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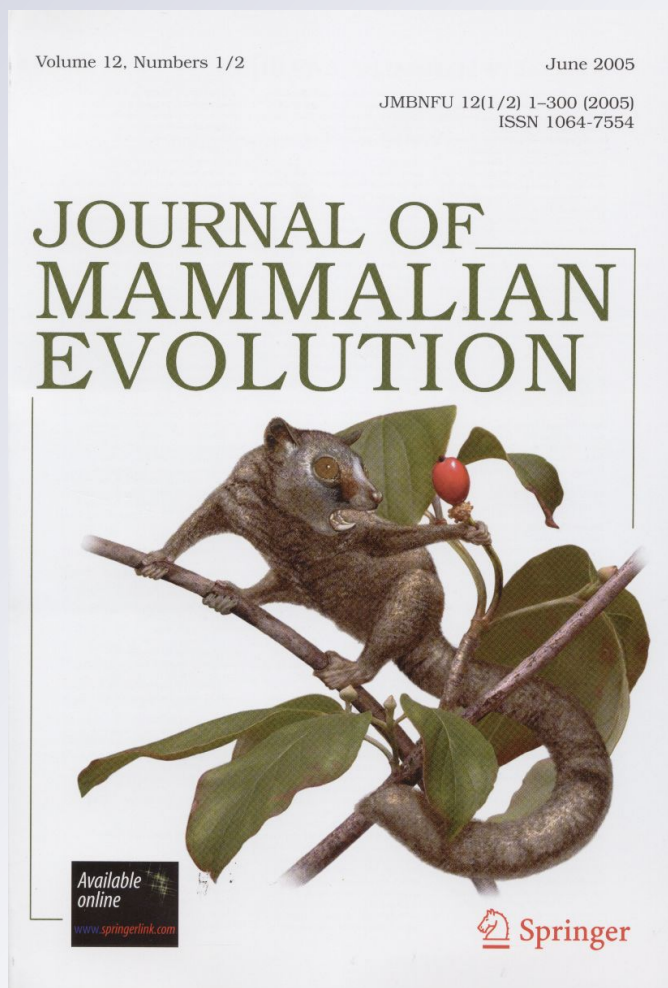
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Life on the Half-Shell: Consequences of a Carapace in the Evolution of Armadillos (Xenarthra: Cingulata)

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Abstract Without doubt, the possession of an armored carapace represents one of the most conspicuous morphological features of all cingulates. Here, we review some of the many ways in which the carapace may have influenced the evolution of other features of extant armadillos (Xenarthra: Cingulata). Effects range from physiological impacts on respiration and thermoregulation, to mechanical and other constraints on reproduction. Additionally, in mammals, armor has been linked with relatively slow plantigrade locomotion, which in turn may have promoted the low metabolic rate and exploitation of a low quality diet typically observed in armadillos. Finally, this network of relationships may help to explain the lack of any obvious kin-selected altruism in the polyembryonic armadillos, such as the nine-banded armadillo (*Dasypus novemcinctus*), because of time and energy constraints associated with a short active period devoted almost exclusively to feeding. In mammals, there has been growing interest in describing an ecological “lifestyle” as the particular way in which each species makes its living, and how this lifestyle constrains the evolution of other phenotypic traits. Based on our review, it appears the carapace has been a major determinant of the lifestyle of armadillos and has played a

central role in shaping the evolution of many other features of these animals.

Keywords Cingulata · Hypoxia · Kin selection · Reproduction · Thermoregulation

Introduction

All cingulates (armadillos, glyptodonts, and pampatheres) are identifiable by the possession of an armored carapace constructed of ossified dermal tissue (i.e., osteoderms or “scutes”, Gaudin and McDonald 2008; Fig. 1). In the extant armadillos, this conspicuous morphology was long viewed as the defining feature of the animals, leading to their name (armadillo = “little armored one”) and fanciful interpretations of their origin and relationships with other vertebrates (Capanna 2009).

In a modern context, the possession of such a distinctive phenotype seems likely to have had widespread consequences in shaping the evolution of many other features of armadillos. This should not be surprising given the well-established view that few traits evolve in isolation (e.g., Gould 2002). Consistent with this line of thinking, Sibly and Brown (2007, 2009; see also Dobson 2007) have proposed the notion of an ecological lifestyle, defined as “a unique combination of morphological, physiological and behavioral traits that is evolutionarily conservative within particular taxonomic groups and serves as a major constraint on the evolution of various life-history characteristics.” In this paper, we propose that the carapace may represent a key determinant of the armadillo lifestyle, acting as a major constraint on the evolution of many other characters.

What, then, constitutes the armadillo lifestyle? Undoubtedly, there are a number of ways this question could be

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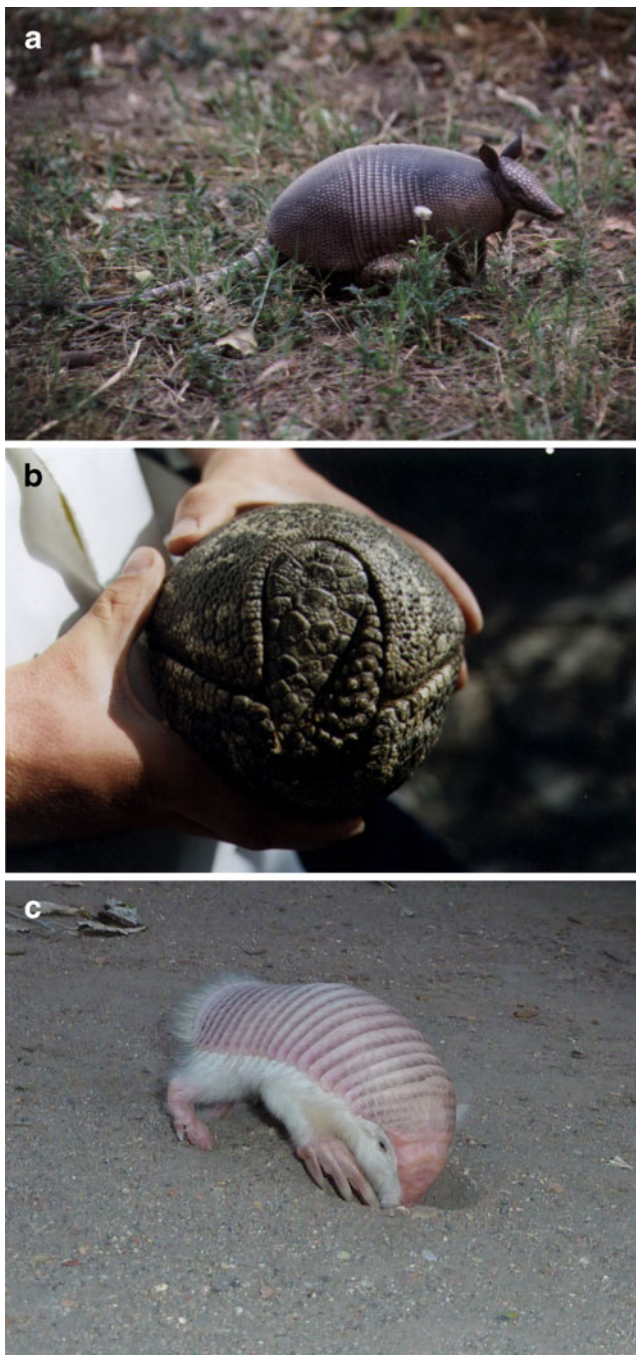


Fig. 1 The 21 extant armadillo species possess a formidable variety of carapaces. Shown are representatives of each of the three sub-families recognized by Gardner (2005). **a** Although commonly called the nine-banded armadillo, *Dasypus novemcinctus* (sub-family Dasypodinae) can have from seven to ten bands separating the scapular and pelvic shields. **b** Three-banded armadillos (*Tolypeutes matacus*; sub-family Tolypeutiinae) have a dome-shaped carapace consisting of rigid scapular and pelvic shields and, on average, three movable bands. They can roll up into a perfect ball. **c** The carapace morphology of pink fairy armadillos (*Chlamyphorus truncatus*; sub-family Euphractinae) is unusual among euphractines and armadillos in general. The carapace is attached to the body through a thin membrane along the spinal column. Silky white hair covers their body beneath the carapace

answered; additionally, any answer would also vary depending on which of the 21 extant species (Gardner 2005) was being discussed. Nonetheless, there are a few key traits that seem broadly applicable to most species. First, most armadillos are burrowing animals frequently exposed to hypoxic conditions (Scholander et al. 1943; Dhindsa et al. 1971). Indeed, many species may even experience hypoxia above ground, because they often forage with the nose immersed in soil. Armadillos feed this way because of the second point, which is that they are insectivores, although the degree of specialization on this resource varies widely among species (Redford 1985). Third, like all xenarthrans, armadillos have low metabolic rates (McNab 1980, 1985) and exhibit low, and often highly variable, body temperatures (McNab 1985). Fourth, armadillos are relatively solitary, asocial animals (McDonough and Loughry 2008). Finally, most species reproduce just once per year; with the exception of the polyembryonic species in the genus *Dasypus*, litter size is usually only one or two offspring (Superina 2000).

In what follows we provide examples of how the carapace may have influenced, directly or indirectly, the ways in which the above lifestyle characteristics have evolved. We conclude with a more detailed discussion of one species, the nine-banded armadillo (*Dasypus novemcinctus*; Fig. 1a), in an attempt to explain some unusual features of its biology. Ultimately, we hope to provide testable hypotheses that will inspire future analyses of the evolutionary relationships among various features of the armadillo phenotype.

Ecological Impacts

It seems obvious that a major benefit to armadillos of possessing a carapace is protection. This could include protection from the thorny vegetation found in many of the habitats armadillos occupy, as well as to minimize the potential for injury during aggressive interactions with conspecifics (McDonough 1994; Loughry et al. 2002; Blanco et al. 2009; Superina et al. 2009b). Another form of protection may involve limiting attachment sites for external parasites. Although ectoparasite prevalence (i.e., percentage of individuals exhibiting infection) can be rather high (e.g., 60% in *Zaedyus pichiy*, Superina et al. 2009b; 74% in *Euphractus sexcinctus*, Medri 2008; and 100% in *Tolypeutes matacus*, Deem et al. 2009), the number of ticks or fleas per individual is usually low and restricted to the soft skin on the animal's ventral side. Consequently, armadillos are typically regarded as suffering minimally from ectoparasitic infections (Forrester 1992).

While the above all represent plausible protective functions of the carapace, conventional wisdom normally

attributes the main function to protection from predators. While this certainly seems reasonable, we would point out that, to date, there are no data available to test this assumption, e.g., by showing that armadillos experience a lower risk of predation than similarly-sized, non-armored mammals occupying the same habitats and active at the same times of day (e.g., opossums, *Didelphis* spp.). Should the antipredator hypothesis be confirmed, then subsequent studies should examine how variation in the thickness of the carapace influences predation risk, both within (e.g., between age groups, see below) and between species.

Testing the antipredator benefits of the carapace will be important because these benefits are argued to lead to other evolutionary consequences. Specifically, Lovegrove (2000, 2001) showed that, in mammals, the possession of armor is linked with plantigrade locomotion. Presumably, armored species can afford this relatively slow mode of locomotion because they do not need to rely on speed to escape predators. Such an argument is further consistent with the aerobic capacity model proposed by Bennett and Ruben (1979), in which species that rely on speed to escape predators (or capture prey) must have a high aerobic capacity. This, in turn, requires that these animals exploit a high-quality diet and have high metabolic rates to fuel such an antipredator strategy. In contrast, armored species are freed from such considerations and are expected to exhibit lower metabolic rates and utilize lower-quality prey.

The ecological lifestyle of armadillos described earlier fits nicely with the predictions of Lovegrove (2000, 2001) and Bennett and Ruben (1979). Recall that armadillos have some of the lowest metabolic rates reported for any placental mammal (McNab 1980, 1985) and typically exploit prey of low energy density (McNab 1984). While it is thus tempting to view the carapace as the key characteristic that promoted the evolution of plantigrade locomotion, low metabolism, and the diet of armadillos, it is important to stress that the causal relationships among these traits remain unresolved. The earliest fossil remain from a cingulate is a scute from an armadillo dated to about 55 mya (Scillato-Yané 1976), which suggests the carapace arose early in the evolution of the group. Likewise, plantigrade locomotion seems typically regarded as ancestral in vertebrates, and a low metabolic rate is plesiomorphic within Xenarthra (McNab 1985). Consequently, at present we cannot say whether possession of a carapace drove the evolution of the other traits as opposed to some other causal scenario. Nonetheless, it seems clear that the carapace was a central component in unifying the evolution of key features of the armadillo lifestyle. Indeed, it is difficult to envision how the animals could jointly possess all of these features without bearing armor.

Physiological Impacts

The carapace, in conjunction with an associated low metabolic rate, has generated numerous ramifications for how armadillos function physiologically. Here, we highlight two of these, namely consequences for dealing with hypoxia and influences on thermoregulation.

At least some species of armadillos can function for extended periods of time at an atmospheric pressure of oxygen about half that of normal (Boggs et al. 1998). Presumably, they are able to do this in part because of their low metabolic rate, which would reduce the demand for oxygen. The carapace may also influence responses to hypoxia. Boggs et al. (1998) showed that, unlike most animals that respond to hypoxia by taking deeper breaths, armadillos breathed more rapidly. Frappell et al. (1998) argued that this was necessary because the carapace greatly increased the rigidity of the thorax, thus precluding the possibility of breathing more deeply.

Just as with hypoxia, the carapace has important consequences for how the animals thermoregulate. In particular, the high thermal conductance of the carapace (McNab 1980; Tattersall and Cadena 2010), coupled with a low metabolism and the absence of much insulating fat or fur, may provide benefits to armadillos in maximizing heat loss and minimizing heat production in hot environments. However, these same features would seem to make it difficult for armadillos to survive for prolonged periods of time in cold climates. Thus, the carapace, through its impacts on thermoregulation, may have played an important role in determining the distributional limits of many species (e.g., Humphrey 1974; Taulman and Robbins 1996). Burrows may represent a means by which armadillos compensate for some of the thermoregulatory consequences of a carapace. If so, then one could argue that the carapace has potentially influenced the evolution of burrowing behavior and the design of burrows. Fossoriality might even have been further promoted by the carapace providing protection during burrow collapses.

Another aspect of thermoregulation in cold environments is the utilization of fat for insulation or as an energy reserve (Grigg et al. 2004). Meritt (2008) noted that three-banded armadillos (*T. matacus*) fed *ad libitum* in captivity failed to add fat. He argued that in this particular case, the reason was not related to thermoregulation, but rather that adding fat would have prevented the animals from using their famous antipredator strategy of rolling up into an impregnable ball (Fig. 1b). This hypothesis indicates a potential for the carapace to act as an important constraint on fat deposition and, thus, to influence the resource allocation strategies of armadillos. Obesity is, however, a common problem in captive armadillos that do not rely on the tight-ball strategy used by *Tolypeutes* (Superina et al.

2008; Rossetto 2009). In addition, wild pichis (*Z. pichiy*), the armadillo naturally occurring at the highest latitudes today (53°S), are known to build up considerable fat reserves before entering hibernation (Superina and Boily 2007; Superina 2008). It is therefore probable that such a constraint is restricted to only a few species.

A more widespread constraint on insulation concerns the impact of the carapace on the production of fur. Vickaryous and Hall (2006) pointed out that the osteoderms of the carapace bear a limited number of foramina that allow the passage of caudally directed hairs. Although some species of armadillos (e.g., *Chaetophractus nationi* and *Dasyopus pilosus*) possess conspicuous fur, it seems likely that, due to the carapace, the density of hair is substantially less than in other fur-bearing mammals. The case of the pink fairy armadillo (*Chlamyphorus truncatus*; Fig. 1c) seems to support this hypothesis. Its carapace is attached to the body only through a thin membrane on the dorsal mid-line, and the animal is insulated by silky white hair growing beneath the carapace. Constraints on fur production would lead yet again to impacts on thermoregulation, with subsequent evolutionary consequences similar to those already described.

Reproductive Impacts

Possession of a carapace has likely shaped several aspects of how armadillos reproduce. Most obviously, the reduced flexibility of the pelvic shield represents a severe hindrance during mounting. Armadillos have overcome this obstacle through the evolution of a penis that is one of the longest relative to body size among mammals. It can reach approximately 50% of body length in *T. matacus* (Herrick et al. 2002) and 60% in *Chaetophractus vellerosus* and *Z. pichiy* (Superina, unpublished data). This long penis allows males to extend beyond the female's bony armor, reach the vaginal opening, and achieve intromission. In addition to length, the distinctive penile anatomy of armadillos may have evolved because of similar considerations. Owing to a parallel and perpendicular arrangement of collagen fibers to the long axis of the corpus cavernosum, the erect armadillo penis can reach a reproducible maximum size with resistance to bending forces (Kelly 1997, 1999).

The presence of a fully developed, rigid carapace in armadillo fetuses would make passage through the birth canal difficult, if not impossible. It is therefore no surprise that the carapace is considerably softer in fetuses and newborns than in adults. The reason for this is that ossification of the dermal scutes commences during the fetal period (Vickaryous and Hall 2006; see Fig. 2), but does not conclude until after birth (Anderson and Benirschke 1966). As a consequence, the carapace of



Fig. 2 **a** The general shape of the carapace, including its division into pectoral, pelvic, and banded shields, is well established and clearly visible in newborn pichis (*Zaedyus pichiy*), but its pinkish color and softness are indicative of the lack of cornification of the epidermal scales and of the small osteoderms. **b** External examination indicates that, in pichis (*Zaedyus pichiy*), the carapace is yellow and relatively hard by 2 weeks of age. However, due to the lack of histological or radiographic studies, it is not known when the development of the carapace is concluded

armadillo fetuses is much more flexible, because their osteoderms are small and separated from each other by loose connective tissue (Vickaryous and Hall 2006), while those of adults are tightly sutured (Hill 2006). This increased flexibility facilitates parturition, but may expose the offspring to a higher risk of predation (McDonough and Loughry 1997). Parturition therefore normally occurs inside burrows, and, in many species, the offspring do not leave the protective den until they are weaned (Superina et al. 2009a).

Lactation is an energetically costly process for all mammals (Gittleman and Thompson 1988). In armadillos, maternal investment must cover the usual energy requirements related to infant growth and maintenance. However, in contrast to other mammals, mothers must also provide their offspring with sufficient minerals, especially calcium and phosphate, for the development and hardening of the carapace. Barclay (1994) proposed

that calcium, and not energy, was the most critical resource limiting litter size in insectivorous bats. Similarly, in armadillos, the availability of calcium (and phosphate) may have had important ramifications for the evolution of maternal investment strategies, juvenile ontogeny, and litter size. Once again though, the more important, general point, is that these effects occurred because of the presence of the carapace.

At present, it is unknown whether lactating females obtain needed minerals through dietary changes, demineralization of their own carapace or endoskeleton, or both. According to Abba et al. (2011), the diet of *C. vellerosus* contains a considerably higher proportion of mammals during summer than in any other season. Lactation occurs during the summer months. Thus, it seems possible that the change in diet composition is related to the reproductive status of females. Further studies are, however, needed to confirm this. A comparison of the bone density of lactating versus non-lactating female *Z. pichiy* is currently underway that may help clarify the role of the carapace as a source of minerals during lactation. If demineralization does occur, then the carapace would represent a major influence on patterns of maternal investment in armadillos via both supply and demand.

High maternal investment in armadillos may have further consequences. If lactating females deplete their calcium stores to ensure their offspring receive a sufficient amount of minerals to grow and develop their own carapace, then these stores must be replenished once lactation has terminated. Considering their predominantly insectivorous diet and the fact that insects are a poor source of calcium (Turner 1982; Studier and Sevick 1992), it is possible that not all females are able to replenish their calcium reserves before the next breeding season. Consequently, they may have to forego reproduction that year. Indeed, population and endocrinological studies on *D. novemcinctus* suggest that not all adult females reproduce in a given year (Gause 1980; Truman et al. 1991; Loughry

and McDonough 2012). Studies in captive animals, where the amount of calcium in the diet is manipulated, would be useful in further testing this hypothesis.

Despite additional energetic and mineral requirements, most species of armadillos have relatively short lactation periods and rapid infant growth (Roberts et al. 1982; Table 1). A preliminary analysis suggests that, in armadillos, the lactation period is about half as long as in other mammals (Table 1). Furthermore, no species of armadillo seems to comply with Millar's (1977) and Charnov and Berrigan's (1993) findings that offspring are weaned when they reach one third of adult body mass. *Dasyus novemcinctus* infants barely reach half of this threshold weight, but the lactation period of *C. villosus*, *Z. pichiy*, and *T. matacus* ends at higher infant body masses relative to adult body mass (Table 1). As a result, these three species grow relatively fast (as shown by high daily growth rates after correction for adult body mass), while nine-banded armadillo infants gain weight at a much slower pace. Litter size is larger in nine-banded armadillos than in the other species due to polyembryony (Prodöhl et al. 1996), which may explain why the offspring are weaned at a lower weight. It would be interesting to determine if the other polyembryonic species in the genus *Dasyus* show a similar pattern. In any case, it will be critical to determine the precise role of the carapace in contributing to these differences in offspring development.

Just as with bats (Barclay 1994), it would be worthwhile to perform comparative analyses that examine the influence of calcium limitation on the evolution of litter size, and other reproductive parameters, in armadillos. For example, one might expect less insectivorous species (which, presumably, have more access to calcium) to exhibit larger litter sizes, shorter lactation periods, and faster growth rates. Unfortunately, data on the reproduction of the most insectivorous genera, *Cabassous* and *Priodontes*, are limited to litter size (one offspring in *Cabassous*, one or two in *Priodontes*). Additional data from these species, and

Table 1 Body mass at different developmental stages, age at weaning, and growth rates for several species of armadillos and other mammals

Species	Adult body mass (g)	Body mass at birth (g)	Body mass at weaning (g)	Age at weaning (days)	Body mass at weaning relative to adult weight	Linear growth rate (g/day)	Daily growth rate corrected for adult mass	References
<i>Dasyus novemcinctus</i>	4,000	100	600	50	15%	10	0.25%	(1)
<i>Chaetophractus villosus</i>	3,000	117	1,590	61	53%	25	0.83%	(2)
<i>Tolypeutes matacus</i>	1,500	85	850	59	57%	13	0.86%	(3)
<i>Zaedyus pichiy</i>	1,000	50	400	40	40%	9	0.88%	(4)
Mammals ^a	2,324	110	717	105	33%	13	0.60%	(5)

^a Average values for 22 species of placental mammal with adult body masses between 1,000 g and 4,000 g

References: (1) Loughry and McDonough (2012); (2) averages of values provided by Kühn (1953) and Beck (1972); (3) Meritt (1971); (4) Superina et al. (2009a) and Superina, unpublished data; (5) Jones et al. (2009)

others, will thus be necessary to further test the idea that mineral availability limits reproduction in armadillos.

The Case of the Nine-Banded Armadillo

The nine-banded armadillo, *D. novemcinctus*, is by far the most studied cingulate (McDonough and Loughry 2008). This allows for additional investigation into how the carapace might influence armadillo evolution. For our purposes here, we focus on two important points: (1) nine-banded armadillos are the only free-ranging vertebrates other than humans that exhibit naturally-occurring infections of *Mycobacterium leprae*, the causative agent in producing leprosy (Truman 2005, 2008); and (2) females exhibit obligate polyembryony, whereby they give birth to litters of genetically identical quadruplets when they reproduce (Prodöhl et al. 1996).

The link between leprosy and the carapace is similar to that discussed previously for thermoregulation. Namely, *M. leprae* only propagates at cool temperatures (such as in the extremities of humans, Binford 1956; Brand 1959). The low metabolic rate and high thermal conductance of *D. novemcinctus* generates an animal with a low body temperature that represents an ideal breeding ground for *M. leprae* infection. Indeed, unlike in humans, leprosy is not confined to the extremities in *D. novemcinctus* but is systemic, spreading throughout the body (Truman 2008).

We must point out that, while the carapace and low metabolic rate may facilitate leprosy infection in *D. novemcinctus*, other factors are also important. All armadillos exhibit low body temperatures, leading to the expectation that all should be equally susceptible to infection by *M. leprae*. However, to date, *D. novemcinctus* is the only species known to exhibit infections in the wild (Truman 2008). In addition, experimental inoculations have only been successful in members of *Dasybus* (Convit and Pinardi 1974; Baliña et al. 1985). Current thinking is that there may be genetic factors that increase the likelihood of infection (Fitness et al. 2004; Mira 2006; Velarde-Félix et al. 2009; Molecular Ecology Resources Primer Development Consortium (MERPDC) et al. 2010), and these may not be present in other genera of armadillos.

Because of polyembryony, *D. novemcinctus* has long been regarded as a model system for the study of kin selection (e.g., Dawkins 1976). Yet, extensive, long-term field studies have failed to uncover any evidence that kin selection is occurring or important in wild populations (Loughry et al. 2005; Loughry and McDonough 2012). There is no obvious reason why nine-banded armadillos should be somehow incapable of exhibiting forms of cooperation seen in other mammals. Thus, the lack of kin-selected altruism, particularly given the high level of genetic relatedness among clonemates, is puzzling. How

might the carapace help explain this? Our argument hinges on a point first made by Dunbar (1992), that social interactions are costly in terms of time and energy. Thus, complex social behavior, such as kin-selected altruism, might not evolve in species that are time- or energy-limited.

We have argued above for linkages between possession of a carapace, plantigrade locomotion, low metabolic rate, and reliance on a low-quality diet. In nine-banded armadillos, these characteristics appear to have resulted in an animal that spends virtually all of its short active period (normally just 4–6 h/day, Prudom and Klemm 1973; Twyver and Allison 1974) feeding. Ancona and Loughry (2009) reported that *D. novemcinctus* spent somewhere between 80% and 90% of its active time above ground feeding and that this was among the highest values reported for any mammal. Not only that, but there was limited variation in time allocation between individuals or due to environmental variables (Ancona and Loughry 2010), which suggested all individuals faced a high premium on finding sufficient food, regardless of individual identity or daily circumstances. If so, then it seems possible that nine-banded armadillos may not have the “time” to be social, thus precluding the evolution of kin-selected behaviors (see also Loughry et al. 2005; Loughry and McDonough 2012).

Other factors, such as juvenile mortality and dispersal patterns of littermates, also influence the potential for kin selection in populations of *D. novemcinctus* (Loughry et al. 2005), so the time constraints hypothesis may be just one aspect of a broader explanation for social evolution in armadillos. Nonetheless, to the extent the time constraints hypothesis has validity, it ultimately traces back to the influence of the carapace in determining many key features of the armadillo lifestyle.

Conclusion

Space limitations preclude further elaboration of our thesis. Nonetheless, we hope this cursory review has been sufficient to illustrate the multiple ways in which the carapace may have influenced the evolution of armadillos. The most important task for the future will be to critically test the ideas we have presented here, thereby generating a far better understanding of the evolutionary role of this remarkable structure.

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References

- Abba AM, Cassini GH, Cassini MH, Vizcaíno SF (2011) Historia natural del piche llorón *Chaetophractus vellerosus* (Mammalia: Xenarthra: Dasypodidae). *Rev Chil Hist Nat* 84:51–64
- Ancona KA, Loughry WJ (2009) Time budgets of wild nine-banded armadillos. *Southeast Nat* 8:587–598
- Ancona KA, Loughry WJ (2010) Sources of variation in the time budgets of wild nine-banded armadillos. *Mammalia* 74:127–134
- Anderson JM, Benirschke K (1966) The armadillo, *Dasypus novemcinctus*, in experimental biology. *Lab Anim Care* 16:202–216
- Baliña LM, Valdez RP, de Herrera M, Cordova HC, Bellocq J, García N (1985) Experimental reproduction of leprosy in seven-banded armadillos, *Dasypus hybridus*. *Int J Lepr* 53:595–599
- Barclay RMR (1994) Constraints on reproduction by flying vertebrates: energy and calcium. *Am Nat* 144:1021–1031
- Beck U (1972) Ueber die künstliche Aufzucht von Borstengürteltieren (*Euphractus villosus*). *Zool Garten* 41:215–222
- Bennett AF, Ruben JA (1979) Endothermy and activity in vertebrates. *Science* 206:649–654
- Binford CH (1956) Comprehensive program for inoculation of human leprosy into laboratory animals. US Public Health Service, Report 71:995–996
- Blanco R, Jones W, Rinderknecht A (2009) The sweet spot of a biological hammer: the centre of percussion of glyptodont (Mammalia: Xenarthra) tail clubs. *Proc R Soc Lond B Biol Sci* 276:3971–3978
- Boggs DF, Frappell PB, Kilgore DL Jr (1998) Ventilatory, cardiovascular and metabolic responses to hypoxia and hypercapnia in the armadillo. *Respir Physiol* 113:101–109
- Brand PW (1959) Temperature variation and leprosy deformity. *Int J Lepr* 27:1–7
- Capanna E (2009) South American mammal diversity and Hernandez's *Novae Hispaniae Thesaurus*. *Rendiconti Lincei* 20:39–60
- Charnov E, Berrigan D (1993) Why do female primates have such long lifespans and so few babies? *Evol Anthropol* 1:191–194
- Convit J, Pinardi ME (1974) Inoculación del *M. leprae* en dos especies de armadillo: *D. sabanicola* y *D. novemcinctus*. *Acta Cient Venezol* 25:51–54
- Dawkins R (1976) *The Selfish Gene*. Oxford University Press, Oxford
- Deem SL, Noss AJ, Fiorello CV, Manharth AL, Robbins RG, Karesh WB (2009) Health assessment of free-ranging three-banded (*Tolypeutes matacus*) and nine-banded (*Dasypus novemcinctus*) armadillos in the Gran Chaco, Bolivia. *J Zoo Wildl Med* 40:245–256
- Dhindsa DS, Hoversland AS, Metcalfe J (1971) Comparative studies of the respiratory functions of mammalian blood VII: armadillo. *Respir Physiol* 13:198–208
- Dobson FS (2007) A lifestyle view of life-history evolution. *Proc Natl Acad Sci USA* 104:17565–17566
- Dunbar RIM (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49
- Fitness J, Floyd S, Wamdorff DK, Sichali L, Mwaungulu L, Crampin AC, Fine PE, Hill AV (2004) Large-scale candidate gene study of leprosy susceptibility in the Karonga district of northern Malawi. *Am J Trop Med Hyg* 71:330–340
- Forrester DJ (1992) *Parasites and Diseases of Wild Mammals in Florida*. University Press of Florida, Gainesville
- Frappell PB, Boggs DF, Kilgore DL (1998) How stiff is the armadillo? A comparison with the allometrics of mammalian respiratory mechanics. *Respir Physiol* 113:111–122
- Gardner AL (2005) Order Cingulata. In: Wilson DE, Reeder DM (eds) *Mammal Species of the World: A Taxonomic and Geographic Reference*. The Johns Hopkins University Press, Baltimore, pp 94–99
- Gaudin TJ, McDonald HG (2008) Morphology-based investigations of the phylogenetic relationships among extant and fossil xenarthrans. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 24–36
- Gause GE (1980) Physiological and morphometric responses of the nine-banded armadillo to environmental factors. PhD Dissertation. Department of Biology, University of Florida, Gainesville, 124 pp
- Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. *Am Zool* 28:863–875
- Gould SJ (2002) *The Structure of Evolutionary Theory*. Belknap Harvard University Press, Cambridge
- Grigg GC, Beard LA, Augee ML (2004) The evolution of endothermy and its diversity in mammals and birds. *Physiol Biochem Zool* 77:982–997
- Herrick JR, Campbell MK, Swanson WF (2002) Electroejaculation and semen analysis in the La Plata three-banded armadillo (*Tolypeutes matacus*). *Zoo Biol* 21:481–487
- Hill RV (2006) Comparative anatomy and histology of xenarthran osteoderms. *J Morphol* 267:1441–1460
- Humphrey SR (1974) Zoogeography of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *BioScience* 24:457–462
- Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme DL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648
- Kelly DA (1997) Axial orthogonal fiber reinforcement in the penis of the nine-banded armadillo (*Dasypus novemcinctus*). *J Morphol* 233:249–255
- Kelly DA (1999) Expansion of the tunica albuginea during penile inflation in the nine-banded armadillo (*Dasypus novemcinctus*). *J Exp Biol*:253–265
- Kühn E (1953) Zum Wachstum männlicher Borstengürteltiere (*Chaetophractus villosus*). *Zool Garten* 20:82–85
- Loughry WJ, McDonough CM (2012) *The Nine-Banded Armadillo*. University of Oklahoma Press, Norman
- Loughry WJ, Prodöhl PA, McDonough CM (2005) The inadequacy of observation: understanding armadillo biology with molecular markers. In: Pandalai SG (ed) *Recent Research Developments in Ecology*. Transworld Research Network, Kerala, India, pp 55–73
- Loughry WJ, Robertson EG, McDonough CM (2002) Patterns of anatomical damage in a population of nine-banded armadillos *Dasypus novemcinctus* (Xenarthra, Dasypodidae). *Mammalia* 66:111–122
- Lovegrove B (2000) The zoogeography of mammalian basal metabolic rate. *Am Nat* 156:201–219
- Lovegrove B (2001) The evolution of body armor in mammals: plantigrade constraints of large body size. *Evolution* 55:1464–1473
- McDonough CM (1994) Determinants of aggression in nine-banded armadillos. *J Mammal* 75:189–198
- McDonough CM, Loughry WJ (1997) Patterns of mortality in a population of nine-banded armadillos, *Dasypus novemcinctus*. *Am Midl Nat* 138:299–305
- McDonough CM, Loughry WJ (2008) Behavioral ecology of armadillos. In: Vizcaíno SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 281–293
- McNab BK (1980) Energetics and the limits to a temperate distribution in armadillos. *J Mammal* 61: 606–627
- McNab BK (1984) Physiological convergence among ant-eating and termite-eating mammals. *J Zool* 203:485–510

- McNab BK (1985) Energetics, population biology, and distribution of Xenarthrans, living and extinct. In: Montgomery GG (ed) *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington and London, pp 219–232
- Medri IM (2008) Ecologia e história natural do tatu-peba, *Euphractus sexcinctus* (Linnaeus, 1758), no Pantanal da Nhecolândia, Mato Grosso do Sul. Master's thesis. Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, pp 167
- Meritt DA Jr (1971) The development of the La Plata three banded armadillo, *Tolypeutes matacus* at Lincoln Park Zoo, Chicago. *Int Zoo Yb* 11:195–196
- Meritt DA Jr (2008) Xenarthrans of the Paraguayan Chaco. In: Vizcaino SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 294–299
- Millar JS (1977) Adaptive features of mammalian reproduction. *Evolution* 31:370–386
- Mira MT (2006) Genetic host resistance and susceptibility to leprosy. *Microbes Infect* 8:1124–1131
- Molecular Ecology Resources Primer Development Consortium (MERPDC) et al. (2010) Permanent genetic resources added to Molecular Ecology Resources database 1 April 2010–31 May 2010. *Mol Ecol Res* 10:1098–1105
- Prodhöhl P, Loughry WJ, McDonough CM, Nelson WS, Avise J (1996) Molecular documentation of polyembryony and the micro-spatial dispersion of clonal sibships in the nine-banded armadillo, *Dasypus novemcinctus*. *Proc R Soc Lond B Biol Sci* 263:1643–1649
- Prudom AE, Klemm WR (1973) Electrographic correlates of sleep behavior in a primitive mammal, the armadillo, *Dasypus novemcinctus*. *Physiol Behav* 10:275–282
- Redford KH (1985) Food habits of armadillos (Xenarthra: Dasypodidae). In: Montgomery GG (ed) *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*. Smithsonian Institution Press, Washington and London, pp 429–437
- Roberts M, Newman L, Peterson G (1982) The management and reproduction on the large hairy armadillo *Chaetophractus villosus* at the National Zoological Park. *Int Zoo Yb* 22:185–194
- Rossetto L (2009) Tatu com obesidade mórbida faz tratamento no Ibama. In: Globo. <http://g1.globo.com/Noticias/Brasil/0,,MUL1399246-5598,00-TATU+COM+OBESIDADE+MORBIDA+FAZ+TRATAMENTO+NO+IBAMA.html> Accessed: December 1 2009
- Scholander PF, Irving L, Grinnell SW (1943) Respiration of the armadillo with possible implications as to its burrowing. *J Cell Comp Physiol* 21:53–63
- Scillato-Yané GJ (1976) Sobre un Dasypodidae de edad Riochiquense (Paleoceno superior) de Itaboraí (Brasil). *An Acad Bras Cienc* 48:527–530
- Sibly RM, Brown JH (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proc Natl Acad Sci USA* 104:17707–17712
- Sibly RM, Brown JH (2009) Mammal reproductive strategies driven by offspring mortality-size relationships. *Am Nat* 173:E185–E199
- Studier EH, Sevick SH (1992) Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. *Comp Biochem Physiol A Comp Physiol* 103:579–595
- Superina M (2000) *Biologie und Haltung von Gürteltieren (Dasypodidae)*. Doctoral thesis. Institut für Zoo-, Heim- und Wildtiere, Universität Zürich, Zürich, 250 pp
- Superina M (2008) The ecology of the pichi *Zaedyus pichiy* in western Argentina. In: Vizcaino SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 313–318
- Superina M, Boily P (2007) Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comp Biochem Physiol A Comp Physiol* 148:893–898
- Superina M, Carreño N, Jahn G (2009a) Characterization of seasonal reproduction patterns in female pichis, *Zaedyus pichiy* (Xenarthra: Dasypodidae) estimated by fecal sex steroid metabolites and ovarian histology. *Anim Reprod Sci* 116:358–369
- Superina M, Garner MM, Aguilar RF (2009b) Health evaluation of free-ranging and captive pichis, *Zaedyus pichiy* (Mammalia, Dasypodidae) in Mendoza Province, Argentina. *J Wildl Dis* 45:174–183
- Superina M, Miranda F, Plese T (2008) Maintenance of Xenarthra in captivity. In: Vizcaino SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 232–243
- Tattersall GJ, Cadena V (2010) Insights into animal temperature adaptations revealed through thermal imaging. *Imaging Sci J* 58:261–268
- Taulman JF, Robbins LW (1996) Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *J Biogeogr* 23:635–648
- Truman RW (2005) Leprosy in wild armadillos. *Lepr Rev* 76:198–208
- Truman RW (2008) Leprosy. In: Vizcaino SF, Loughry WJ (eds) *The Biology of the Xenarthra*. University Press of Florida, Gainesville, pp 111–119
- Truman RW, Kumaresan JA, McDonough CM, Job CK, Hastings RC (1991) Seasonal and spatial trends in the detectability of leprosy in wild armadillos. *Epidemiol Infect* 106:549–560
- Turner AK (1982) Timing of laying by swallows (*Hirundo rustica*) and sand martins (*Riparia riparia*). *J Anim Ecol* 51:29–46
- Twyver JV, Allison T (1974) Sleep in the armadillo *Dasypus novemcinctus* at moderate and low ambient temperatures. *Brain Behav Evol* 9:107–120
- Velarde-Félix JS, Cázarez Salazar SG, Castro Velázquez R, Rendón Maldonado JG, Rangel Villalobos J (2009) Association between the TaqI polymorphism of vitamin D receptor gene and lepromatous leprosy in a Mexican population sample. *Salud Publica Mex* 51:59–61
- Vickaryous MK, Hall BK (2006) Osteoderm morphology and development in the nine-banded armadillo, *Dasypus novemcinctus* (Mammalia, Xenarthra, Cingulata). *J Morphol* 267:1273–1283