chested buzzard eagle), and mammals such as *Lycalopex culpaeus* (Andean fox), and *Puma concolor* (puma) (Hiraldo et al., 1995; Zapata et al., 2005; Zanón et al., 2012; Superina and Abba, 2014). *Zaedyus pichiy* is preyed by Black-chested buzzard eagles, Crowned solitary eagles, Andean fox, puma, and *Lycalopex griseus* (South American grey fox) (Zapata et al., 2005; Zanón et al., 2012; Superina and Abba, 2014).

3. Regional setting

The studied breeding areas of the Crowned solitary eagle are located in central-western La Pampa Province, in an area of 15,000 km², and central-eastern Mendoza Province in the protected “Nacuan Biosphere Reserve”, in an area of 123 km² (Fig. 1, Table 1). These areas include the southern limit of the distribution range of this eagle, corresponding from east to west to the Espinal and Monte Desert ecoregions, respectively (Burkart et al., 1999). The Espinal has a warm and semi-desert climate, sandy soils, and the vegetation is mainly characterized by deciduous xerophytic forest with “Caldén” (*Prosopis caldenia*) as the dominant tree. The Monte, coincident with the South American Arid Diagonal, has warm-desert climate, sandy soils, and the vegetation is mainly composed of xerophytic shrubs such as *Larrea* spp. and isolated trees such as *Prosopis* spp. and *Geoffroea decorticans* (Burkart et al., 1999; Abraham et al., 2009).

Table 1
Identification of 13 breeding areas and frequencies of Dasypodidae.

Locality	Beeding areas ID	Ecoregion	Dasypodidae remains
La Mota	1	Espinal	17
La Pelegrina	2	Espinal	13
Las Nutrias	3	Espinal	10
La Gitana	4	Espinal	1
San José	5	Espinal	50
Campomar	6	Espinal	14
Nafra	7	Espinal	3
San Eduardo	8	Espinal	13
Torres	9	Monte Desert	19
Ventrecó	10	Monte Desert	35
Vicente	11	Monte Desert	20
El Tres	12	Monte Desert	22
Nacuñan	13	Monte Desert	83

4. Material and methods

Between 2010 and 2012, we collected all pellets and prey remains of Crowned solitary eagles from one nest (and perches around it) from 12 breeding areas in La Pampa Province and two nests (one active and the other inactive) for Nacuñan Reserve, Mendoza Province (Table 1, Fig. 1). In general, we found one or two pellets per nest, and five only once. They are very fragile, poorly consolidated and break down quickly. Prey remains include all the uneaten items accumulated on the surface of the nest, and under roosting sites and perches of the surrounding area. Skeletal accumulations are not randomly scattered and depend on the nesting

site, mostly on the vegetation physiognomy around the nest: number and distance of perches around the nest. In the Nacuñan Biosphere Reserve, armadillo remains were recovered from both active and abandoned nests in order to make taphonomic comparisons, including weathering variables (Behrensmeyer, 1978).

The dorsal armor or carapace is one of the most conspicuous features of armadillos. The main function was conventionally attributed to protection from predators: however, this seems not to be its primary function (see Superina and Loughry, 2012). The carapace consists of four clearly distinguishable regions, cephalic shield, scapular shield, flexible bands (of variable number) and pelvic shield, and a caudal armor (Vizcaino and Bargo, 1993; Soibelzon et al., 2013). They are composed of bony dermal scutes or osteoderms covered by epidermal scales (Fig. 2). The different regions of the carapace were analyzed to evaluate degree of completeness/incompleteness and breakage. In addition, the type of marks (e.g., punctures, irregular holes, crenulated) produced in the carapace and endoskeletal elements during handling and ingestion of prey were evaluated (*sensu* Loveras et al., 2014). These modifications were observed with a Leica Ms5 stereomicroscope.

Taxonomic identifications were made by comparison with specimens housed in the mammal collection of Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (La Pampa, Argentina) as well as with specific literature (e.g., Vizcaino et al., 1995; Soibelzon et al., 2013). The minimum number of individuals (MNI, Grayson, 1984) was calculated using the shield region, most frequent in the breeding areas. To have an estimate of the total number of

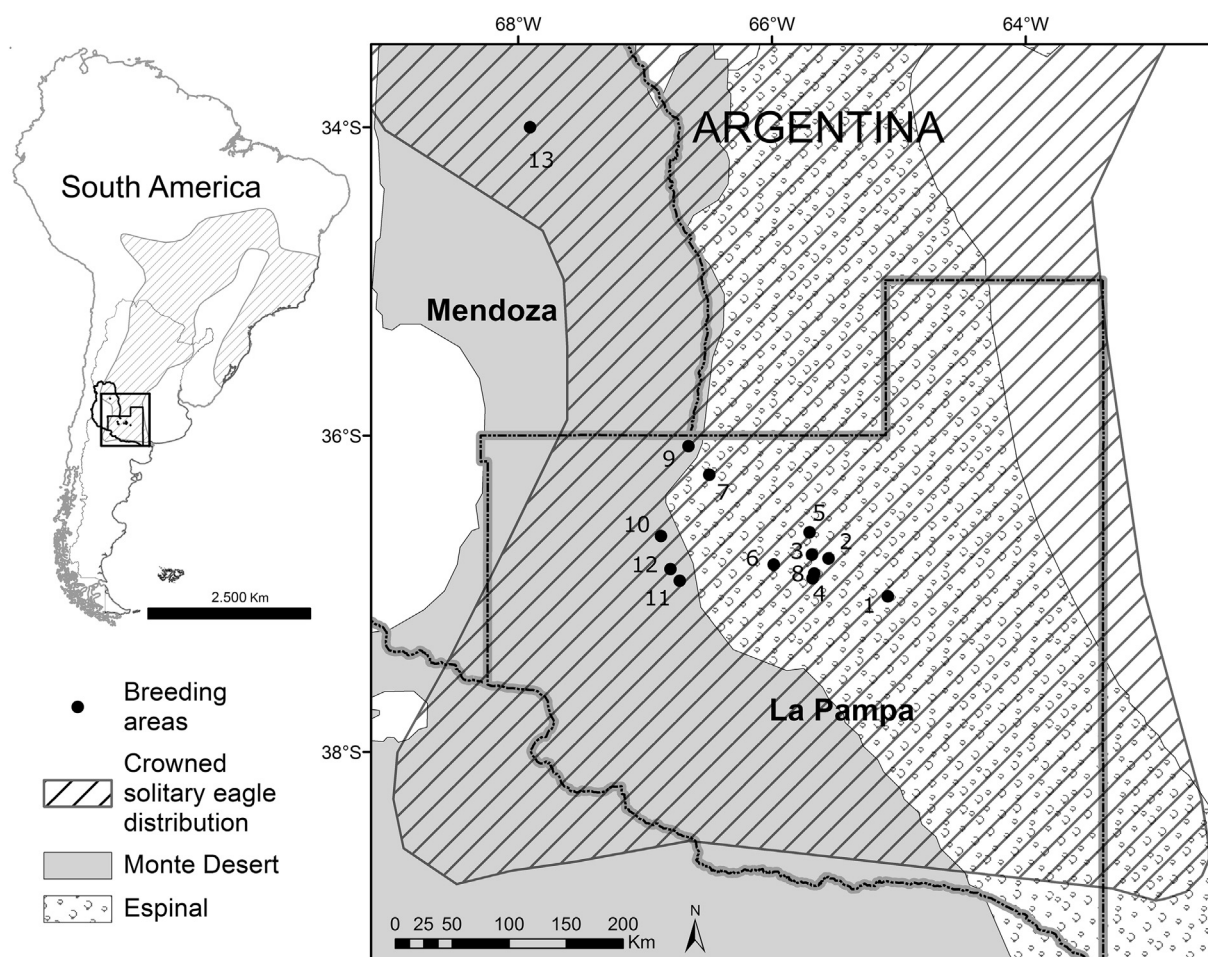


Fig. 1. Distribution of *Buteogallus coronatus* in South America and map of the study area, including La Pampa and Mendoza provinces, Argentina. The map (IUCN) shows the location of breeding areas superimposed on the main ecoregions (according to Burkart et al., 1999). Numbers (ID) are those used in Table 1.

osteoderms of the armors, they were counted in six individuals of *Zaedyus pichiy*, and four of *Chaetophractus vellerosus* and *C. villosus*.

5. Results

5.1. Taxonomic representation in the total sample

Three hundred and nine prey remains, belonging to eight taxa of vertebrates, were recovered from 13 breeding areas (Fig. 1). The three species of dasypodids (*Zaedyus pichiy*, *Chaetophractus villosus* and *C. vellerosus*) constituted 97.08% of prey remains. *Zaedyus pichiy* was the most frequent, followed by *C. villosus* and *C. vellerosus* (Fig. 3). Other vertebrates were represented by nine prey remains recovered from four breeding areas (6, 7, 8, 13), including two isolated skulls of *Tupinambis* sp. (lizard) and *Conepatus chinga* (Hog-nosed skunk), four isolated mandibles of *Tupinambis* sp., *C. chinga* and *Lepus europeus* (European hare), two isolated skulls of *Galictis cuja* (Lesser grisson), and articulated vertebrae of *Serpentes* indet.

5.2. Anatomical representation, articulation and breakage degree in all samples

The dasypodids sample included 300 prey remains represented by complete carapaces, isolated shields, skulls, mandibles, and other scarce skeletal elements, with and without soft tissues; 130 carapaces retained epidermal scales, 82 preserved hair, 9 ears, and 8 some areas with skin. Table 2 shows the proportion of different elements recovered, discriminated by taxon.

A hundred armor remains retained the four regions of the dorsal carapace (Fig. 4a), and only four included the caudal armors. Two hundred were incomplete carapaces; 36 lacked the cephalic shield, but other shields were complete (Fig. 4b), and 13 were only represented by cephalic shields (Fig. 4c). The rest of prey remains consisted of the following structures: cephalic and scapular shields (Fig. 4d), scapular shield and flexible bands (Fig. 4e), and flexible bands and pelvic shield (Fig. 4f).

When evaluating the representation of each region of the carapace, cephalic shields were preserved in 128 prey remains (60.16% complete and 39.84% incomplete); scapular shields in 183 (65.03% complete and 34.97% incomplete); flexible bands in 201 (51.24% complete and 48.76% incomplete) and pelvic shields in 191 (66.49% complete and 33.51% incomplete). Incomplete regions included shields lacking several osteoderms (Fig. 4g), and carapace borders with lost or broken osteoderms (Fig. 4h). In several cases, broken edges were irregular and crenulated, affecting one or two osteoderms or the whole osteoderm line. There were some differences in carapace preservation between fresh prey remains (with epidermal scales, skin, and hair) and those exposed for a longer period to atmospheric conditions. In the first case, the completeness of all shields was higher, and shields remained attached. In the other case, a high degree of shield and osteoderm disarticulation and dispersion was observed. Very incomplete shield portions or completely isolated osteoderms were also found.

Ninety-five armadillo skulls were recovered: 75 were still articulated with the cephalic shield (Fig. 4i) and 21 had the mandibles articulated (Fig. 4j). Regarding the degree completeness of the

Table 2

Number percentage, and marks of complete or incomplete portions of armadillos carapace, skulls and mandibles, discriminated by taxon.

			<i>Zaedyus pichiy</i>	<i>Chaetophractus villosus</i>	<i>C. vellerosus</i>	Dasypodidae indet.
Cephalic shields	Complete	NR	59	10	4	4
		%	62.77	52.63	66.67	44.44
	Incomplete	NR	35	9	2	5
		%	37.23	47.37	33.33	55.56
Scapular shields	Marks	NR	15	3	3	0
		%	15.96	15.79	50	0
	Complete	NR	95	17	2	5
		%	69.85	68	50	27.78
Flexible bands	Incomplete	NR	41	8	2	13
		%	30.15	32	50	72.22
	Marks	NR	18	5	2	3
		%	13.24	20	50	16.67
Pelvic shields	Complete	NR	82	19	1	1
		%	45.81	73.08	25	6.67
	Incomplete	NR	74	7	3	14
		%	41.34	26.92	75	93.33
Skulls	Marks	NR	35	3	4	2
		%	19.55	11.54	100	13.33
	Complete	NR	96	18	2	11
		%	53.63	78.26	22.22	61.11
Mandibles	Incomplete	NR	45	5	7	7
		%	25.14	21.74	77.78	38.89
	Marks	NR	25	5	4	6
		%	13.97	21.74	44.44	33.33
Mandibles	Complete	NR	17	3	3	4
		%	33.33	18.75	33.33	21.05
	Incomplete	NR	34	13	6	15
		%	66.67	81.25	66.67	78.95
Mandibles	Marks	NR	1	13	6	4
		%	1.96	81.25	66.67	21.05
	Complete	NR	18	4	13	12
		%	66.67	100	81.25	63.16
Mandibles	Incomplete	NR	9	0	3	7
		%	33.33	0	18.75	36.84
	Marks	NR	9	0	3	7
		%	33.33	0	18.75	36.84

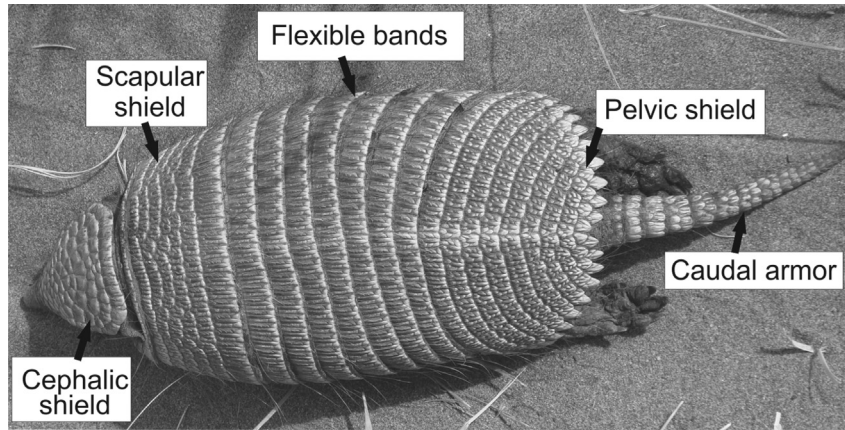


Fig. 2. Dorsal view of the carapace regions of Dasypodidae.

skulls, 68 lacked the rostral portion, the posterior portion or both (Fig. 4k), two lacked the cranial roof, and the remainder were complete. Several skulls showed the parietal, occipital and posterior area of the palate broken, and lacked some molariforms (Fig. 4k). Twenty carapaces were found completely flattened (Fig. 4b and i); 47 were book-shaped folded (along the midline or transverse to the body) (Fig. 5a) and five showed a depressed area (Fig. 5b). Numerous incomplete scapular shields with their anterior region broken or missing areas with irregular edges were also found (Fig. 5b–c). In addition, 66 mandibles were recovered: 26 showed both hemimandibles articulated (Fig. 4j), seven had the symphyseal portion broken and 14 the angular area and/or coronoid process broken. The articulated or associated postcranial elements are listed in Table 3. Cervical vertebrae were the most frequent element, generally attached to the skulls retained in the carapace. Vertebrae show little damage, and in several cases, they were protected by soft tissue.

Table 3

Postcranial elements recovered in the total sample of armadillos (NR, number of remains).

Skeletal elements	NR
Scapulae	2
Vertebrae	76
Ribs	10
Pelves	16
Sinsacrum	2
Femora	2
Whole hindlimbs	5

5.3. Marks

Although the eagle holds the carapace with claws and pulls the soft tissues with beak, only light beak or talon marks on the osteoderms were observed in all samples. However, numerous fractured carapaces and irregular and crenulated borders on fractured osteoderms were identified (Table 2, Fig. 6a). Some skulls, mandibles, and postcranial elements showed broken areas with irregular or stepped fractures (Fig. 6b–c; *sensu* Marshall, 1989). There were puncture marks with bone collapse and irregular edges in five skulls, two scapulae, and one pelvis. These marks appeared as perforations in thin portions of these bones. In skulls, the largest marks were 9.70 mm (Fig. 6c–d and e), located in the dorsal region (braincase), and a single skull had three marks in the occipital

region (Fig. 6e). Several carapaces displayed circular holes (diameter = 2 mm) in some osteoderms. These marks were either isolated or occurred in more than one osteoderm of the same carapace (Fig. 6f).

5.4. Ñacuñan Biosphere Reserve sample

This locality (13) had the highest number of prey remains of armadillos in the whole sample accumulated in the breeding area (two nests), including complete and incomplete carapaces, osteoderms and other skeletal elements. It yielded 83 armadillo remains (*Zaedyus pichiy*, 48.19%; *Chaetophractus villosus*, 13.25% and *C. vellerosus* 9.64%; the remaining specimens were assigned to Dasypodidae indet.). Only 36% of the carapaces had epidermal scales, 20.5% hair, and 3.6% ears.

The nests were identified as active and abandoned according to bone features, nest locations, and collection date. In the active nest, with 18 prey remains, more than 55% were carapaces with the four regions of the carapace. Five of them retained the skull articulated with the cephalic shield. Pelvic shields were the most represented (in 16 prey remains), while flexible bands were present in 12, and cephalic and scapular shields were recovered in 14. The remaining 45% of this sample were isolated portions of shields with different degrees of completeness. All remains retained epidermal scales and more than 50% of this sample retained hairs. Two complete skulls and five without the posterior region, and seven hemimandibles

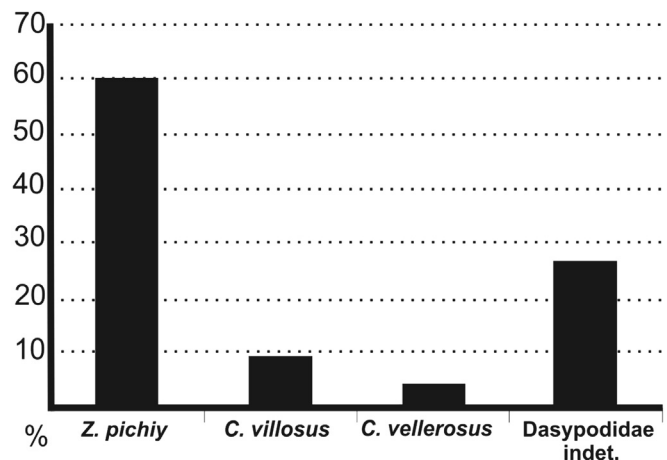


Fig. 3. Percentage of armadillos remains in the total sample.

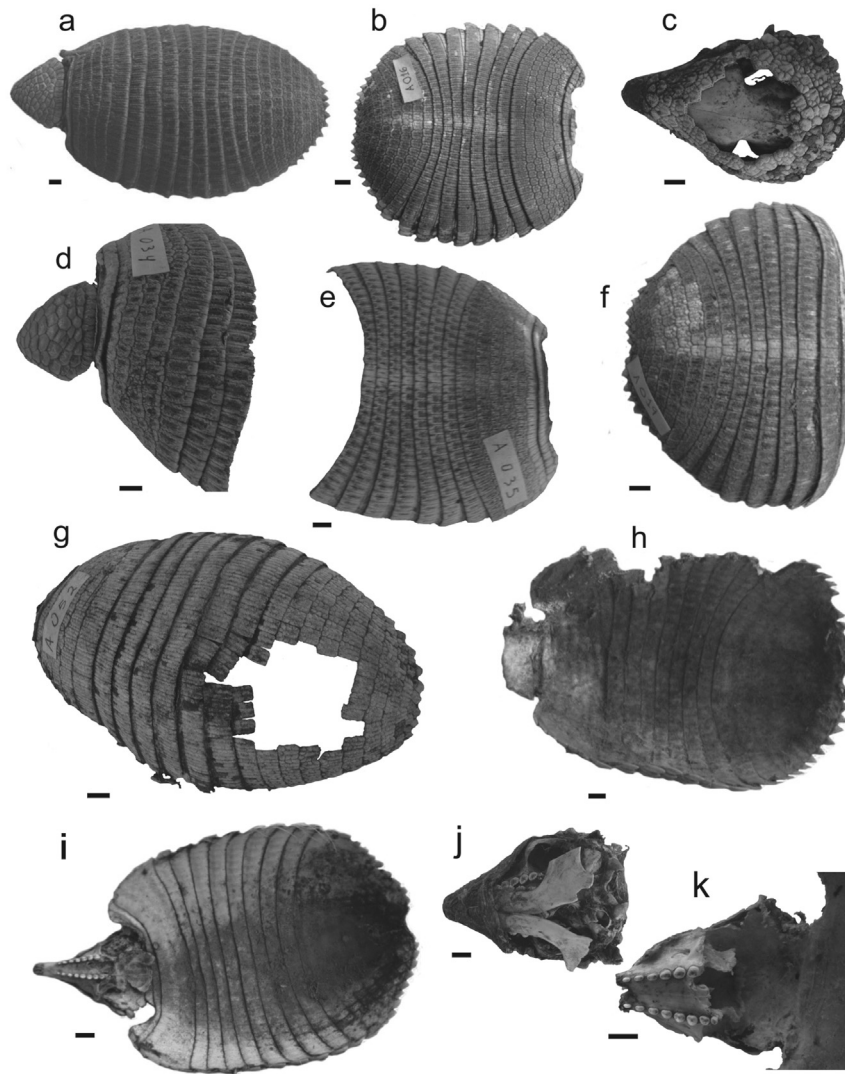


Fig. 4. Examples of prey remains. a. Complete carapace (12); b. carapace lacking cephalic shield (13); c. only cephalic shield (1); d. cephalic and scapular shields (11); e. scapular shield and flexible bands (5); f. flexible bands and pelvic shield (13); g. incomplete carapace including shields without several osteoderms (1); h. carapace borders with broken and lost osteoderms (2); i. skull articulated with carapace (13); j. skull and articulated hemimandibles (1); k. skull without anterior and posterior portions (13). The numbers in brackets correspond to the breeding area locality (ID). Scale bar = 1 cm.



Fig. 5. a. Book-shaped folded carapace (10); b. carapace with a depressed area and scapular shield with missing areas defined by irregular edges (5); c. scapular shield with missing areas defined by irregular edges (11). The numbers in brackets correspond to the breeding area locality (ID). Scale bar = 1 cm.

were recovered. In the abandoned nest, 65 armadillo prey remains were recovered; 32.30% with the four shields, but none of them was complete. Less than 50% of the carapaces retained epidermal scales and only 21.5% had hair. Flexible bands were the most preserved shields, with different degree of completeness in 55 prey remains.

Cephalic shields were less frequent, and present in 30 prey remains. Scapular and pelvic shields were recovered in 44 and 43 prey remains, respectively. The incomplete shields were mainly represented by portions lacking many osteoderms. The endoskeletal elements were represented by one femur, 10 hemimandibles, and

38 skulls (six complete, 14 with the anterior region broken and 18 with the posterior region broken). Of the total skulls, 20% showed cracking, flaking, desquamation, and open sutures (Fig. 6g–h and i).

Table 4 shows the mean values of osteoderms of each carapace for the three species of dasypodids. This allows estimating an average of 860.33 osteoderms per individual. Furthermore, in order to estimate the number of osteoderms present in each nest, the minimal number of armadillo individuals (MNI) in both nests was calculated. The result was 16 individuals in the active nest (based on pelvic shields) and 55 individuals in the abandoned nest (based on flexible bands). Considering the mean number of osteoderms per armadillo, a value of 13,765 osteoderms in the active nest and 47,318 osteoderms in the abandoned nest was obtained. These values confirm the high accumulation of osteoderms produced by the Crowned solitary eagle in the depositional environment, at least at the time of collection.

mechanical action of teeth, beaks or talons before or during ingestion, and the subsequent damage produced by the corrosion effect during digestion (Andrews, 1990). Diurnal raptors, including the Crowned solitary eagle, yield a substantial amount of bone destruction during prey consumption (Mayhew, 1977; Hoffman, 1988; Andrews, 1990). The bones not consumed are discarded at roost or nest sites, which yields bone assemblages produced these uneaten remains (Hockett, 1995; Bochenski et al., 1999). Therefore, this type of accumulation has a different survival and tends to be less fragmented than bones recovered from pellets (Lloveras et al., 2008).

The taxonomic structure of the prey remains of the Crowned solitary eagle was similar to those documented in previous studies. Sarasola et al. (2010) and Pereyra Lobos et al. (2011), based on remains from pellets and prey, reported a high frequency of armadillos, with an extremely high predominance of carapaces and

Table 4
Amount of osteoderms from each carapace of the three species of dasypodids present in the sample.

	Cephalic shield	Scapular shield	Flexible bands	Pelvic shield	Total
<i>Zaedyus pichiy</i>	90	237	270	185	782
<i>Chaetophractus villosus</i>	123	259	319	239	940
<i>Chaetophractus vellerosus</i>	113	253	299	194	859

6. Discussion

All predators produce modifications on the bones of their prey. The main alterations consist of breakage and fragmentation by

osteoderms over other endoskeleton elements. Although the modifications of ingested bones were not studied here, a preliminary analysis of the remains recovered from pellets of some nests, showed that only a few had armadillo remains, mostly

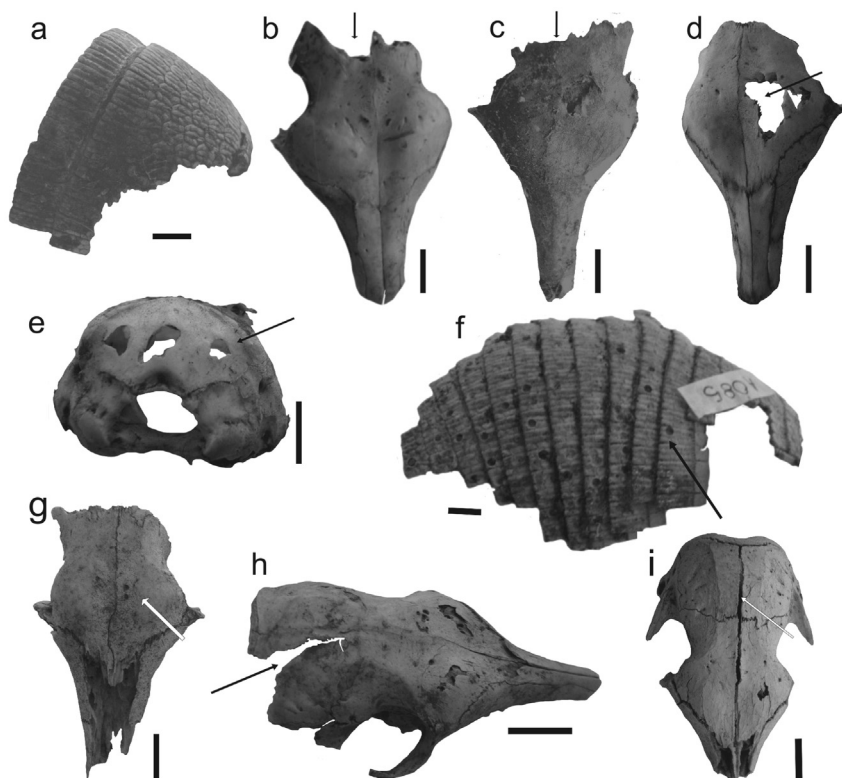


Fig. 6. a. Prey remain with crenulated and irregular borders (10); b. skull with broken areas with irregular fractures (5); c. skull with broken areas with stepped fractures and puncture mark with irregular edges (13); d. skull with puncture marks with irregular edges (13); e. skull with three puncture marks with irregular borders (13); f. carapace with circular holes in some osteoderms (5); g, h and i. skulls with cracking, flaking, desquamation and open sutures (13). The numbers in brackets correspond to the breeding area locality (ID). Scale bar = 1 cm.

osteoderms, with heavy evidences of corrosion by digestion. Their presence in the pellets of the eagle could be interpreted as accidental ingestion. These osteoderms showed more evidence of digestive action than those described by Montalvo et al. (2007) from samples of puma (*Puma concolor*) scats, and by Ballejo et al. (2012) from pellets of the American black vulture (*Coragyps atratus*), which exhibited strong modifications produced by digestive acids.

The armadillos lack carapace in the underside of the body, where soft, naked skin is present. This region is the most accessible for predators (Saggese and de Lucca, 2004). The high abundance of skeletal elements in the nests of the Crowned solitary eagle may be related to the way in which these birds access the body of the armadillos. This raptor strikes a death blow in the cephalic region and access the body by breaking the neck (M. Galmes pers. obs., Fig. 7a–c). This action may explain the high frequency of scapular shields with broken anterior portion, and the low frequency of cephalic shields. As well, the high frequency of carapaces with the four regions, but none complete, suggests that there was loss of osteoderms almost from the beginning of the prey handling to eat the soft tissues. The postcranial elements recovered belonged mainly to the posterior region, and in some cases included their articulations (e.g., whole hindlimb), indicating exploitation of the whole anterior body of the prey. The rapid consumption of all soft tissues during prey handling may cause the carapaces to acquire flattened or folded (book-shaped) appearances, with depressed areas. The raptor eagle probably rests on the carapace while tearing off all soft tissue with the beak. However, typical evidences of trampling, subparallel fine scratches described by Fiorillo (1989), both in outer and inner surface of the carapace, were not recognized. Apparently, the presence of scales, hair and connective tissue precludes the production of such marks. The described breakage of the weakest parts of the carapace (crenulated and irregular osteoderm borders, broken osteoderms or broken shields and junction area between the shields), could have been produced by trampling and handling. The rare presence of caudal armors in the whole sample may be associated with the rapid disarticulation of this region, or because they were eaten by the eagle. The presence of fragments of caudal armor was observed on preliminarily reviewed pellets.

The high percentages of skulls with the posterior region broken or absent, and skulls with beak marks on the dorsal and posterior region, are probably related to the consumption of the brain. Broken skulls had irregular and crenulated borders. Regarding the mandibles, 20% had their posterior area broken or absent. The

postcranial elements showed little evidence of modification, excluding marks produced by beak action on scapulae and pelves.

The frequency of carapaces, osteoderms, cranial elements and several postcranial elements of armadillos is undoubtedly one of the most distinctive features to identify an accumulation of the Crowned solitary eagle. The significant amount of osteoderms that they can accumulate in nests was evident. The type of breakage in skulls and mandibles (mainly in the posterior portion of these elements) would be a consequence of the Crowned solitary eagle mode of feeding, which occurred while the animal was stripping the masseter muscle and breaching the occipital region to extract the brain. There is no information about the modifications that other predators may produce on the carapaces and osteoderms of armadillos. Marks (mainly breakage and punctures) produced by the Crowned solitary eagle on skulls, mandibles and endoskeletal elements are similar to those produced by several eagles from other parts of the world. For instance, bone damage (mandibles with broken ascending rami, skulls represented by maxillae with molars) was described by Schmitt (1995) for leporid remains accumulated by the Golden eagle (*Aquila chrysaetos*) from North American and Eurasia. The Crowned hawk-eagle (*Stephanoaetus coronatus*) from Africa produces similar puncture marks in skulls, scapula and pelves of monkeys. In addition, skulls, hindlimb elements, and scapulae survive predation better than other bones. Crania and mandibles of adults are typically complete, while crania of young individuals are usually dissociated from mandibles and lack basicrania and rostra. Long bones are often complete or show minimal damage. Thin bones, such as crania and pelves, are marked by numerous nicks, punctures, and “can-opener” perforations (Sanders et al., 2003). The mammalian prey remains recovered from nests of the African Verreaux's eagle (*Aquila verreauxii*) showed similar types of modifications (punctures, pits, scores, crenulated edges) in several bones (Armstrong and Avery, 2014). Finally, the marks in several remains recovered from nests of the Bonelli's eagle (*Aquila fasciata*) presented crenulated edges, notches and punctures (Lloveras et al., 2014). These authors pointed out that no reliable criteria allow discrimination of marks produced by beaks from those yielded by talons.

In the Nacuñan Biosphere Reserve locality, the active and the abandoned nests showed different features. The carapaces and endoskeletal elements exposed to weathering in an open environment with scarce vegetation cover (the abandoned nest site) suffered damages due to the combination of temperature and moisture fluctuations leading to bone decomposition at the ground surface (Behrensmeier, 1978). The abandoned nests showed higher

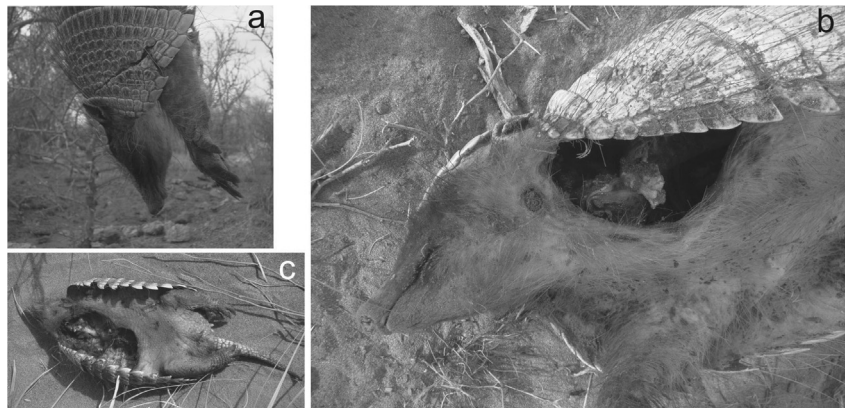


Fig. 7. *Zaedyus pichiy* killed by *Buteogallus coronatus* a. prey remain with broken scapular shield; b and c. prey remains with broken neck area in their ventral region.

loss of osteoderms and carapace portions, loss of 50% of epidermal scales, less cephalic shields, higher number of flexible bands, higher disarticulation and bone dispersion, and cracking, flaking, desquamation and open sutures in skulls (Fig. 6g–h and i), apparently associated with weathering and dispersion action. Muñoz (2015) examined naturally dead armadillos exposed to weathering and dispersion agents in the seacoast of southern Patagonia. Compared to our study, he pointed out a severe delay in the time of bone dispersion and weathering, related to the armadillo carapace. Our observations suggest that the Crowned solitary eagle produces modifications in carapaces during the consumption that could accelerate the bone weathering and dispersion.

No signs of modifications were identified on armadillo leftover remains caused by other organisms after the consumption by the Crowned solitary eagle. The circular holes observed in some osteoderms were caused by the parasitic fleas of the genus *Tunga* (Siphonaptera, Tungidae), whose gravid females bury themselves into the carapace of armadillos, perforating the osteoderms (Ezquiaga et al., 2015). Therefore, these holes could have been produced before the capture of the armadillo by the eagle. Similarly, Hammond et al. (2014) found some osteoderms of *Zaedyus pichiy* with circular perforations from a Holocene archaeological site in the seacoast of southern Patagonia made by the fleas *Tunga*. Their taphonomic study resolved an equifinality problem of whether the perforations were produced by tools of humans or by natural agents. Frontini and Vecchi (2014) noted another equifinality problem about a great accumulation of osteoderms and endoskeletal elements of *C. villosus* from a Holocene archaeological site of the seacoast of the southern Pampean region. In this case, non-uniformly burned osteoderms (mainly on the external region) and scarcely burned endoskeletal elements were interpreted as derived from human consumption of this armadillo, instead of the natural death in burrows as observed in a nearby archaeological site (Frontini and Escosteguy, 2012). However, as fire is frequent in central-western La Pampa Province (Fischer et al., 2012), burned carapaces are found below Crowned solitary eagle nests or perch sites. Thus, the external region of osteoderms is the most affected, probably by being in contact with the ground (M. Galmes pers. obs.). Moreover, Fernández et al. (in this volume) documented both natural death in burrows and human consumption of *C. villosus* in a Holocene archaeological site of northwestern Patagonia, based on findings of an articulated skeleton, and cut marks and burnt osteoderms. The actualistic results presented here together with these archaeofaunistic examples provide valuable information about how to evaluate natural action (death *in situ* and predation) vs. human subsistence.

7. Final remarks

This contribution reported the first actualistic study about the taphonomic modifications of armadillo carcasses produced by the action of raptor birds, specifically the crowned solitary eagle. This eagle produces great accumulations of osteoderms and endoskeletal elements of armadillos in their nests. These accumulations are taphonomically characterized by the presence of: 1) complete or almost complete flattened, depressed or book-shaped folded carapaces; 2) scarce caudal armors and cephalic shields; 3) flexible bands, and scapular and pelvic shields well represented; 4) anterior region of scapular shields usually broken; 5) many isolated osteoderms broken, crenulated or with irregular borders; 6) posterior regions of skulls often with crenulated, broken or missing borders; 7) skulls with beak marks in the dorsal and posterior parts of the braincase, and in the palates; 8) some mandibles with the posterior part broken; 9) scarce, but well preserved limb bones; and 10) beak marks on scapulae and pelves. In addition, the information obtained from abandoned nests showed that these taphonomic features could have been altered by weathering, common in open

environments with scarce vegetation cover, such as desquamation of the skulls and loss of portions of the carapace.

These taphonomic features will allow assessment of equifinality between this diurnal raptor and humans. Therefore, the results could be used in subsequent studies of bone accumulations of armadillos from open-air archaeological or paleontological sites, as well as in future revisions of published samples from central Argentina and other parts of South America inhabited by the Crowned solitary eagle.

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