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CHELONOIDIS CARBONARIA (SPIX, 1824) (TESTUDINES: TESTUDINIDAE), ONCE COMMON AND ABUNDANT BECOMES AN ENDANGERED SPECIES IN PARAGUAY

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Abstract.- *Chelonoidis carbonaria* is highly adapted to its habitat in Paraguay. Investigation on wild populations, especially long-term observation is almost completely lacking, even though such data is vital for effective management. The Paraguayan populations show differences in their reproductive behaviour to better studied northern populations of the species, and there are also clear differences in morphology.

Key words: *Reptilia: Chelonii, distribution, ecology, threats, conservation status.*

Resumen.- *Chelonoidis carbonaria* está altamente adaptado a su hábitat en Paraguay. Prácticamente se carece de investigaciones en poblaciones salvajes, especialmente de observaciones a largo plazo, pese a que dicha información es vital para el manejo efectivo de la especie. Las poblaciones paraguayas muestran diferencias en su comportamiento reproductivo respecto a las mejores estudiadas poblaciones norteñas de la especie, existiendo también diferencias claras en la morfología.

Palabras clave: *Reptilia: Chelonii, distribución, ecología, amenazas, estado de conservación.*

The Red-footed tortoise, *Chelonoidis carbonaria*, is widely distributed in South America, its range extending from Panama to Northern Argentina, including Colombia, Venezuela, Guyana, Suriname, French Guyana, Brazil, Bolivia, and Paraguay (Vinke *et al*., 2008). However it can be difficult to understand Chelonian distributions as they are susceptible to anthropochory. The question of whether the sparse findings of *C. carbonaria* in Peru are of autochthonous or allochthonous origin is still unresolved (Carillo de Espinoza & Lamas, 1985; Walker, 1987), and there is also doubt as to the origin of specimens occurring on some islands of the Caribbean (Vinke *et al*., 2008).

Despite the large geographic range and morphological differences apparently related to the tortoises' origin (e.g. Pritchard & Trebau, 1984; Vinke & Vinke, 2004a) no subspecies are currently recognized. It was only following a major analysis by Williams (1960) that the specific distinction between *Chelonoidis carbonaria* and *C. denticulata* was first clarified. In fact Paraguayan *Chelonoidis carbonaria* are quite variable in form, size and coloration (Fig. 1), but common to all specimens is a uniquely dark plastron with brighter spots at the border and the bridge (Fig. 2), and hypertrophied red scales on the forelimbs (Fig. 3), attributes that they do not share with northern populations (Pritchard & Trebau, 1984; Vinke & Vinke, 2004a).

An investigation using sequence data of the mitochondrial cytochrome b gene of 83 *Chelonoidis carbonaria* (five of which originated from two Paraguayan Chaco localities) returned strong evidence for the subdivision of genetically distinct, geographically vicariant populations of which the clade formed by haplotypes from Paraguay constituted a sister clade of all other haplotypes of the species (Vargas-Ramírez *et al*., 2010). However because of incomplete locality sampling and the restriction to mitochondrial data the authors refrained from describing different species or subspecies, suggesting that further research on geographic and taxonomic variation in *C. carbonaria* is necessary to clarify relationships. The study did not rule out the possibility that *Chelonoidis carbonaria* represents a composite of cryptic species.

Figures 1-3. Morphological features of the paraguayan red-footed tortoise (*Chelonoidis carbonaria*). **1)** The individuals are variable in form, size and coloration. **2)** A uniquely dark plastron is typical of Paraguayan populations. **3)** All specimens show hypertrophied red scales on the forelimbs.

Distribution and habitat in Paraguay

Chelonoidis carbonaria occurs in both the Chaco and oriental regions of Paraguay (Fig. 4). In the Chaco *Chelonoidis carbonaria* is present in all three departments (Alto Paraguay, Boquerón, and Presidente Hayes) and is found in different Chaco ecotypes. In the dry Chaco the most northerly Paraguayan localities are from the area of the *Cerro Chovoreca* (Gayet, 2008) and the xerophytic forest between Lagerenza'i and Mendoza in Department Alto Paraguay (pers. obs.). The most south-westerly locality is located on the border with Argentina, at the Río Pilcomayo in the Pozo Hondo region, Dept. Boquerón (Miguel de Machune, pers. comm.).

The transition zone of the Dry Chaco and the Humid Chaco is characterized by a band of saline lagoons bordered by xerophytic forest. In May 2010 we found a population in that region, close to Estancia Campo Maria (Dept. Presidente Hayes, Fig. 5). In the Humid Chaco they have been reported from various localities: San Carlos (80 km west of Puerto Mihanovich); farther south, directly on the banks of the Río Paraguay, between Puerto Sastre and Puerto Casado, Dept. of Alto Paraguay (Müller & Hellmich, 1936); and in Dept. Presidente Hayes at Estancia Kintana (Vinke *et al*., 2008), Estancia Salazar and a little farther east along the Trans-Chaco Highway in the area of the Estación Experimental Chaco at km 295 (Scott & Lovett, 1975, not 245, as published by Pritchard & Trebbau, 1984).

The wide range of *Chelonoidis carbonaria* in the Paraguayan Chaco should not be interpreted as the presence of the species throughout the region, as large portions of the Chaco are not suitable for the species (see section on Natural history), a result of microhabitat requirements that are locally distributed in the harsh Chaco environment.

Much of the oriental region was once covered by Atlantic Forest (94,000 km^2 of 159,800 km^2 Fragano & Clay, 2003; 2005), but the northern departments (Dept. Concepcion, Dept. Amambay, Dept. San Pedro, Dept. Canindeyú) represent the southern limits of the Cerrado, with smaller, isolated patches further south to Dept. Cordillera (Mereles, 2013). In the oriental region *Chelonoidis carbonaria* is known in Dept. Concepción from the hills between "Estancia San Luís de la Sierra (Apá Hills) and Estancia Zanja Moroti" (Müller and Hellmich, 1936), within Serranía de San Luís National Park (John Simmons, pers. comm.) and along the Rio Aquidabán (own findings). In Dept. Amambay, local rangers report it from Cerro Corá National Park. In Dept. San Pedro the species was common in the 1960s in the

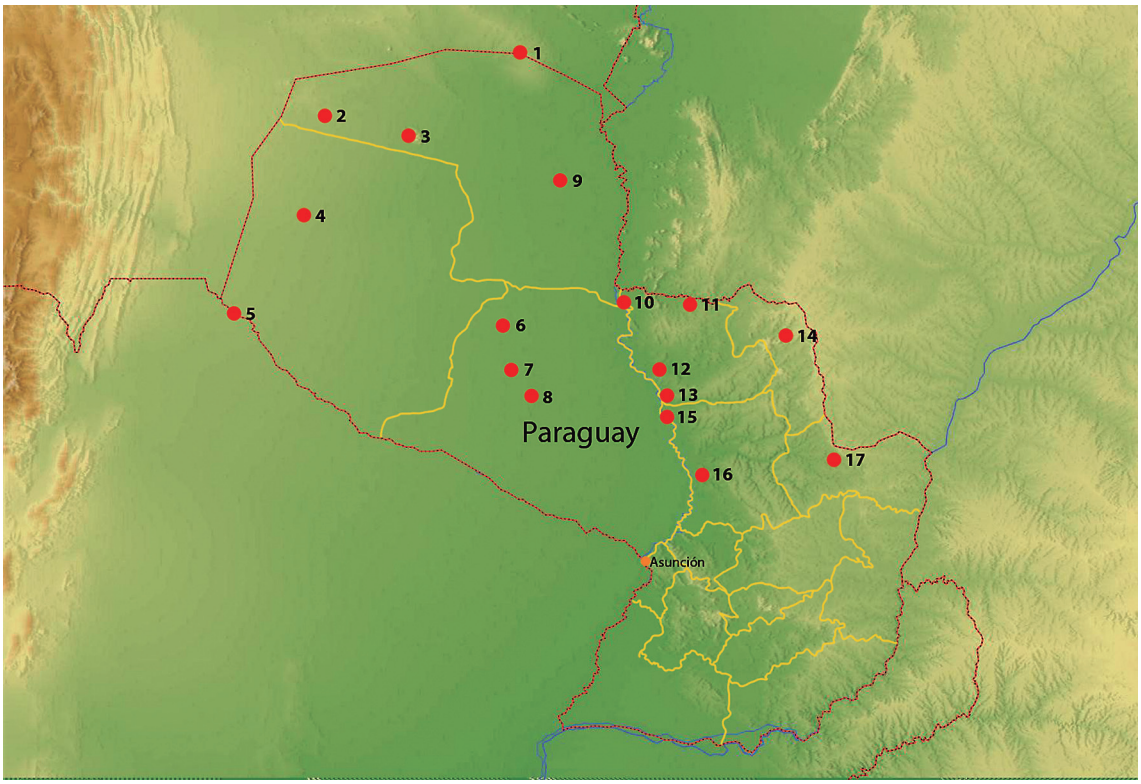

Figure 4. Map of present and former occurrence of *Chelonoidis carbonaria*. Dry Chaco: 1=Cerro Chovoreca, 2=Road between Médanos and Lagerenza'i, 3= Defensores del Chaco National Park, 4=La Patria, 5=Pozo Hondo Region. Transition zone: 6=Estancia Campo Maria, 7=Estancia Salzar, 8=Estación Experimental, Wet Chaco: 9=80 km west of P. Mihanovich, 10=Puerto Casado. Dept. Concepción: 11=Apa Hills, 12=Banks of the Río Aquidabán, 13=Serranías de San Luís National Park. Dept. Amambay: 14= Cerro Corá National Park, Dept.San Pedro: 15=Ybapobó, 16=Volendam. Dept. Canindeyú: 17=Mbaracayú Forest Nature Reserve.

surroundings of Colonia Volendam (Hermann Waldbrunner, pers. comm.), though this area has since been transformed into agriculture and pasture. A specimen was also cited from Puerto Ybapobó (erroneously Ybabopo) by Williams (1960). We are unaware of any recent records of *C. carbonaria* in San Pedro. One *Chelonoidis carbonaria* was hunted by the Ache tribe during sample periods from 1980 to 1996 in the Mbaracayú Forest Reserve (referred to *Geochelone* sp., Hill & Padwe, 2000).

According to Müller and Hellmich (1936) *Chelonoidis carbonaria* prefers open and bushy forests ("lichte Wald- und Buschbestände") and does not occur in grassland or dense forests, which are used habitually by northern populations of the species (Vinke *et al*., 2008). Consequently it seems probable that the distribution of *C. carbonaria* in the Oriental region is limited to the Cerrado and its transition zone to Atlantic Forest and Humid Chaco (Río Aquidabán).

It is unclear whether *Chelonoidis carbonaria* once occurred naturally in southern Paraguay in the region of Ayolas and Encarnación, Depts. Misiones and Itapuá (Cabrera, 1998), but if – as we suppose– the species distribution is limited by Cerrado or the transition zone between Cerrado and Atlantic Forest, it would seem unlikely. The red-footed tortoise is frequently kept in captivity in Paraguay, so single reports must not be understood to necessarily imply native origin, especially when they are close to human settlements. Large scale habitat alteration over much of the oriental region coupled with the paucity of records, means that it is now almost impossible to confidently evaluate the former extent of the distribution.

Figure 5. Two views of a perfectly camouflaged *Chelonoidis carbonaria* in its natural habitat, close to a saline lagoon, Presidente Hayes, Paraguay.

Natural history

According to our field experience of the past 15 years *Chelonoidis carbonaria* prefers a relatively more humid micro-habitat within the xerophytic forest of the Dry Chaco. Typically, these are areas where compacted soils allow water to accumulate, in depressions (*bajantes*), marking the riverbeds of temporary rivers such as the Río Verde or the affluxes of the Río Timané. This may be the reason for the absence of the species in large parts of the western Chaco where there is a predominance of sandy soils (e.g. region of Campo Loa, or the Médanos, both Dept. Boquerón). *Chelonoidis carbonaria* is often found in a relatively high density, an experienced person can find 5–10 per hour, in areas where populations are healthy.

With a high domed, black carapace and slender limbs unsuitable for digging, *Chelonoidis carbonaria* does not appear to be morphologically well adapted to life in a hot and arid environment. The flattened, light-coloured carapace and thick-scaled forelimbs of the Chaco tortoise (*C. chilensis*), represented in parallel evolution on other continents by the North American desert tortoise (*Gopherus agassizii*), the African spurred tortoise (*Geochelone sulcata*), and the central Asian steppe tortoise (*Testudo horsfieldii*) are more usually associated with arid environments. *C. carbonaria* however employs an interesting behavioural adaptation to compensate for these apparent morphological deficiencies, using abandoned burrows of the giant armadillo (*Priodontes maximus*) as protection from unfavourable weather conditions such as heat, drought, and cold (Vinke & Vinke, 2003, Fig. 6). Similar findings were also described from the Bolivian Chaco (Noss et al., 2013) where tortoises occupied burrows with a width of 20–100 cm (x = 39.7 cm, standard deviation 19.8) and a height from 17–200 cm (37.5 cm, 34.0). Eight of 27 surveyed burrows had been originally dug by a giant armadillo; the origin of the others is not mentioned. In the Paraguayan Chaco we have found up to five tortoises occupying a burrow at the same time – adults and subadults of both sexes together.

Red-footed tortoises are sedentary in the Paraguayan Chaco (Vinke & Vinke, 2003). In the Bolivian Chaco the home-range is between 50–600 ha (Noss *et al*., 2013, Montaño *et al*. 2013). In a restricted environment each tortoise seems to continually re-use the same burrow (Vinke & Vinke, 2012). Radio-tracked animals in the Bolivian Chaco used between 4–18 burrows over the course of a year (Noss *et al*., 2013). *Chelonoidis carbonaria* do not maintain their burrows; should they become unsuitable (by human or natural influence) they move to another one. If burrows fail to provide sufficient shelter for all the inhabitants, then some of them may move and others remain. We never have found young juveniles (< 20 cm) in a burrow that was occupied by adult tortoises. Under semi-natural conditions we have never observed aggressions between larger and smaller animals, so this may not be a mechanism of active displacement. One explanation is that large burrows with their larger entrances are less secure for smaller tortoises which are under greater predation pressure than adults. Furthermore juveniles can more easily find suitable shelters

under vegetation and in smaller burrows.

In the palm savannahs of the Humid Chaco the species is frequently found in higher grounds with both open and denser forests. The palm savannah frequently floods during the summer and these higher "islands" of bushy forest act as refuges for the tortoises. Within the forests the tortoises prefer places that contain a dense undergrowth of *Aechmea distichantha* ("karaguata") or other species of Bromeliaceae, which provide both food and shelter.

When foraging tortoises create clearly visible paths between their burrows and grazing and basking areas (Fig. 7). As the terrain which they inhabit is typically flat with sparse vegetation, the paths appear to serve primarily for orientation, providing visual and olfactory markers that help the tortoises to find their shared burrows in this monotonous landscape (Moskovits, 1985; Vinke & Vinke, 2003). However this does not mean that *Chelonoidis carbonaria* has a poor sense of direction or poor learning capability (Wilkinson *et al*., 2007). Standardized tests showed the species to be capable of social learning (Wilkinson *et al*., 2010) and solution of the reversal discrimination task (Smith, 2012).

Activity levels change according to environmental conditions. In winter the tortoises are relatively inactive, but they do not hibernate in its strict sense. Whenever the weather permits, they leave their burrows, and even when the forest is mostly bare of leaves, succulent plants provide them with food.

Unlike in other areas of the wide distribution, Paraguayan male *C. carbonaria* do not engage in combat when they meet and are tolerant of other individuals. Courtship behaviour is also significantly different (Vinke *et al*., 2008) lacking the ritualised head movements described by Auffenberg (1965) and Colvée (2002). There is no information about egg-laying and incubation times for wild Paraguayan populations, but observations of a group under semi-wild conditions revealed significant differences to the reproduction cycle published for populations of northern South America (Vinke & Vinke 2004b, Vinke *et al*. 2008).

Most egg laying takes place in late summer (late February to April) with isolated cases of eggs being laid during warm periods of winter (June–August). Clutch size in Paraguayan red-footed tortoises is is low in comparison to other

Figures 6-8. Natural history traits of *Chelonoidis carbonaria*. **6)** An abandoned den of a giant armadillo was used by a group of 4 *Chelonoidis carbonaria,* Defensores del Chaco National Park, Dept. Alto Paraguay. **7)** Broad paths made by *Chelonoidis carbonaria* serving for orientation. Defensores del Chaco National Park, Dept. Alto Paraguay. **8)** Hatchling leaving the breeding chamber.

tortoises of similar size, being 5–8 eggs (Vinke & Vinke, 2004b). The number of clutches laid in a year is unknown, but at least two seems likely. Hatching in Chaco populations takes place after the onset of the rains, which may start as early as September or as late as December. A clutch monitored under natural conditions hatched after

Figures 9-10. Threatening situations for *Chelonoidis carbonaria*. **9)** Remains of a barbecued individual at Defensores del Chaco National Park, Dept. Alto Paraguay. **10)** Individual resting during winter in an inappropriate shelter after the dens in the surrounding area had been destroyed, Defensores del Chaco National Park, Dept. Alto Paraguay.

322 days of incubation, in further clutches the exact data was not available, but seem to be between 10 months and a year (Vinke *et al*. 2008). Hatchlings leave the eggs with a weight of 17–45 g (mean 29.9 g Vinke *et al*. 2008, Fig. 8).

Threats

At first glance the conservation situation of *Chelonoidis carbonaria* does not seem to be of high concern. The species is present in several protected areas and has previously been considered "Least Concern" at the national level in Paraguay (Motte *et al*., 2009). Subsequently however the species was designated as "Vulnerable" during the **"**IUCN South American Turtle and Tortoise Red List Workshop, Rio Trombetas, Brazil, 10-14 Oct 2010" (van Dijk, pers. comm.) and "Endangered" due to habitat loss and degradation (A1c, A2c) in the Southern Cone at the IUCN Red Listing and Action Planning Workshop for Chelonians of the Southern Cone" in Filadelfia, Paraguay in 2012 (Vinke and Van Dijk, in preparation). The species is presumably in rapid decline in the oriental region where habitat alteration has been extreme and 97.3 % of the Paraguayan human population (approx. 6,562,000) live (Martí *et al*., 2011). The situation in the Chaco is more promising, but threats are increasing. By mid-2009 19.1 % of the Chaco territory had been converted to pasture and the process is accelerating, with deforestation rates often exceeding 1.000 hectares/day. It has been estimated that by 2025 all land that is suitable for agriculture and cattle farming outside of protected areas will have been cleared (Yanosky, 2013). With the distribution of *Chelonoidis carbonaria* closely associated with the developing area of the Chaco, pressure on the species is increasing rapidly.

As *Chelonoidis carbonaria* is unable to adapt to altered habitat, including the extensive cattle farms in the Chaco (Vinke *et al*., 2008), accelerating loss of habitat represents the most serious threat to the species. This can have a number of unforeseen consequences, for example on the genetic health of populations (Vargas-Ramírez *et al*., 2010). A 16 year population study in an insular forest fragment in Amazonia revealed a significant shift in population structure towards juveniles and significantly slower growth rates (Aponte *et al*., 2003).

Though the species is present in protected areas, it is worthy of note that effective enforcement of environmental law in these areas is not existent. Two rangers manage three National Parks (Medanos del Chaco, Defensores del Chaco, and Río Negro, Benítez, 2013), with a combined area of 13,580 km^2 (Torres s.a.).

In Paraguay the red-footed tortoise is consumed by the Aché (Hill & Pawde, 2000) and Ayoreo ethnic groups (Gayet, 2008). The Ayoreo consider the species a delicacy and this is true both for the Totobiegosode tribe, the last existing traditional nomadic Ayoreo group, as well

as Ayoreo groups which have adopted a settled lifestyle in towns (Fig. 9). Demands of indigenous hunting can effect tortoise populations and in the current conditions may be considered unsustainable, even when traditional methods are used (Strong, 2005). Gayet (2008) notes that large numbers of tortoises may be harvested during such trips (as many as 169 in a single day) and that dens, already in short supply, are habitually destroyed in the process thereby creating a longer term impact than the collecting trip itself (Fig. 10).

The third threat for *Chelonoidis carbonaria* is the pet trade. Although trafficking of wildlife without permits is strictly prohibited, *C. carbonaria* is frequently offered for sale door to door in the Chaco settlements. In the local market "Mercado 4" in Asunción (Paraguay's capital city) tortoises are offered for sale by wildlife dealers. During The Virgin of Caacupé festival (8 December), an event with up to 2,500,000 visitors, the species is traded in the city of Caacupé along with other native wildlife. During the CITES moratorium (September 2003 to February 2014) in combination with the CITES listing at Apendix II, the legal international market was closed so no trade statistics are available. However small numbers of Paraguayan Redfooted Tortoises, continued to be smuggled out of the country into the black market and make their way into the international pet trade.

Actions recommended

The most significant threat to the species is habitat destruction and degradation. For that reason the strengthening of the protected areas system is vital for the conservation of *Chelonoidis carbonaria*, thereby eliminating illegal trade through the effective enforcement of environmental law. Educational efforts should be undertaken to sensitize people against the purchase of wild animals at illegal markets and their removal from nature.

A good knowledge of the biology of the species is essential for effective conservation. *Chelonoidis carbonaria* was included as one of four Chelonians as a priority for research in the Southern Cone during the IUCN Red Listing and Action Planning Workshop for Chelonians of the Southern Cone, Filadelfia, Paraguay, April 2012 (Vinke & Van Dijk, in prep.). The taxonomic status of the Paraguayan populations requires investigation, even if the description of new species can sometimes imperil species (Stuart *et al*. 2006), this being especially important for possible repatriation of seized animals (Gaur *et al*. 2006). Population studies were also highlighted as a priority for investigation during the IUCN workshop (Vinke and Van Dijk, in prep.).

Regarding a possible reliance on the burrows of the Giant armadillo (*Priodontes maximus*), combined conservation efforts of herpetologists and mastozoologists could be productive.

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