NINE-BANDED ARMADILLO

Dasypus novemcinctus Linnaeus, 1758

**FIGURE 1** - (FPMAM68PH) Adult, Estancia Nueva Gambach, PN San Rafael, Departamento Itapúa (Hans Hostettler undated).

**TAXONOMY:** Class Mammalia; Subclass Theria; Infraclass Eutheria; Order Cingulata; Family Dasypodidae; Subfamily Dasypodinae (Myers et al 2006, Möller-Krull et al 2007). Seven species are recognised in this genus, three are present in Paraguay. *Dasypus* is derived from a Greek translation of the Aztec name "Azotochtli" which roughly means "tortoise-rabbit"; *novemcinctus* means "nine bands", in reference to the movable bands across the back. There are seven subspecies, the nominate subspecies *D.n.novemcinctus* Linnaeus 1758 is present in Paraguay (Gardner 2007). Examination of cranial characteristics is necessary to assign specimens to subspecies. Desmarest’s (1804) description was based on de Azara’s (1801) "Le Tatou Noir" and Buffon’s (1776) "Le Tatuete et Cachicame" Larrañaga’s (1923) description was based on de Azara’s (1802) "Negro". Synonyms adapted from McBee & Baker (1982) and Gardner (2007): [Dasypus] novemcinctus Linnaeus 1758:51. Type locality "in America Meridionali" restricted to Pernambuco, Brazil by Cabrera (1958).
Tatus minor Fermin 1769:110. Unavailable.
Dasypus octocinctus Schreber 1774: pl.lxxxiii. No locality given.
Dasypus longicandatus Kerr 1792:112. Type locality "America".
Dasypus longicandatus Daudin in Lacépède 1802:173. Based on Buffon’s "Le Tatou á Longue Queue". Preoccupied.

Dasypus octocinctus Schreber 1774: pl.lxxxiii. No locality given.
Dasypus longicandatus Daudin in Lacépède 1802:173. Based on Buffon’s "Le Tatou á Longue Queue". Preoccupied.

Tatus minor Fermin 1769:110. Unavailable.
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Dasypus octocinctus Schreber 1774: pl.lxxxiii. No locality given.
Dasypus longicandatus Daudin in Lacépède 1802:173. Based on Buffon’s "Le Tatou á Longue Queue". Preoccupied.

Dasypus octocinctus Schreber 1774: pl.lxxxiii. No locality given.
Dasypus longicandatus Daudin in Lacépède 1802:173. Based on Buffon’s "Le Tatou á Longue Queue". Preoccupied.
Dasypus mazzai Yepes 1933:226. Type locality "Tabacal, Departamento de Orán" Salta, Argentina.


GUARANÍ COMMON NAMES: Tatu hu MPA (Neris et al 2002, Villalba & Yanosky 2000), Tatú-hu (Redford & Eisenberg 1992) Tatú-hú (Parera 2002), Tatu MPA (Villalba & Yanosky 2000), Chachú Ac (Villalba & Yanosky 2000). The Guarani name is the most frequently utilised in Paraguay for this species, the Spanish names rarely being heard in everyday speech. Tatu hu means "black armadillo" in reference to the dark colouration of the carapace.

DESCRIPTION: "Long-nosed" Armadillos have a broad, depressed body, an obtusely-pointed rostrum, long, pointed ears (40-50% head length) and short legs. The carapace consists of two immobile plates, the scapular and pelvic shields each with 18-20 rows of ossified scutes and separated by 8 or 9 movable bands connected to each other by a fold of hairless skin. The vast majority of Paraguayan individuals possess 8 movable bands, despite the common name, and the average number of movable bands across the entire range is 8.3. The carapace is mostly blackish, hairless and with the scales of the anterior edge of the movable bands diagnostically pale yellowish-white in colour. Paler scales are also present on the lower halves of the scapular and pelvic plates, generally with broad blackish margins. Scutes on the movable bands are triangular in shape, but those on the main plates are rounded. The number of scutes present on the fourth movable band varies from 54 to 65, typically 60 (Díaz & Barquez 2002). The head is thin and triangular with a sloping forehead and long, mobile ears with rounded tips that are not separated by armour at the base. The head plate is generally pale and pinkish-yellow, often slightly darker and blacker on the crown. Scutes of the head plate are heavy and closely attached to the skull. The tail is long (equal to or greater than body length) with 12 to 15 rings of bicoloured scutes giving it a banded appearance along the basal 60% and narrowing towards the tip where it terminates in irregular scutes. There are four toes on the forefoot (characteristic of the Subfamily Dasypodinae), the middle two much the longest, and five on the hindfoot. The underside is naked and pinkish with only a light covering of coarse greyish hair sprouting from regularly-spaced papillae. Sexes are barely distinguishable, though males may be slightly hairier along the lateral part of the venter. Females have four nipples, two pectoral and two inguinal. Males lack a scrotum and the testes descend no further than the pelvis. Males have an average body temperature of 33.4ºC and females 31.3ºC, males also have a consistently faster heart rate.

SKELETAL CHARACTERISTICS: Steeply descending frontal bone and an almost horizontal rostrum with a triangular tip in lateral profile. Occipitonasal Length 90mm (Díaz & Barquez 2002). Genoways & Timm (2003) give the following cranial measurements for males and females from Nicaragua (ssp. fenestratus): Occipitonasal Length male 99mm (+/-0.86; n=14), female 98.1mm (+/-1.12; n=7); Condylobasal Length male 89.1mm (+/-0.72; n=13), female 89.7mm (+/-1.2; n=7); Length of Nasals male 32.4mm (+/-0.5; n=14), female 32.2mm (+/-0.51; n=7); Zygomatic Width male 43.1mm (+/-0.40; n=10), female 41.8mm (+/-0.66; n=6); Postorbital Width male 23.5mm (+/-0.15; n=14), female 23.2mm (+/-0.37; n=7); Mastoid Width male 28.3mm (+/-0.19; n=13), female 28.2mm (+/-0.7; n=7); Length of Palate male 64mm (+/-0.65; n=14), female 63.7mm (+/-0.81; n=7); Length of Mandible male 77.9mm (+/-0.62; n=14), female 77.9mm (+/-0.99; n=7); Length of Rostrals male 59.5mm (+/-0.84; n=14), female 59.4mm (+/-1.1; n=7).
Vizcaino et al (1999) give the following ulnar dimensions (n=17): Ulnar Length 68.7mm (+/-3.5); Olecranon Length 26.7mm (+/-2.1). The trend towards fossoriality is correlated with relative development of the olecranon process, and the ratio of the ulnar length to olecranon length is the Index of Fossorial Ability. An IFE above 0.70 is considered indicative of a highly fossorial species and one below 0.55 of a cursorial species. This species has an IFE of 0.64 (+/-0.06).

Vickaryous & Ball (2006) describe the morphology of the osteoderms. Most of the osteoderms on the cephalic, pelvic and pectoral shields are equidimensional pentagons and hexagons which form a mosaic when ordered. Each has a series of foramina interconnected by grooves that form a rosette-like pattern. Osteoderms are not articulated and eventually disarticulate after death. Osteoderms of the bands are roughly rectangular with elements having up to a 5 to 1 length to width ratio. The anterior portion overlaps the posterior of the following band. Tail osteoderms are also rectangular but only twice as long as they are wide. They completely encircle the tail forming a series of nested rings. Hill (2006) compared the osteoderms of this species with several extinct forms.

**DENTAL CHARACTERISTICS:** Armadillos lack true teeth. "Long-nosed" armadillos have single-rooted, peg-like teeth that lack enamel. 7-9/7-9 = 28-36 - most often 8/8=32. Genoways & Timm (2003) noted that at least in Nicaragua (subspecies *fenestratus*) juveniles have just 7 deciduous teeth in each toothrow. These are replaced by 7 permanent teeth with the addition of one or two permanent teeth which lack a deciduous precursor to give the full adult complement.

Genoways & Timm (2003) give the following cranial measurements for males and females from Nicaragua (ssp. *fenestratus*): Length of Upper Toothrow male 24.2mm (+/-0.54; n=13), female 24mm (+/-0.48; n=7); Length of Lower Toothrow male 26mm (+/-0.25; n=12), female 25.9mm (+/-0.28; n=7).

Green (2009) looked for a link between the orthodentine microwear of this species and its diet, but found considerable intertooth variation, possibly related to the uneven distribution of bite force on the dentition of long-faced animals, though food texture and intraspecific variation likely also play a role.

**GENETIC CHARACTERISTICS:** 2n=64, FN=80. Redi et al (2005) gives the genome size as 5.41pg (+/-0.27) or 5291 Mbp. Autosomes separable into five groups: two large pairs of metacentrics, four large pairs of acrocentrics, six pairs of medium metacentrics, fourteen pairs of medium acrocentrics and five pairs of small acrocentrics. The X chromosome is a large metacentric with a medial centromere. The Y chromosome is a small acrocentric. North American armadillos display moderate microsatellite allelic variability (Beath et al 1962, Prodöhl et al 1996).

Frutos & Van den Bussche (2002) noted that the Paraguay River did not act as barrier to gene flow between populations in the Chaco and Oriental regions of Paraguay. Paraguayan populations are characterised by a high number of closely-related haplotypes, with 25 haplotypes found among 75 individuals sampled. Nested clade analysis revealed a continued range expansion, isolation by distance and long distance dispersal of females.


**TRACKS AND SIGNS:** *Dasypus* prints can be distinguished from those of other armadillos by their long, pointed toes with four toes on the forefoot and five on the hindfoot. However they generally leave the impression of only the two central toes on the forefoot (though sometimes the outer toe is also visible) and three central toes on the hindfeet. Given a full print, the hindfoot has a pointed heel with three long, somewhat pointed central toes and two, much shorter, outer toes set well back towards the heel. The forefoot has the inner toe much reduced and it rarely leaves an impression. **FP:** 4.8 x 3.5cm **HP:** 6 x 4.8cm. **PA:** 25cm. (Villalba & Yanosky 2000). Footprints are approximately 50% larger than those of *D.septemcinctus*. Faeces resemble those of *Tamandua tetradactyla*, being composed largely of ant and termite remains, but they are generally more elongated and also contain soil and elements of vegetable matter. Typically no more than 2 or 3 pellets are dropped in one place. Faeces are usually deposited along runways in forested areas, making them difficult to locate (Taber 1945, Anacleto 2007).
EXTERNAL MEASUREMENTS: The largest of the "long-nosed armadillos" in Paraguay. Males slightly larger than females. TL: 64.57 (60-100cm - generally in the range 60-85cm) Adult size is not reached until the animal is 3 to 4 years old (Redford & Eisenberg 1992); HB: 41.03cm (32.4-57.3cm); Height at Shoulder 155-230mm; TA: 30.18cm (21.1-45cm); FT: 87.5cm (5.9-11.4cm); EA: 4.32cm (3.3-5.9cm); WT: 3.91kg (2.9-8.3kg - generally between 3-6.5kg) Carapace accounts for c16% of body weight; WN: 85g. (Parera 2002, Nowak 1991, Emmons 1999, Ceresoli et al 2003, Redford & Eisenberg 1992, Díaz & Barquez 2002, McBee & Baker 1982).

McDonough (2000) noted significant sexual dimorphism in mass of individuals in Texas, with males heavier than females: WT: male 4.69kg (+/-0.55; n=48), female 4.41kg (+/-0.51; n=45). Breeding males were also heavier than non-breeding males WT: breeding male 4.98kg (+/-0.28), non-breeding male 4.20kg (+/-0.54). Mass also increased with age WT: adult 4.6kg (+/-0.4; n=19), 1-2 year-olds 4kg (+/-0.4; n=7). Masses of males paired with one female did not differ significantly from males that paired with two or more females WT: male with single mate 4.92kg (+/-0.26; n=4), male with multiple mates 5.07kg (+/-0.29; n=9).

Morgan & Loughry (2009) give the following external measurements for leprous (male n=10, female n=22) and non-leprous (male n=107, female n=103) armadillos from Mississippi, noting no sexual differences in size, but that leprous females were larger than non-leprous females in front carapace, back band and tail base measurements: WT: male leprous 4.35kg (+/-0.26), male non-leprous 4.19kg (+/-0.39), female leprous 4.20 (+/-0.36), female non-leprous 4.03kg (+/-0.42); Front carapace length male leprous 21.32cm (+/-0.87), male non-leprous 20.85cm (+/-0.83), female leprous 21.06cm (+/-0.84), female non-leprous 20.54cm (+/-0.72); Front band length male leprous 33.05cm (+/-1.31), male non-leprous 32.77cm (+/-1.20), female leprous 33.05cm (+/-1.5), female non-leprous 32.59cm (+/-1.23); Back band length male leprous 36.93cm (+/-1.13), male non-leprous 36.44cm (+/-1.32), female leprous 37.12cm (+/-1.52), female non-leprous 36.44cm (+/-1.36); Tail base circumference male leprous 15.67cm (+/-0.56), male non-leprous 15.62cm (+/-0.68), female leprous 15.76cm (+/-0.53), female non-leprous 15.45cm (+/-0.62); TA: male leprous 31.26cm (+/-2.13), male non-leprous 30.05cm (+/-1.89), female leprous 32.15cm (+/-1.86), female non-leprous 31.84cm (+/-2.22).

Morgan & Loughry (2009) give the following external measurements for leprous and non-leprous females at varying reproductive stages. Leprosoy was associated with larger size and lactation due to increased progesterone levels: WT: leprosy lactating (n=15) 4.30kg (+/-0.35), leprosy possibly lactating (n=3) 4.08kg (+/-0.24), leprous not lactating (n=4) 3.81kg (+/-0.21), non-leprous not lactating (n=44) 4.09kg (+/-0.40), non-leprous possibly lactating (n=51) 4.19kg (+/-0.43), non-leprous not lactating (n=8) 3.93kg (+/-0.42); Front carapace length leprous lactating 21.10cm (+/-0.87), leprous possibly lactating 21.10cm (+/-1.06), leprous not lactating 20.80cm (+/-0.70), non-leprous lactating 20.56cm (+/-0.76), non-leprous possibly lactating 20.45cm (+/-0.66), non-leprous not lactating 20.54cm (+/-0.71); Front band length leprous lactating 33.29cm (+/-1.54), leprous possibly lactating 33.03cm (+/-1.64), leprous not lactating 31.90cm (+/-1.99), non-leprous lactating 32.72cm (+/-1.22), non-leprous possibly lactating 32.50cm (+/-1.32), non-leprous not lactating 32.52cm (+/-1.24); Back band length leprous lactating 37.38cm (+/-1.52), leprous possibly lactating 36.47cm (+/-1.23), leprous not lactating 36.47cm (+/-1.86), non-leprous lactating 36.73cm (+/-1.38), non-leprous possibly lactating 36.17cm (+/-1.37), non-leprous not lactating 36.26cm (+/-1.32); Tail base circumference leprous lactating 15.93cm (+/-0.53), leprous possibly lactating 15.53cm (+/-0.08), leprous not lactating 15.13cm (+/-0.12), non-leprous lactating 15.58cm (+/-0.64), non-leprous possibly lactating 15.44cm (+/-0.52), non-leprous not lactating 15.35cm (+/-0.61); TA: leprous lactating 32.31cm (+/-1.97), leprous possibly lactating 30.90cm (+/-0.56), leprous not lactating 32.63cm (+/-2.04), non-leprous lactating 31.09cm (+/-2.09), non-leprous possibly lactating 32.42cm (+/-1.91), non-leprous not lactating 32.27cm (+/-2.26).

Genoways & Timm (2003) give the following external measurements for males and females from Nicaragua (ssp. fenestratus) noting no significant difference between the sexes, though measurements of males tend to be slightly larger: TL: male 807mm (+/-18.47; n=8), female 785mm (+/-38.27; n=5); TA: male 359mm (+/-12.45; n=8), female 365mm (+/-7.34; n=7); FT: male 88.44mm (+/-4.78; n=7), female 81.88mm (+/-5.96; n=6); EA: male 41.4mm (+/-1.00; n=7), female 39.8mm (+/-1.72; n=6).

McDonough et al (1998) studied growth rates of captive litters. Males and female growth was linear during the first year of life, but by the second year female growth was best described by a fourth order polynomial (\( y = 172.659 + 2.422x + 0.06X^2 - 0.0002X^3 + 0.0000001X^4 \); \( r = 1.0, P < 0.0001, n = 436 \)). Full adult size was attained at around 400 days, though some animals continued to increase in size well
into the second year (beyond day 700). Results generally supported the traditional classification of armadillos into age classes by mass (ie juvenile <2.5kg; yearling 2.5-3.5kg; adult >3.5kg). The following results were obtained for captive and wild first year animals caught during the months of June, July and August: wild males June 0.881kg (+/-0.15, n=9), July 1.06kg (+/-0.41, n=23), August 1.72kg (+/-0.53, n=21); wild females June 0.915kg (+/-0.35, n=16), July 1.25kg (+/-0.42, n=59), August 1.59kg (+/-0.57, n=13); captive males June 0.783kg (+/-0.10, n=4), July 1.01kg (+/-0.11, n=4), August 1.39kg (+/-0.14, n=4); captive females June 0.965kg (+/-0.17, n=4), July 1.36kg (+/-0.11, n=4), August 1.49kg (+/-0.11, n=4).

Hind foot and ear lengths can be used to determine fetal age (Rojas-Suárez & Maffei 2003).
50 days HF 7mm; EA 2mm; WT 2g.
70 days HF 13mm; EA 9mm; WT 16g.
90 days HF 20mm; EA 14mm; WT 36g.
120 days HF 27mm; EA 20mm; WT 64g.

**SIMILAR SPECIES:** Adults are much the largest of the "long-nosed armadillos" in Paraguay and can be immediately identified by the number of bands - generally eight or nine (usually 8) in this species and never more than seven in other Paraguayan *Dasypus* (Hamlett 1939). It can be further distinguished by the blackish colouration with yellowish-white triangular scales on the posterior edge of the movable bands and the generally paler-coloured cephalic shield. Of all the *Dasypus* this species has proportionately the longest ears (40-50% of head length) and tail (equal to or greater than body length).

*Dasypus septemcinctus* is much smaller overall, with dark and blackish, lacking the pale edges to the movable bands which also number 6 or 7. It has similar length ears (40-50% head length) but a proportionately shorter tail (80-100% body length) than the Nine-banded. It has a mean of 48.4 scutes along the fourth movable band (Hamlett 1939). Both *D.septemcinctus* and *D.hybridus* have just 6 upper teeth in each jaw.

*Dasypus hybridus* is intermediate in size between *septemcinctus* and *novemcinctus*, though much closer to the former. It has proportionately shorter ears and 6 or 7 movable bands. The ears are shorter, typically 25-30% of head length, as is the tail (67-70% body length). It has a preference for open grassy areas. Using the fourth movable band as a standard, Hamlett (1939) noted that this species has a mean of 60 scutes whereas *D.hybridus* has a mean of 54 scutes. The presence of *hybridus* in Paraguay is by no means clear, though traditionally it has been assumed to occur here, the species name being based on a vague description by d’Azara from Paraguay. Work to clarify the status of this species in Paraguay is ongoing (Owen & Smith in prep.).

**DISTRIBUTION:** This is the most widely distributed of all the armadillos, occurring from the USA south to Argentina, and is actually in the process of expanding its range to the north. The northern and southerly limits of the range are probably defined by cold, lack of insects and drought (Redford & Eisenberg 1992) whilst MacDonald (1985) also notes that competition with other armadillo species may limit its southerly expansion.

In the USA it was recorded in Texas for the first time in 1880; arriving in Arkansas by 1921 (Dellinger & Black 1940); Louisiana by at least 1925 (Strecker 1926); crossing the Mississippi River by 1935 (Lowery 1936) and becoming established in southwest Mississippi by the 1950s (Buchanan 1958); it reached Oklahoma by 1932 (Tyler & Donelson 1932); Colorado by 1963 (Hahn 1966); Kansas by 1970 (Merriam 2002), Nebraska by 1972 (Choate & Flaherty 1975, Freeman & Genoways 1998) and southern Illinois by 1992 (Hoffmann 2009). An isolated population in southern Alabama was established by 1949, but may have been descended from introduced individuals (Fitch et al 1952). The eastern population in Florida originated from escapes from a local zoo in Brevard County in 1922 and later merged with migrants from Texas around 1972 (Humphrey 1974), expanding into Georgia and South Carolina by 1995 (Taulmann & Robbins 1996). Cold is apparently slowing its northward advance (MacDonald 1985).

It is found throughout Central America, some offshore islands (Platt et al 2000) and even some Caribbean Islands. West of the Andes it occurs south to northern Peru, but east of the Andes it reaches...
Uruguay and Argentina as far south as Provincia Entre Rios in the east of the country, though only to the Yungas in the west. The most southerly record in Argentina is from Guisasola, southwestern Province Buenos Aires, with an additional two animals found dead on the Rio de La Plata Coast, but human intervention in their presence, though unlikely, could not be ruled out (Zamorano & Scillato-Yané 2008).

The subspecies found in Paraguay is *D.n.novemcinctus*, which is distributed through most of South America, east of the Andes from Colombia and Venezuela south to Argentina. The remaining subspecies are: *D.n.mexicanus* from the USA south to southern Mexico; *D.n.davisii* from the Balsas Basin to the mountains of Morelos in Mexico; *D.n.baplitensis* from Trinidad and Tobago, Grenada, Barro Colorado Island and Costa Rica; *D.n.aequatorialis* west of the Andes in Ecuador and probably also Peru and Colombia; *D.n.fenestratus* from Oaxaca through Central America to Panama and possibly also across northern South America; *D.n.mexicanus* is endemic to the delta of the Rio Amazonas, Pará, Brazil. The species has been successfully introduced to the Pacific island of Guam some time after 1959 (Long 2003).

In Paraguay it occurs throughout the country in all departments, though it is considerably more sparsely distributed in arid areas. Parera (2002) states that its presence in the Dry Chaco of Argentina requires confirmation, but Neris et al (2002) report multiple records of the species in the Dry Chaco of Paraguay - noting that the species is more common in humid areas. It seems to be relatively common at least in the transitional area around the Mennonite Colonies of the Central Paraguayan Chaco (P.Smith pers.obs.).


**HABITAT:** This adaptable species is able to colonise a variety of habitats from humid Atlantic forest, through grasslands and agricultural areas, to the palm savanna of the Humid Chaco and drier chaco forest and cerradón. It is more common in warm, humid areas and seems to prefer some forest cover, being the most frequently encountered armadillo species in undisturbed humid forest habitats (P.Smith pers. obs) but is generally absent from open, grassy areas where other species of *Dasypus* are present. West of the Paraguay River it reaches its greatest abundance in the Humid Chaco. Merritt (2008) notes it as present in almost every habitat in the Paraguayan Chaco, but absent from the most xeric areas and most common in moister grasslands and shrubby patches that have been converted for use by cattle, with wooded boundaries between fields being ideal for the species. Such strips of wooded land act as biological corridors that encourage the spread of the species.

Anacleto et al (2006) used the genetic algorithm program GARP to predict the species distribution in Brazil, with results suggesting this species would occur in Amazonia, Cerrado Caatinga, Atlantic Forest and Pantanal biomes in that country. Santos-Filho & da Silva (2002) found the species in gallery forest and palm forest dominated by *Orbignia martiniiana* in Mato Grosso, Brazil.

**ALIMENTATION:** Considered a generalist insectivore that exploits the food materials most easily available in any given habitat. Redford (1986) classified them as primarily entomophagous omnivores and opportunistic myrmecophages in North America, noting that the greater abundance and diversity of ants and termites in the tropics may make myrmecophagy more prominent in Central and South American portions of the range.

They begin to forage immediately on leaving the burrow after nightfall and studies suggest that there is a move from more forested to more open habitats as the night progresses (McBee & Baker 1982). Foraging animals are noisy and follow random paths, snorting constantly and investigating every potential source of food. Eyesight is poor and food is located by smell, with most food items taken from the soil surface or by using the claws to dig shallow, triangular feeding holes just below the surface. (Redford & Eisenberg 1992). During June and July 1996 Simkin & Michener (2005) counted a mean of 167 (+/-124.7) armadillo foraging digs per hectare which had a mean depth of 9cm (+/-0.5) in n a Longleaf Pine ecosystem in Georgia, USA.

Nine-banded Armadillos re-use traditional feeding trails and foraging individuals are so preoccupied with the job in-hand that they may even collide with an immobile observer (Emmons 1999). Frequently they will rise up onto the hindlegs, using the tail for balance, and sniff the air. The nose is often pressed into the hole to maintain the scent trail and they may hold their breath for up to 6 minutes to
avoid dust inhalation (MacDonald 1985). Ancona & Loughry (2009) suggested that this species may spend 77 to 90% of its active above-ground time foraging, one of the highest values recorded for any mammal. It was suggested that this intensive foraging regime was consistent with Dunbar’s (1992) time constraints hypothesis as an explanation for why altruism has not involved in this species despite siblings being genetic clones of each other.

Adults have been seen using the forefeet to smash bird’s eggs and to hold down rabbit carcasses whilst ripping off pieces of flesh with the mouth (McBee & Baker 1982). Butler et al (2004) reported them depredating nests of Carolina Diamondback Turtles *Malaclemys terrapin* in northeastern Florida. Staller et al (2005) found them responsible for 16% of 114 examined predated nests of the commercial gamebird Northern Bobwhite *Colinus virginianus* in northern Florida. Typically they consumed all the eggs, breaking holes into them and licking out the contents. Allantoic membranes were left at 11 of 16 nest depredations and a mean of 12.2 minutes (+/-8.7) was required to consume an entire clutch of Bobwhite eggs. Bobwhites attempted to defend their nests from the armadillos on 6 of 11 occasions, resulting in 2 obliterated nests. A total of 63% of armadillo depredations were nocturnal.

Armadillos must drink water frequently and do so by lapping in the manner of a dog, leaving a film of their thick saliva over the water surface. Capable swimmers they may enter water to feed, using the forefeet to search for aquatic invertebrates in the substrate (Parera 2002). It seems that this species feeds largely on coleopterans, ants and termites in the Paraguayan range. Parera (2002) also lists amphibians, reptiles, birds eggs and juvenile micro-mammals in the diet of Argentinean individuals and to a lesser extent fruit, roots and seeds. In the USA it also supplements the diet with carrion, fruit and small vertebrates, but these are less prominent in the diet of South American specimens. Hamilton (1946) found that stomachs of all 8 specimens of this species taken near San Antonio, Texas in August contained black persimmon or chapote fruits *Diospyros texana* and that this fruit was an important dietary item in that area at that time of year accounting for more than 80% of stomach contents. Garcia & Kuprewicz (2009) suggested that the species may play a role in dispersal of Neotropical Ginger *Renealmia alpinia* (Zingiberaceae) in Costa Rica, and probably of other plant species.

An analysis of stomach contents estimated the 93.3% of foods taken were animal in nature (McBee & Baker 1982). Tyler et al (1996) documented the diet in a residential area of Oklahoma, USA. They found Coleoptera, cicada and lepidoptera to constitute 96% of the food volume. Coleoptera of the families Scarabaeidae, Carabidae and Elateridae (larvae only) were found in 92% of all stomachs (n=37), with only trace amounts of Staphylinidae and Histeridae, perhaps suggestive of carrion feeding. Cicada nymphs were present in 82% of samples, though this may have been a result of opportunistic feeding during a time when they were particularly abundant. Lepidoptera larvae were present in 61% of stomachs (6% of total volume) while ants made up only 0.8% of the volume despite being present in 68% of stomachs. Remaining material consisted of myriapods (1% by volume), and small amounts of isopods, orthoptera, wasps, gastropods, hemipterans and a single salamander skull.

Anacletto (2007) studied the diet via faecal samples during the dry season in the cerrado of Mato Grosso, Brazil and found Coleoptera to be the biggest single item in the diet by weight (71.3%) followed by ants (16.5%) and termites (12.2%) of the genera (in order of prominence as biomass) *Nasutitermes, Velocitermes, Rhynochotermes, Cornitermes and Anhangatermes*. The nests of the two most prominent termite species in this study were those that are the most easily opened, suggesting that the species excavates when foraging for termites. Taber (1945) fed captive individuals on bone and fishmeal mixed with sour milk and mash. They also learned how to eat dead chicken, using the foreclaws to scratch meat from the bones and tugging with the mouth to loosen it. When the carcasses became infested with maggots the maggots were preferred to the chicken. Chicken eggs were eaten only when broken first. Watermelon and cantaloupe were taken only when broken and only when other food was unavailable. Cereals were ignored, even when soaked in fish oil, but bread soaked in fish oil was accepted. Beets, potatoes, onions and turnips were never consumed despite being offered for over a month. Carvalho et al (1997) fed captives on 200 to 250g of dog chow daily moistened with water, 50 newborn mice twice a week, 5 adult crickets and 50 mealworms provided alternately every five days. Water was constantly available.

In the “Lauro de Souza Lima” Institute, São Paulo, Brazil captive armadillos were fed a balanced diet of dog food, ground beef, boiled eggs and vitamin C, yet several specimens became anaemic. It was
hypothesised that the amount of iron in the feed was insufficient for the formation of hemoglobin, leading to microcytic anemia. Rosa et al (2009) found that supplementation of the diet with 10 mg/animal of iron sulfate (Hematofer®) diluted in sterile water reversed this state.

Levey (1999) reports on a foraging armadillo in Florida being followed by a Parulid warbler *Seiurus auricapillus*. The bird was in close attendance when the armadillo was moving and disturbing leaf litter, suggesting that it was taking advantage of insects that were flushed by the animal.

**REPRODUCTIVE BIOLOGY:** Females are receptive once a year and the main breeding season in Paraguay is from August to November (Neris et al 2002). Parera (2002) states that in Argentina the females ovulate twice a year and that mating occurs in the summer-autumn season. In Izozog, Departamento Cordillera, Bolivia births were found to be highly seasonal and concentrated from October to December with just a single litter per year (Rojas-Suárez & Maffei 2003). McDonough (2000) found that 96.4% (n=84) of all pairings in Texas occurred from June to November, with 83% of them between June and August which suggested the existence of a defined breeding season. Repeated sightings of some pairs together (n=2-64 days; n=17) was indicative of a courtship period.

Males produce sperm all year-round with testosterone levels highest (around 200ng/ml) during the time of maximum breeding but remaining high throughout the year. Captive born males show a gradual rise in testosterone levels from the 5th month of life, reaching adult levels by the 9th month. Circulating testosterone levels in armadillos are high when compared to most other mammals. (Czekala et al 1980).

Pairs form for a short period during a breeding season. Males are often polygynous, but females almost always take a single mate. Paige et al (2002) found a sex ratio of 1.15 males to every female in Louisiana, USA (n=403). McDonough (2000) noted that though males may have multiple partners during a breeding season (range 2-4), they were only paired with one female at a time. In the study area 59% (10 of 17) of males were observed to have more than one partner, whereas only 16.7% (4 of 24) of females had too a second mate. Paired males were sometimes seen to sleep in the entrance of a burrow of a receptive female and to initiate chases or fights when other males approached within 20m. The proximity of females at this time however provoked no response. This is possibly anecdotal evidence of mate guarding in this species. On at least one occasion the female was usurped by an aggressive male.

Because of the position of the genitalia mating occurs with the female on her back. (McBee & Baker 1982). The gestation period is 8 to 9 months, a remarkably long pregnancy explainable by a 3 to 4 month embryonic diapause (delayed implantation). At 5 to 7 days the ovum forms a blastocyst and passes into the uterus where development ceases, becoming implanted several months later. Neris et al (2002) quotes the gestation period at 120 days, presumably not including the diapause. In common with the other "long-nosed armadillos" this species produces multiple, same sex offspring from a single egg - essentially clones of each other. Rojas-Suárez & Maffei (2003) found a greater proportion of males to females in 44 litters in Bolivia (males 26:14 females), and the proportion was sustained in their sampling of the adult population. Prodohl et al (1996) genetically confirmed polyembryony in this species.

Four young are almost always produced in this species, limited by the number of nipples available on the mother, though Parera (2002) notes that exceptionally litters of 2 to 8 have been recorded. In 300 examined litters there were only four cases of triplets, four cases of quintuplets and one set of twins (McBee & Baker 1982). Because of the polyembryonic breeding strategy there is almost always an even number of offspring.

Vickaryous & Ball (2006) note that the formation of the osteoderms (scales) is in vitro and asynchronous within each shield. The first to mineralise are those of the pectoral shield, followed by elements in the bands, head, pelvic and tail shields. Ossification usually begins craniomedially and proceeds caudally and laterally, though on the head the earliest elements are over the frontal and parietal bones.

Newborns have soft, leathery skin which takes several weeks to harden though the eyes are open from the first day. They are able to walk within a few hours and join their mother on foraging expeditions after a couple of weeks (McBee & Baker 1982). Wild individuals are weaned in three months but the family may remain together for nine months. Jacobs (1979) calculated a linear growth rate of 10.6g per day in wild individuals.

Although genetically identical, differences may exist between litter mates, for example developmental abnormalities may occur in some but not all members of a litter (Loughry et al 2002).
Loughry & McDonough (2002) studied phenotypic variability within and between 36 litters (19 male and 17 female) of 100 total juveniles and 14 litters (13 male and 1 female) of 30 total adults captured in northern Florida, USA. Variation in the measurements taken was greater between litters than within litters. Variability could not be correlated to sex or to the number of litter mates. Phenotypes of littermates do diverge over time, but the differences are not always significant. Differences observed in wild animals were mirrored in two captive bred litters.

McDonough et al (1998) noticed a difference in the timing of developmental events between captive males and females. Males left the nest earlier (day 20 versus day 22), drank water earlier (day 21 versus day 25), ingested solid food earlier (day 35 versus day 42), began weaning earlier (day 82 versus day 140) and ended weaning earlier (day 89 versus day 162). Females however began to include insects in their diet before males (day 71 versus day 74).

Prodohl et al (1996) noted that sibling clones initially maintained a close spatial relationship, but that this disappeared with age. Though juveniles occasionally shared burrows, adults did not, and nor did they indulge in any behaviours that would mutually benefit each other at any age as kin theory might predict (eg foraging strategy, predator avoidance, territoriality).

Females reach sexual maturity and progesterone levels indicative of ovulation (10ng/ml) are seen for the first time at 15 months (Pepperl et al 1986). First-breeding females pair later than multiparous females probably because of the physiological constraints associated with ovulation and not because of a male preference for experienced mates. Males are physiologically capable of breeding at 12 months (McCusker 1977), though it seems they show delayed breeding and do not attempt to breed in the wild until more than 32 months old. In captivity females have been known to bear young 13 to 24 months after capture and isolation from males. (Redford & Eisenberg 1992).

**GENERAL BEHAVIOUR:** Though this is by far the most well-studied Dasypodid, much of what is known about the biology of this species in the wild comes from studies performed in the North American part of the range, particularly by investigators at Valdosta State University.

This is a solitary and largely nocturnal armadillo, though occasionally active at dusk and during the day (P.Smith pers.obs.). Activity levels are likely determined by ambiental factors, particularly temperature and they may become more diurnal during the reproductive season (Parera 2002). Peaks of activity usually occur around 21-22.00h. They are not well-adapted to cold conditions and are able to lower the body temperature by only around 2.5°C, resulting in periods of inactivity during cold spells. Rain does not affect activity unless accompanied by cold weather (Taber 1945). The lifespan is 12 to 15 years.

Ancona & Loughry (2009) performed time budget studies on this species in western Mississippi during two successive summers. They found that in observed individuals the following percentages were devoted to these defined behaviours (n=260): Amicable (social interactions related to proximity maintenance) 0.03% (+/-0.37); Bipedal Sniffing 1.11% (+/-2.02); Chasing 0.07 (+/-0.56); Digging 0%; Foraging 89.32% (+/-11.71); Fighting 0.09% (+/-1.07); Going to Burrow 0.01% (+/-0.13); Pair Maintenance Behaviour 0.12% (+/-0.86); Pausing 3.48% (+/-5.29); Running 0.71% (+/-2.19); Walking 6.36% (+/-10.91). The vast majority of the time was spent foraging or walking, and if it is reasonably assumed that walking involves moving between foraging sites, almost all the active time is spent in activities associated with feeding. Vaughan & Schoenfelder (1999) found that peak activity in dry forests of Costa Rica was from 18-21.00h, with high levels of activity from 21-0300h and no activity from 06-15.00h, this lack of diurnal activity likely being due to the harsh, hot, dry climate in the study region.

Robertson et al (2000) noticed a decline in observability of this species during their annual study period of June to August. They hypothesised that the decline may be seasonal but there results did not discount an "observer effect" ie that the armadillos learn to become wary of the observer as they become more exposed to him/her. They suggested that their capturing and marking of the animals may have exacerbated the observer effect, while stress caused by noises made by walking may also operate in uncaptured animals.

Rocha et al (2006) noted a significant difference in the abundance indexes of this species between the dry season (April to September) 0.50 (+/-0.49) and the wet season (October to March) 1.54 (+/-0.61) in Mato Grosso, Brazil in a study based on footprints. They speculated that this may be due to a greater availability of resources during the wet season.
Home Range

Population density has been estimated at 0.36/km$^2$ in the cerrado of Brazil (suboptimal) to 50/km$^2$ in the coastal prairies of Texas and may be even higher in tropical forest areas (MacDonald 1985). Cullen et al (2001) reported varied densities in Atlantic Forest patches in São Paulo State, Brazil from 9.6/km$^2$ in an area that was heavily hunted to 23.63/km$^2$ in a protected area. Crude biomass estimates calculated that they made up between 0.4 and 16% of the biomass in the five study sites. Naughton-Treves et al (2003) estimated a density of 21.9/km$^2$ (+/-21.1) in slash-and-burn fields in Tambopata, Peru. Timock & Vaughan (2002) recorded a density of 0.094/ha (+/-0.12) in Provincia Puntaarenas, Costa Rica, but this estimate was based solely on 8 visual records along walked transects and likely greatly underestimates the true density.

McDonough (2000) estimated a density of 1.45/ha at Rob and Bessie Welder Wildlife Refuge in Texas. It was noted that in this riparian habitat the home range was smaller than most other published sources and that armadillos inhabiting more mesic habitats tend to have smaller home ranges than those occurring in more open habitats. This pattern would be expected if home range size reflected resource requirements and mesic habitats were richer in resources.

Home range size was found to increase with age with adults holding greater home ranges than either juvenile or 1-2 year-olds. Differences in the size of male and female territories were not found to be statistically significant within the age groups sampled. Breeding males were found to hold larger territories than non-breeding males. The following home range size estimates were obtained for different age and sex classes: all adults 2.82ha (+/-1.01; n=19); adult males 3.41ha (+/-0.67; n=6); adult females 2.54ha (+/-1.04; n=13); all 1-2 year-olds 1.48ha (+/-0.86; n=7); 1-2 year-old males 1.49ha (+/-0.94; n=6); 1-2 year-old females 1.43ha (n=1); all juveniles 0.94ha (+/-0.53; n=10); juvenile males 1.18ha (+/-0.65; n=5); juvenile females 0.71ha (+/-0.28; n=5); breeding males 3.88ha (+/-1.22; n=6); breeding females 1.96ha (+/-0.65; n=7). McDonough (2000)

Territories of breeding males did not overlap with each other, but did overlap with those of females and non-breeding males. Home ranges of adult females overlapped extensively both with other females and with breeding and non-breeding males. Females (n=14) had a mean exclusive home range of 26.7% (+/-19.9), overlapping with other females in 29.8% (+/-8.3) of their range, breeding males 44.8% (+/-14) and non-breeding males 25.5% (+/-13.2). Breeding males (n=6) had a mean exclusive home range of 69.2% (+/-13.9), overlapping with females in 32.5% (+/-7.3) of their range, other breeding males 11.8% (+/-4.9) and non-breeding males 23.3% (+/-5.2). Non-breeding males (n=9) had a mean exclusive home range of 49.6% (+/-209), overlapping with females in 35.9% (+/-11.2) of their range, breeding males 41% (+/-18.4) and other non-breeding males 24.2% (+/-9.5). (McDonough 2000).

Loughry & McDonough (1998) studied spatial patterns of Nine-banded Armadillos near Tallahassee, Florida, USA. They found the mean movement of individuals between successive sightings to be <200m (range 0-1180.8m). Analysis of within-year movement showed that adults generally moved more than juveniles, but there were no differences between sexes in any age class. Both adults and juveniles moved significantly farther between years. The following results were obtained for distances between first and last sighting: adult males (n=43) distance moved 179.7m (+/-23.19; range 2.3-688.1m); adult females (n=37) distance moved 159.6m (+/-15.36; range 21.8-1022.9m); juvenile males (n=11) distance moved 127.2m (+/-37.80; range 10.7-328m); juvenile females (n=25) distance moved 81.3m (+/-20.05; range 10.2-527.2m). The results suggested that a significant portion of any population are faithful to their home range, but it was noted that a majority of animals were captured only once, indicating that transient individuals are also present in a population.

McDonough et al (2007) expanded on this study by collecting data for a removal experiment during an attempt to cull armadillos from the Tallahassee study area to eliminate nest predators of Northern Bobwhite Colinus virginianus. The population of armadillos that had been marked in previous years studies was very quickly eliminated, with 32 of the 41 marked animals killed in the first year of the cull, 5 in the second and 4 in the third. Total numbers killed however remained constant over the three years with figures of 149, 149 and 153 respectively. Numbers of juveniles harvested were low with 33 in the first year, 25 in the second year and 16 in the third year, suggesting that there was no increase in recruitment by birth during the cull. The remarkable constancy of the population despite the intensive harvesting is therefore attributable to immigration from surrounding areas.
Vaughan & Schoenfelder (1999) found radio-tagged individuals to move between 133 and 835m per night (n=16) in Costa Rican dry forest. Mean distance moved was 388.2m.

**Refuges** Typically this species spends the day in self-dug burrows 0.5-6m long (mean 1.25m) which are usually located in forested areas close to a water source. Any one animal may have a mean of 4.5 to 8.5 burrows depending on locality (Taber 1945).

Burrows are dug by wedging the nose and forefeet into the soil to loosen it, then scratching with the forefeet to position it below the abdomen. Using the forefeet and tail for balance, the hindfeet are brought forward in front of the pile of dirt, the back is arched and then suddenly thrust straight so that the loose soil is propelled behind the animal. (McBe & Baker 1982). Burrows generally have multiple entrances 17-20cm in diameter and contain a grass nesting chamber c34cm in diameter which is used for reproduction, sleeping and refuge during colder periods. Average vertical depth to the nest chamber is 50cm, but an extreme of 151cm has been recorded.

Taber (1945) noted that nests of this species have no structure and rather are piles of leaves into which the animal buries itself. As a result occupied burrows often appear to have the entrance plugged with plant material, a fact that may serve a purpose for camouflage as well as providing insulation to prevent over-heating or heat loss. (Taulman 1994). Plant material is carried between the chin and forelegs, the animal zig-zagging backwards, at which time the tail may serve a tactile function. On arrival at the burrow the armadillo enters backwards, raking the plant material into the hole with the nose and feet. (McBe & Baker 1982).

In Arkansas Taulman (1994) observed somewhat different nest-building behaviour. He noted that collecting material involved 3 to 5 scrapes lasting about 3 to 5 seconds and amassed a bundle of leaf litter c20cm in diameter. The armadillo made several collecting trips, each in different directions, and return trips followed the same direct path as the outward journey, with the animal hopping backwards to its burrow. Between collecting bouts (approximately once a minute) the animal paused to sniff the air before continuing with its task. The animal only turned to face the burrow upon arrival, when it used the forefeet and snout to push material into the hole. The material from the last trip (the fifth) was simply dumped at the burrow entrance, the hole apparently being completely full with material, and the armadillo then walked away.

Zimmerman (1990) reported the following burrow dimensions for Oklahoma, USA (n=113): entrance 19.8cm (+/-4.24) high x 21.9cm (+/-3.64) wide; 10cm inside burrow 17.5cm (+/-3.41) high x 20.5cm (+/-3.43) wide.

In Belize Platt et al (2004) found 70.5% (74 of 105) burrows to be located in pine forest compared to adjacent savanna. Mean burrow density was 27/ha (+/-3.2) in pine forest compared to 5.8/ha (+/-2.1) in savanna. Burrow dimensions were 8.6 to 22.9cm high x 13.5 to 30.5cm wide at the entrance, with a mean of approximately 13.6 (+/-2.5) x 18.75 (+/-3.1) cm. These measurements were significantly smaller than those reported by Zimmerman (1990) for North American Dasypus from Oklahoma. Mean burrow temperatures were 3 to 4°C lower than mean air temperatures when measured just inside the burrow entrance. Kinlaw (2006) also found a mesic habitat preference for burrow location for animals in Florida, with pine forest being preferred over a variety of scrubby habitats.

Few studies have investigated burrow orientation in this species, but what little data exists appears to suggest a random orientation (Zimmerman 1990), unlike those of savanna species which typically have the entrance to the burrow sheltered from the prevailing winds. It has been hypothesised that their preference for forested environments provides the necessary protection from prevailing winds, liberating them from constraints affecting burrow orientation (Platt et al 2004).

Several individuals may use the same burrow, but these are likely members of the same family, though usually all of the same sex. Burrows are frequently used by other species. In areas that are subject to periodic flooding (eg Humid Chaco) nests are frequently built above ground to avoid drowning and resemble miniature haystacks (Nowak 1991).

Platt et al (2004) found burrows in Belize to be utilised by a variety of reptiles including three species of snake that occur in Paraguay, Tropical Rattlesnake *Crotalus durissus*, Black Rat Snake *Spilotes pullatus* and *Boa constrictor*. Vaughan & Schoenfelder (1999) found that individuals in the dry forest of Costa
Rica used a mean of 2.3 burrows each and shared dens with reptiles (*Ctenosaura similis*), rodents (*Sigmodon hispidus*), opossums (*Didelphis marsupialis*) and a skunk (*Mephitis mephitis*).

Carvalho et al (1997) provide guidelines for the housing and breeding of this species in captivity, using both indoor and outdoor enclosures.

**Range size and territorial behaviour** Home ranges of males often overlap considerably without antagonism and may encompass the ranges of several females. The size of the range varies depending on the carrying capacity of the habitat, with figures of 3.4ha suggested for prime habitat and 15ha for suboptimal habitats having been suggested (Redford & Eisenberg 1992, Nowak 1991), with male ranges up to 50% larger than those of females (MacDonald 1985). This species possesses glands on the ears, eyelids, anus and soles of the feet which play an advertising role warning of the presence of the individual in the area. Upon meeting they frequently sniff the anal regions and to further mark territories they defecate and urinate on prominent posts and along feeding trails (MacDonald 1985). The yellowish glandular secretions may also be used to deter predators, producing a nauseating effect if inhaled in quantity. Animals have been seen to feed in close proximity to each other without signs of aggression, though sick or injured animals have been reported to victims of mutilation or even cannibalism by conspecifics (Mc Bee & Baker 1982).

**Swimming and Bathing** Nine-banded Armadillos are capable of swimming short distances by gasping to inflate the stomach and intestine with air for buoyancy - upon first entering the water they are almost completely submerged, but ride higher on the water surface the longer they swim (McBee & Baker 1982). Swimming armadillos fold the ears back against the head, kick all four legs in doggy fashion and periodically raise the nose to breathe before lowering it again (Taber 1945). Though by no means a common occurrence, the ability to hold the breath and accrue a considerable oxygen debt means they can also cross streams and small rivers by walking along the river bed (MacDonald 1985) - in fact they may even feed in the water (Parera 2002).

Taulman (1994) described an individual seen bathing in a large puddle 15-28cm deep. The animal dipped its snout into the water and raised the head quickly so that water dripped backwards over the carapace, before systematically shaking in a front to back sequence lasting 1 to 2s. The animal then rolled onto its back and writhed briefly as if rubbing mud onto its dorsal surface. Each rolling sequence lasted approximately 4 seconds and it was repeated three times before the animal trotted away.

**Aggressive Behaviour** Aggression is commonly observed during the breeding season. Male aggression likely assures exclusivity of mates, female aggression may be a result of competition for limited resources or to stimulate dispersal of the previous year’s young (McDonough 1994). Adults have been observed chasing juveniles at high speed for a period of up to 35 minutes, presumably to displace them (Breece & Dusi 1985). Fights are rare but generally take the form of one individual leaning back on the hind feet and clawing with the forefoot or clawing at the sides of another individual with the hind feet whilst rolling and flipping (McDonough 1994).

**Defensive Behaviour** As defined by McDonough & Loughry (1995), vigilance in this species consists of three different behaviour patterns: 1) Pausing - The cessation of movement; 2) Quadrupedal Sniffing - Elevation of the snout parallel to the ground with all four feet in contact with the floor; 3) Bipedal Sniffing - Raising up balancing on the tail and hind legs and sniffing around. These patterns act to obtain aural and olfactory information from the environment because the sense of sight is poor.

McDonough & Loughry (1995) found that vigilance was influenced by both social and anti-predator concerns. It was not influenced either by age, sex, time of year or breeding status in the case of solitary individuals. Exposure to a potential predator increased vigilance. Armadillos involved in social interactions were more vigilant than solitary animals, primarily due to an increase in Pausing after aggressive and proximity maintenance interactions. Quadrupedal Sniffs also increased significantly following proximity maintenance interactions. Individuals were more vigilant during aggressive interactions than during other social interactions. Bipedal and Quadrupedal Sniffs correlated positively with flight distance. Flight distances were shorter at night and following rain, possibly because the noise of rain and increased humidity at night made observes less audibly "detectable". Flight distances were shorter by males in the breeding season, possibly because males wait to see if the disturbance is caused by a female, a competitor or a predator.
Surprised animals frequently explode into a run, crashing through the undergrowth towards their nest burrow. One animal at Itabó Itapú Reserve, Departamento Alto Paraná was observed to run and collide with a tree when disturbed, stopping momentarily before continuing on (K. Atkinson pers. comm.). Animals frightened at close range may perform remarkable vertical jumps with arched back prior to fleeing or when pursued (Emmons 1999) and if overtaken may attempt to curl up to protect as much of the body as possible (Nowak 1991). When pursued into a burrow they may arch the back, digging the scales of the carapace into the tunnel roof and make it impossible to pull them out (McBee & Baker 1982).

**Mortality**

McDonough & Loughry (1997) documented mortality patterns in a population of this species in Texas by studying carapaces of dead individuals. Though juvenile made up only a third of the live population (111 of 338 individuals) the number of dead individuals was 43, much higher than the expected 23.6. The adult population consisted of 227 individuals and their mortality was 29, much lower than the expected 48.4. Of 21 juvenile carcasses examined for predation, 15 exhibited bite marks, whilst none of the 8 adult carcasses showed signs of predation. Juvenile mortality was highest from June to September when juveniles are beginning to seek independence, but lower during the rest of the year. Adult mortality was five times higher during a period of drought.

Loughry & McDonough (1996) sampled roadkill armadillos over three years in Texas. They found that the sex ratio and reproductive condition of females was comparative to the results found by live sampling. However almost no juvenile (2 of 27 individuals) or yearling (2 of 27) armadillos were found killed on roads compared to the number of adults (23 of 27). It was hypothesised that adults are more at risk from traffic as they range further during the breeding season than do juveniles which initially tend to remain closer to the natal burrow. They concluded that examination of roadkill provided a representative picture of adult demography but was misleading in regards to age structure of a population.

Smith-Patten & Patten (2008) counted 284 roadkills of this species along >16,500km of surveys in the southern Great Plains from March 2004 to March 2007, making it the third most frequently killed mammal on the roads in that area. There was a distinct seasonal peak of kills in August, with higher kill rates in spring and summer related to their reproductive cycle when young animals and their mothers become motile. Virtually no roadkill armadillos were found during the winter months.

Inbar & Mayer (1999) found that armadillos in Florida were more diurnal from November to March and hence less likely to be victims of roadkill. Additionally their habitat preference was more closely tied to dense woodlands at this time. They found 143 roadkill individuals during 49 surveys of a 168.9km stretch of road, with a mean of 3.7 dead per survey during the summer months compared to just 1.95 dead per survey in the winter. Peak roadkill was from June to August, declining from September onwards.

Kalmbach (1944) noted that even if not killed by the wheels of a vehicle, armadillos have a tendency to jump upwards when passed over by a vehicle and may kill themselves against the undercarriage. Armadillos do not generate eye shine and so may be less visible on roads at night than other mammals (P. Smith pers. obs.).

Loughry et al (2002) summarised the types of anatomical damage experienced by a population in Florida, USA. They found that of 631 animals (444 adults, 31 yearlings, 156 juveniles) 70.21% (443 individuals) showed anatomical damage. Predictably adults showed more total damage than juveniles and yearlings, being more prone to tail loss, carapace notches and torn and missing ears. There was no significant difference across age classes between the occurrence of band abnormalities, number of scars and distribution of scars. No differences in damage type according to sex were recorded. The following results were obtained for adults, yearlings and juveniles (sexes combined): Total showing some kind of damage: adults 358, yearlings 20, juveniles 65; Total showing no damage: adults 66, yearlings 11, juveniles 91; Carapace notches adults 181, yearlings 10, juveniles 19; Ears torn adults 89, yearlings 1, juveniles 3; Ears missing adults 35, yearlings 1, juveniles 0; Large scars adults 451, yearlings 2, juveniles 8; Small scars adults 126, yearlings 8, juveniles 40; Band abnormalities adults 31, yearlings 2, juveniles 10; Loss of tail tip adults 51, yearlings 2, juveniles 0; Loss of greater proportion of the tail adults 93, yearlings 1, juveniles 0. Juveniles had a full complement of 15 tail segments. Mean numbers for yearlings (male 14.69 +/- 1.01, female 14.93 +/- 0.26) and adults (male 13.66 +/- 2.71, female 13.77 +/- 2.58) shows a higher incidence of tail breakages with age. Tail breakages were possibly a result of unsuccessful predation attempts, the lower incidence in juveniles being consistent with the fact that predation attempts on juveniles are more likely to be successful.
In Belize this species constitutes 54% of the diet of the Jaguar *Panthera onca* (Rabinowitz & Nottingham 1986) and in Campeche, Mexico it makes up 12% (Aranda 1994). Remains have also been found in the nests of Harpy Eagles. Juveniles are likely taken by Lesser Grison *Galictis cuja*, foxes, small cats and Black Tegu *Tupinambis merianae*. Garla et al (2001) found *Dasypus* sp (likely principally or entirely this species) to make up 15% of the diet of Jaguar in the Atlantic Forest of Southeastern Brazil, being taken in all months and present in 23.2% of 56 examined scats. Azevedo (2008) calculated relative frequencies of 9.8% in 51 Jaguar scats and 3.7% in 54 Puma scats from Iguaçu National Park, southern Brazil.

Martins et al (2008) found this species in 1 of 12 (8.3%) scats of Puma *Puma concolor* and 1 of 14 (7%) scats of Ocelot *Leopardus pardalis* in São Paulo, Brazil. This represented 6.1% of the relative biomass consumed by Puma and 5.5% of the relative biomass consumed by Ocelot in the study area. Moreno (2008) found it in 1 of 15 scats of Puma and absent from 9 Jaguar scats in Darién, Panama.

**Parasites** Relatively few parasites have been documented for this species despite its extensive range. All ticks reported on armadillos are Ixodidae in the genus *Amblyomma*, with the species *A.concolor* and *A.pseudoconcolor* documented on this species. Guglielmone & Nava (2006) added *A.parvum* for this species in Argentina. Additionally Nava et al (2007) listed *Amblyomma auricularium* on this species in Paraguay and Szabó et al (2007) the same species for the Goiás, Brazil. Guglielmone et al (2003) note that the close association between this species and *A.auricularium* may be responsible for the wide geographic range of that tick (Nearctic and Neotropical). In the collections they examined they found 384 *A.auricularium* associated with this species compared to just one *A.pseudoconcolor*. Both of these tick species are associated with armadillos, but the Neotropical distribution of the latter suggests that *Dasypus* is not a preferred host it.

Fleas are rarely but found the following species have been reported: *Echidnophaga gallinacea, Ixodapus pinetorum, Polygenis roberti, P.occidentalis and Tunga travassosi*. Antunes et al (2006) report the first record of *Tunga terama* on this species in Brazil. It is also known as a carrier of the protozoan *Trypanosoma cruzi* which is responsible for Chaga’s Disease, probably becoming infected by eating insect carriers. It is susceptible to infection by *Schistosoma haematobium* but develops no symptoms and the eggs and parasites do not reach the urogenital system.


Fujita et al (1995) reported the following nematodes from two specimens in Paraguay: Anclylostoma sp., *Aspidodera esperanzae* (described as a new species in the same paper paper - but later proposed as a junior synonym of *A.binansata* by Jimenez-Ruiz & Gardner 2003), *Moennigia complexus, M.pintoi* and an unidentified species of Heterakinae. The two specimens were infected with 69 specimens of four species and 3 specimens of one species respectively. Navone (1990) recorded the nematode *Aspidodera vagz* (Aspidoderidae) and the cestode *Mathevotaenia surinamensis* (Anoplocephalidae) in the Paranaense and Chaco regions of Argentina, with *Aspidodera fasciata* (Aspidoderidae) additionally recorded in the Chaco region.

Jimenez-Ruiz & Gardner (2003) reported Aspidoderid nematodes *Aspidodera binansata* (n=173) and *Lauroia bolivari* sp. nov (n=22) from a specimen in Santa Cruz, Bolivia. 


This species exhibits low and highly variable base and peak metabolic rates and low body temperatures consistent with the pattern for other armadillos. The armoured carapace causes low predation risks so that selection for high aerobic capacity is weaker than the opposing selection for energy conservation. Boily (2002) measured BMR at 8.6 to 19.5mlO$_2$min$^{-1}$ and PMR ranged from 47.3 to 147.3mlO$_2$min$^{-1}$ both being correlated positively with body mass. BMR and PMR also correlated positively with each other supporting the aerobic capacity model. Rectal temperatures varied from 32.7–35.3°C.

Leprous armadillos may show much higher BMR, with Steuber (2007) recording a BMR 23.9% above normal. Given the normally low BMR of this species, this symptom of infection may represent a considerable cost (Morgan & Loughry 2009).

**VOCALISATIONS:** Though it does not generally vocalise, the Nine-banded Armadillo is one of the noisiest forest inhabitants given its snorting foraging style and clumsy form of ambulation with complete disregard for the noise created by snapping branches, dry leaves and moving undergrowth. A medium-sized animal charging through the undergrowth of humid forest at high speed at night is likely to be this species (Emmons 1999).

**HUMAN IMPACT:** This species is one of the principal prey items of the Aché Guaráni who prize it for its white meat (Esquivel 2001). Representatives of the Mbyá Guaráni in PN San Rafael hunted this species using dogs to locate the armadillos and killed them via a machete blow to the head (P.Smith pers. obs.). In the period 1980 to 1996 a total of 1500 individuals of this species were taken by the Aché in the Mbaracayú Biosphere Reserve, representing 5,750kg of meat or 35.2% of the biomass that they consumed (Cartés 2007). The species has become more prominent in the diet of the Aché since 1994, when it represented 43.1% of the wild game in their diet compared to just 13.5% in 1980, a change likely related to deforestation and the reduction in numbers of larger prey species such as White-lipped Peccary which declined from 22% to 2% of the diet over the same period (Cartés 2007).

In other areas Nine-banded Armadillos is one of the preferred wild game food items over much of its range with the meat being considered a substitute for chicken (Neris et al 2002) and the species is customarily cooked in its "shell" (McBee & Baker 1982). Merritt (2008) notes the species as frequently offered for sale as game meat on roadside poles along the Ruta Trans-Chaco. A campesino community in Departamento Caazapá took 66 individuals of this species over a four year period, making it the third most frequently hunted species and representing 21% of all animals taken, though this corresponded to only 5% of the total biomass (Cartés 2007). In the Argentine Chaco it made up <1% of the diet of local people and was consumed a mean of 0.3 days per year (+/-0.03) (Altrichter 2006).

Fat is used as a remedy for the treatment of coughs, bronchitis, asthma, rhematism, open wounds, appendicitis and concussion (Cartés 2007, Neris et al 2002), making it the second most utilised mammal species for medicinal purposes in Paraguay after the Capybara. The carapace may be used to fashion wallets as a cheap substitute for leather and the species is often taken as a pet (Neris et al 2002). Alves et al (2007) note that in Mexico the carapace and tail are used to treat diahorea, tuberculosis and whooping cough, and to accelerate parturition. Alves & Rosa (2006) state that the tail is used as an amulet to protect against the "evil eye" in Maranhão and Paraíba States, Brazil and the skin drunk in a tea as a treatment for asthma. Alves & Rosa (2007) state additionally that street traders in the city of São Luís, Maranhão sell the fat for treatment of diahorea, headache and swelling. The tail is introduced into the ear to combat deafness in Ceará State, Brazil (Ferreira et al 2009b). In the same area fat is rubbed onto burns and inflammations, and the meat is eaten without salt to combat pains in the bones. (Ferreira et al 2009a).

With the reduction in populations of other myrmecophagous species, Nine-banded Armadillos probably play an important role in population control of ants and termites. Though easily tamed they do not adapt well to captivity (Nowak 1991). They have been falsely accused of attacking domestic poultry in some areas of their range (McBee & Baker 1982), though they do predate the nests of wild gamebirds (Staller 2001, Staller et al 2005).

The species is considered a minor agricultural pest in the southern USA on account of its burrowing activities which affect fruit and agricultural plantations and apparently affect dykes, fences and undermine buildings (Long 2003). Gammons et al (2009) demonstrated that translocation of pest
individuals from one area to another is not an effective means of control. Of 12 armadillos that were translocated in Georgia, USA, 92% left the release site within a few days and some even returned to their original site of capture. They compared these results with 29 resident armadillos, 12 of which remained in their original territory, 11 of which moved on a mean of 245 days after capture (range 117 to 322 days), and six of which died. They noted that the highly dispersive nature of armadillos meant that territories vacated by translocation would likely be very quickly re-occupied by other individuals.

The species has been used in laboratory studies of in birth defects, multiple births and organ transplants (Nowak 1991). Additionally the species is a natural reservoir and research subject for several serious illnesses that affect humans such as leprosy, trichinosis, coccidioidomycosis, Chaga’s disease and typhus. Nine-banded Armadillos captured near Sao Paulo, Brazil all showed the same Duffy phenotype Fy (a+b+). The protein encoded by this gene is a glycosylated membrane protein and a non-specific receptor for several chemokines, as well as for plasmodium parasitic protozoans (Silva et al 2005).

Other than humans, armadillos are the only animals known to carry the bacteria Mycobacterium leprae, which causes leprosy. As this bacterium has never been successfully cultured, the utility of this armadillo as a laboratory animal cannot be underestimated (Vijayaraghavan 2009). Transmission from armadillos to humans is rare and typically caused by the consumption of undercooked meat. Leprosy rates in armadillos are high in the USA and likely also in much of the rest of the range, but at least 15% of animals are completely resistant to the disease and are useful for understanding the mechanisms of resistance which may, in part, be genetic. Clark et al (2008) found a significant correlation between contact with armadillos and the human disease in USA.

Depst et al (2007) reported an infection rate of 29.7% in 34 individuals from Espirito Santo, Brazil in an area where local populations consume the animal. Paige et al (2002) calculated infection rates in Louisana, USA to be steadily around 19%, varying from 18.4-19.7% over the four year study, similar to the 16% infection rate by Truman et al (1991) for Louisiana and Texas. Infection rates in western Mississippi were 7 to 12% (Loughry et al 2009). The disease appears to be spreading eastwards in the USA and has now crossed the Mississippi River (Loughry et al 2009). Animals found in Colombia, Venezuela and Paraguay are reportedly free from infection, though it is present in Argentina (Vijayaraghavan 2009). Zumarraga et al (2001) found 9 of 132 armadillos positive for the disease in Corrientes, Argentina an area where the human prevalence is in the order of 6 per 100,000.

The time from infection to the development of the disease is six months to four years in this species (3 to 6 years in humans), with the spectrum of the disease similar to that in humans. Although a majority of the infected animals develop lepromatous disease, borderline leproma is also fairly common. Armadillos develop severe disseminated leprosy when inoculated with human leprosy bacilli. (Vijayaraghavan 2009).

Truman et al (1991) noted that all infected in Louisana and Texas were adults, but that there was no significant sexual difference between infection rates (15.3% in males, 17.5% in females). They found a positive link between leprosy infection and lactation as infected females had higher progesterone levels than uninfected females. Prevalence rates were higher in winter and summer and lower in spring, related to the fact that juveniles show no signs of the disease and that females hide themselves away during breeding.

Similar results were found by Morgan & Loughry (2009) in western Mississippi where no juvenile or yearling armadillos were leprous, but 10 of 107 (9.35%) males and 22 of 103 (21.36%) females were positive for the disease. They detected no morphological size differences between leprous and non-leprous animals, though leprous animals exhibited greater phenotypic damage than negative males and no observable differences in behaviour were detected in infected animals. The results surprisingly suggested that leprosy infection had few ecological consequences for the population studied.

This species has been experimentally infected with the fungus Mycobacterium ulcerans, causal agent of the disease Buruli ulcer (Walsh et al 1999). As with leprosy armadillos develop symptoms similar to humans and the species has become an important study subject for treatment of the disease. The disease is rarely fatal but can cause considerable disfigurement.

da Costa et al (2001) detail a fatal case of an armadillo hunter infected with pulmonary coccidioidomycosis in Ceará State, northeast Brazil. The disease is caused by the inhalation of arthrospores of the fungus Coccidioides immitis. The hunter had participated in an armadillo hunt 5 days prior to showing
symptoms and a second participant had also shown similar symptoms, though these later spontaneously disappeared. Eulálio et al (2000) found that 3 of 26 armadillos of this species captured in Piauí State, Brazil were infected with *Coccidioides immitis*, this representing the first documented case of infection in *Dasypus novemcinctus*.

Paracoccidioidomycosis (PCM) is the most important and prevalent systemic mycosis in Latin America where it has been recorded principally in Brazil, Colombia and Venezuela. The etiological agent of the disease is the fungus *Paracoccidioides brasiliensis* and infection is primarily through inhalation of the spores (Restrepo et al 2001). This species is a natural reservoir and sylvan host of the fungus (Bagagli et al 1998, Nishikaku et al 2008). Bagagli et al (2003) found that *P. brasiliensis* occurs preferentially in humid and shady disturbed forests in strong association with armadillos, with positive animals found with greater frequency near water in sites with disturbed vegetation such as riparian forests and plantations of *Eucalyptus* and *Pinus*. Soil types were mainly sandy with medium to low concentrations of organic matter and typically acidic pH. In Colombia human incidence is greater in communities in contact with armadillos than those with little or no contact with armadillos (Cadavid & Restrepo 1993). Hebeler-Barbosa et al (2003) confirmed the high level of virulence isolated from armadillos.

Richini-Perreira et al (2008) found a roadkill individual of this species in São Paulo State, Brazil with *P. brasiliensis* amplicons in the lungs, spleen, liver, kidney and mesenteric lymph node and Silva-Vergara & Martinez (1999) report 1 of 21 individuals infected in Minas Gerais State. Corredor et al (1999) first isolated the fungus from 1 of 2 Colombian animals. Richini-Perreira et al (2009) found 7 of 20 individuals of this species to be infected, a prevalence of 35%, though in hyperendemic areas infection rate may be much higher (72% - Bagagli et al 1998). Armadillos develop PCM disease at a low frequency when compared to the high infection rate. Infection rate in armadillos is $10^3$ to $10^4$ times higher than the infection rate for humans (Bagagli et al 2003).

The causative agent of Chaga’s disease is *Trypanosoma cruzi*, a digenetic kinetoplastid and enzootic parasite of almost 100 mammal species, includign humans. Though typically transmitted to humans via the Reduvid bug *Triatoma infestans*, oral infection with the disease does occur and is often associated with acute forms of the disease. *T. cruzi* has two intraspecific subdivisions, with TCII being most associated with armadillos and associated with less severe human symptoms. TCII has been isolated from armadillos in the Paraguayan Chaco (Yeo et al 2005) and Pará, Brazil (Marcili et al 2009).

Roque et al (2008) captured a specimen of this species that was infected with *Trypanosoma cruzi* in an area of Pará State, Brazil that had recently suffered an outbreak of Chagas disease and 1 of 1 specimen from the Pacific coast of Colombia was found to be infected by Travi et al (1994). Paige et al (2002) calculated infection rates in Louisiana, USA to be 3.9%, varying from 0.47-7.28% over the four year study. Three armadillos infected with this agent were also infected with *Mycobacterium leprae*. The consumption of undercooked armadillo meat in rural areas is a potential source of infection with this disease.

Toxoplasmosis is a widespread zoonosis that affects wild animals and man, caused by the protozoan *Toxoplasma gondii*. Da Silva et al (2006) recorded positive tests for *Toxoplasma* in two specimens of this species tested. Infection of humans via the consumption of undercooked meat is a possibility.

Leishmaniasis is a disease caused by protozoans in the genus *Leishmania* and transmitted to humans via the bite of sandflies principally of the genus *Lutzomyia* (Phlebotominae). The principal infective agent in armadillos is *Leishmania naiffi* (Grimaldi et al 1991). Naiff et al (1991) reported that 10 of 64 armadillos from Amazonian Brazil were infected with *Leishmania naiffi*, one of the causal agents of cutaneous leishmaniasis in humans, a prevalence of 15.6%. Medina (1966) reports on successful laboratory inoculation of this species with *Leishmania mexicana* in Venezuela.

Histoplasmosis is a disease that affects principally the lungs and is caused by the fungus *Histoplasma capsulatum*. Naiff et al (1996) found only one female from Rondônia out of 11 tested specimens (6 males and 5 females) to be infected with *Histoplasma* in the Brazilian Amazon.

St Louis encephalitis is a *Culex* mosquito-borne viral disease caused by a Flavivirid virus that occurs mainly in the USA, with occasional cases in Canada, Mexico and South America (Brazil). Day et al (1995) reported that 59 of 189 armadillos (31%) captured in southern Florida had antibodies to the St Louis encephalitis virus, proving that they were fed upon my infected mosquitoes.
Three of six animals experimentally infected with *Schistosoma haematobium* causal agent of schistomiasis haematobia died, though not necessarily as a result of infection. Parasites were present in all of the dead animals but none exhibited pathology associated with the disease. It was concluded that this species is only moderately susceptible to infection and can accommodate a large parasite load of *Schistosoma haematobium*. It was not considered a practical candidae for studies of the disease as no pathology developed and mature mparasites did not produce eggs. (Kuntz et al 1975).

**CONSERVATION STATUS:** The Nine-banded Armadillo is considered Lowest Risk, least concern by the IUCN (Abba & Superina 2010), see http://www.iucnredlist.org/search/details.php?6290/all for their latest assessment of the species. The Centro de Datos de Conservación en Paraguay consider the species to be secure in Paraguay but with the potential to become threatened in the future and give it the code N4. The species is not listed by CITES.

The species is able to coexist with humans in rural areas because of its largely nocturnal habits and large litter size, but has declined over much of its range in eastern Paraguay as a result of destruction of optimal habitat and hunting pressure.

McDonough & Loughry (2005) found that armadillos in Florida were not adversely affected by fire, being able to hide in their burrows to escape. Initial avoidance of burnt areas for foraging was exhibited, but this was only a temporary effect. They did however decline during a period of drought and populations were impacted during a period of intensive logging. The species is extremely susceptible to leprosy both under captive conditions and in the wild (Nowak 1991).

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FIGURE 4 - (FPMAM70PH)
Nine-banded Armadillo
Dasypus novemcinctus.
Adult cephalic shield. Estancia Nueva Gambach, PN San Rafael, Departamento Itapúa, undated.
Photo Hans Hostettler.

FIGURE 5 - (FPMAM895PH)
Nine-banded Armadillo
Dasypus novemcinctus.
Forefoot. Estancia Kanguery, PN San Rafael, Departamento Itapúa, November 2010.
Photo Paul Smith.

FIGURE 6 - (FPMAM896PH)
Nine-banded Armadillo
Dasypus novemcinctus.
Hindfoot. Estancia Kanguery, PN San Rafael, Departamento Itapúa, November 2010.
Photo Paul Smith.
**FIGURE 7**

Nine-banded Armadillo

*Dasypus novemcinctus.*