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Origins of the Extinct, Subfossil Galápagos Giant Tortoises (*Chelonoidis niger*) of the Post Office Lava Tube (Inferior) of Floreana Island: Voluntary or Accidental Occupancy?

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ABSTRACT.– The origins of the remains of giant tortoises that have accumulated in vast quantities on the floors of caves in some locations where giant tortoises once lived have received only scant attention to date. The subfossil Galápagos Giant Tortoises (*Chelonoidis niger*) of Floreana Island's Post Office lava tube (inferior) are the main focus of this paper with supporting data obtained from other tortoise populations and locations. These remains have historically been explained, if at all, as the result of accidental falls (e.g., via pitfall traps). With the accumulation of greater knowledge of tortoise ecology and paleoecology the likelihood of voluntary cave entry and exit, sometimes by large numbers of giant tortoises (e.g., the Aldabra Atoll Giant Tortoises), also seems plausible. If followed by occasional blockages of exits by geological phenomena such as roof collapse the tortoises could be trapped within as well. An inquiry into the available evidence for the occurrence of both phenomena is the subject of this paper.

KEY WORDS: giant tortoises, lava tubes, subfossils, Floreana

INTRODUCTION

The Giant Galápagos Tortoises (*Chelonoidis niger* species complex) of Ecuador's Galápagos Islands are among the largest of extant land tortoises. They are also long famous for their role as ships' fare in the age of sail due to their ability to survive without sustenance for months in the ships' holds. A more detailed knowledge of their biology has gradually accumulated in more recent times (e.g., Blake et al., 2012; Blake et al., 2013; Blake et al., 2015; Caccone et al., 2002; Caccone et al., 1999; Pritchard, 1996, 2007; Rick and Bowman, 1961). However, relatively little has been published concerning the extinct subfossil forms including the specimens of *Chelonoidis niger* obtained from the Post Office lava tube of Floreana Island (= Charles or Santa Maria) in the Galápagos Archipelago. Hundreds of their remains are scattered on the floor of this cave-like lava tube. Townsend (1928) and Steadman (1986) suggested the tortoises fell through the ceiling "pitfalls" and became trapped, resulting in death from injuries sustained in their fall or eventual starvation. We herein challenge their explanation of the tortoises' means of entry, and suggest an alternative explanation for some of the tortoises present in the lava tube.

MATERIALS AND METHODS

Literature Search

The methodology of Brown et al. (2008) was employed to obtain a maximum number of relevant references concerning the subject matter of this paper. Searches employing numerous combinations of search words and the search engines Google, Google Scholar (Advanced Scholar Search), and JSTOR Advanced Search were used along with traditional library-based searches of paper sources at Illinois State University's Milner Library, and in LEB's and DM's personal herpetological and paleontological libraries.

Scientific and common names follow those designated by the Turtle Taxonomy Working Group (2017).

Collecting History and Location of Specimens

In 1928, Townsend (Director of the New York Aquarium) visited Floreana, one of the southern Galápagos Islands (Latitude: -1° 17' 30.60" S; Longitude: -90° 26' 1.79" W), where he observed hundreds of subfossil fragments of tortoises in a lava tube cave (Post Office lava tube [inferior]) on the northwest side of the island, and collected 12 nearly complete shells of extinct Giant Tortoises (*Chelonoidis niger*). The following year, 1929, K. P. Schmidt (Field Museum of Natural History) and S. N. Shurcliff also explored this same lava tube and found three additional shells in "perfect condition" which had apparently been overlooked previously (Shurcliff and Schmidt, 1930). The Field Museum tortoises with nearly complete shells include FMNH 13522 (now MCZ Herpetology R-32098) and FMNH 13523 (2 specimens). A number of carapaces and other subfossil material are held by the American Museum of Natural History and Harvard University's Museum of Comparative Zoology (D. Dickey, pers. comm.; Poulakakis et al., 2008).

Description of Study Area

Lava tubes are cave-like structures associated with effusive volcanic eruptions of low viscosity basalt lavas (Carlquist, 1980). They are formed by flowing lava and may be subterranean or formed by crusting-over of surface lava channels. They may have complex branching and can have a more or less horizontal or downslope surface opening (i.e., window) through which the liquid lava within may escape, leaving a hollow tube. It has also been observed that if a surface window does form, the still-flowing lava may rebuild it and not flow out. At other times, overflow may occur draining the tube (Greeley, 1971a; Jagger, 1921). Roof collapse may eventually block the tube when it is void of lava. When this occurs near the original surface opening, a secondary opening may split off creating a steep, vertical, well-like hole.

Post Office lava tube was described in detail by Townsend (1928) and Steadman (1986). There are two elongate branches ("inferior" and "superior") that are now separated from one another by a massive roof collapse. The inferior branch contains most of the tortoise remains. Its opening to the surface was also formed by a roof collapse. This opening is ca. 12 ft. (3.7 m) in diameter and was half-concealed by bushes. Ground level beneath the entrance is ca. 20 ft. (6.1 m) deep. One side of the opening has a steep slope (Townsend, 1928).

RESULTS AND DISCUSSION

The Tortoise Turnstile Scenario

Townsend (1928), echoed by Steadman (1986), stated that the tortoises found in the Post Office lava tube (inferior) must have entered by falling through the near-vertical opening left by the collapsed roof section described previously. This would presumably have occurred after the major roof rock fall blocked the liquid lava exit pathway that previously allowed any tortoises to enter and leave the lava tube at will.

Townsend (1928) suggested that, "With a steep slope at one side the unluckly [*sic*] tortoise that tumbled in did not necessarily strike bottom with a fatal crash but rather rolled down an incline it could not ascend." As the shells of most Giant Galápagos Tortoises are thick, hard, and tough (except the Pinta Tortoises [*Chelonoidis abingdonii*]), most individuals falling ~6 m into the lava tube in this manner would be unlikely to be seriously injured, if at all. Without an accessible exit these tortoises would be doomed to eventually die of starvation or other stresses in the lava tube. (The collapsed roof section in the Post Office lava tube [superior] descended at a shallower angle, resulting in fewer tortoises being trapped than in the inferior tube [Steadman, 1986]).

When Townsend (1928) and even Steadman (1986) conducted their research there was very limited ecological or paleo-ecological information available concerning Giant Galápagos Tortoises, or, indeed, tortoises in general. As more knowledge has accumulated it has become apparent that another explanation for some of the tortoises present in the Post Office lava tube is plausible: the tortoises could have voluntarily entered the lava tube, and were subsequently trapped within by some geological phenomenon such as a roof collapse or landslide.

Caves provide favorable environments for some species of extant tortoises. The caves' other fauna may benefit from their presence also. For example, the large amount of dung produced by Aldabra Tortoises in the caves they visit seems to feed resident crabs and insects (Baxter, R.; Blake, S. and Hansen, D. *in* [Bittel, J., 2016]). It is reasonable to assume that this could have been the case for some extinct species also.

Moll and Brown (2017) reviewed and summarized examples of several extant tortoise species known to utilize different forms of rock shelters, from large caves to crevices. This depended on the size, and sometimes age of the species in question. Protection from predators, heat and humidity fluctuation, cold temperatures, and use as hibernacula are common benefits for these species. Most interesting in the context of this discussion was the discovery of two caves on Grande Terre, Aldabra Atoll by D. Hansen and his research team from the University of Zurich that are used by many Giant Aldabra Tortoises (*Aldabrachelys gigantea*) to escape the potentially lethal afternoon heat on the atoll (see photos and text in Bittel [2016], Warne [2016], and photo by Dr. Dennis Hansen in Moll and Brown [2017]). Dennis Hansen (*in* Bittel, 2016) believed the use of these caves by tortoises was quite ancient based upon the extent of wear of the rock surfaces in and around the caves. The mid-day heat of Aldabra Atoll is an existential threat to tortoise survival there and shade is necessary for coping with the hottest parts of the day. As Bittel (2016) stated, "For giant tortoises living in the tropics you either find a way to get out of the sun or you die." Naturalists have observed small juvenile, and larger adult tortoises on Aldabra Atoll utilizing shade in rock crevices and under clumps of Tussock Grass, *Sclerodactylon macrostachyum*, or other shade-producing plant clumps (Bittel, 2016; Coe and Swingland, 1984; Pritchard, 2007). The Grande Terre caves, however, provide considerably more shade space in addition to those previously known shaded areas (accommodating up to 85 tortoises in the larger cave [Bittel, 2016]).

As the Galápagos, Seychelles, and Mascarene archipelagos are within the tropical latitudes, the resident giant tortoises must have coped with periods (if not daily exposure) of extreme heat. The use of caves would have been a natural, simple, behavioral mechanism to cope with heat stress where accessible caves are available.

Other reasons for tortoise aggregations in caves, related to possible social interactions among tortoises, and not just benefits provided by the cave itself are also possible, but have not yet been identified in tortoises (e.g., group mating behavior, kleptothermy, etc., have been observed in other reptiles congregating in caves and cave-like structures [S. Blake, *in* Bittel, 2016]).

There are few other recent observations of extant giant tortoises in caves. Pritchard (2007) recorded one very large, seemingly "deranged" Galápagos Tortoise (presumably *Chelonoidis becki*) encountered by a BBC film crew in a lava tube on Volcan Wolf, Isabela Island (=Albemarle Island). It was presumed to have fallen in from an opening above, but was unable to ascend the steep slope leading back to the surface.

Giant extinct tortoises which may have used caves for shelter (or were victimized by them) are known from Madagascar (two species of *Aldabrachelys*). One species, *A. grandidieri*, may have been associated with the caves of Andranoboka (north of Mahanjanga) according to Cheke and Bour (2014).

The Mascarene Islands (La Réunion, Mauritius, and Rodrigues) were inhabited by five species of giant tortoises of the genus *Cylindraspis* (one, two, and two species, respectively – Gerlach [2014]). All are now extinct, but one live female (species unknown) was captured in a cave on Round Island (22.4 km off the north coast of Mauritius) sometime after 1844 (Barkly, 1870 *in* Bour et al., 2014). Large deposits of their fossil and (mainly) subfossil remains litter the cave floors of all three main islands and some of their smaller satellites, including caves of limestone karst and volcanic (including lava tube) origin. The condition of the remains vary greatly due to the environments of the caves, the age of the remains, and the degree of disruption of the cave floors by animal and/or human traffic. In *Cylindraspis,* the generally more fragile morphology of the thin carapaces and lighter skeletal structure are quite different from most other tortoises (Bour et al., 2014; Hume, 2014). Moll and Brown (2017) found *C. vosmaeri* and *C. peltastes* of Rodrigues particularly interesting in regard to their possible voluntary use of caves as shelters since their remains are often extremely well preserved and articulated, with numerous complete or nearly complete sets of remains on cave floors despite their aforementioned fragility. Signs of damage which would probably result from falls are often not present, suggesting the possibility of voluntary entry into the caves.

Despite the long history of association between humans and *Cylindraspis* on the Mascarenes, and the existence of numerous published and unpublished accounts of observations of their natural history (e.g., Cheke and Bour, 2014), we are aware of only one historical observation related to voluntary cave use. Bellanger de Lespinay (1671) wrote (on La Réunion) "through an instinctual sense, two or three days before bad weather (referring to a cyclone), the birds, tortoises and other animals, withdraw into rocks or caves from which they do not leave until the bad weather has passed" (*in* Bour et al., 2014). Perhaps this should not be too surprising since scores of naturalists and trained researchers who have observed the Giant Tortoises of Aldabra Atoll over a period of many years failed to detect their impressive daily migrations to and from the caves of Grande Terre.

Shell fragments of the Giant North American Tortoise, *Hesperotestudo* sp., have been found in Crevice Cave and Tom Moore Cave in Perry County, south-eastern Missouri (Hawksley, 1986). The latter specimen was collected from the clay and gravel of a stream in the cave.

The remains of *Meiolania mackayi*, an Australasian Horned Turtle, have been discovered in the Pindaï Caves of New Caledonia (Bauer and Sadlier, 2000).

Finally, a bone of the Radiated Tortoise (*Astrochelys radiata*) with a tool cut on it was found in a cave on La Réunion. As this cave is beyond the range of this tortoise, and the cave had been disturbed previously by cave explorers (Bour, 1981), its transport to the site by humans is considered likely.

Before the Fall

A related issue when considering the origin of tortoise remains in caves is, why are there so many tortoises that have presumably fallen in? An obvious, partial answer is that animals have steadily fallen in through the pitfalls described above by Townsend (1928), Steadman (1986) and others in the Galápagos Islands, and *in* Bour et al. (2014) and Hume (2014) in the Mascarene Islands over the millennia that tortoises and caves have been present. Additional contributions could have been made through water transport of already dead animals into the caves (Hume, 2014), human transport for butchering, cooking, etc. (Bour, 1981; Cheke and Bour, 2014), or in the case of small tortoises, perhaps transfer as prey by cave-dwelling owls (Steadman, 1986). The sheer quantity of the remains which have been discovered in caves in the Galápagos and Mascarenes alone is staggering, however, and begs further inquiry.

Early observations by Gilbert White in Carr (1952) suggested that a pet tortoise was "… much too wise to walk into a well" and was perceptive enough to retreat from the rim of a precipice it had encountered. Yerkes (1904) conducted research that suggested terrestrial turtles hesitated to walk off platforms a foot (.305 m) in height and became even more apprehensive at greater heights, while aquatic turtles showed little concern about leaving the platform at similar heights. Case (1969), Patterson (1971) and Routtenberg and Glickman (1964) demonstrated experimentally that a variety of terrestrial turtles and tortoises were able to perceive and avoid deep visual cliffs. This degree of visual acuity, depth perception and judgement should make the likelihood of accidentally tumbling into a pitfall extremely unlikely, yet evidence in the caves suggests otherwise.

Golubović et al. (2013) conducted experimental studies of willingness to "step" off a 50 cm high step by Hermann's Tortoises (*Testudo hermanni*) from a rocky, rugged, island habitat compared to those from a lowland plain habitat in Macedonia. They found that significantly more tortoises from the rugged habitat were willing to take the plunge compared to those from the plain. Golubović et al. (2013) believed that the more rugged habitat required greater boldness in its resident tortoises in order to accomplish essential tortoise requirements (compared to lowland plain tortoises) even though risks were involved. Indeed, they observed tortoises in the field losing their balance and falling from steep cliffs they were attempting to ascend (non-fatally). They also found dead tortoises at the foot of 15-30 m high cliffs atop which they previously observed living, active tortoises had been present. Griffiths (2014) also recorded a fatal fall of an introduced Radiated Tortoise (*A. radiata*) a month after its release on Round Island in the Mascarenes. It had tumbled about 71 m down a rock slab and she considered such falls "… not uncommon for tortoises."

Many tortoise populations live in rocky, uneven environments and individuals must often travel extensively to meet their needs in spite of the possible dangers along the way (Calzolai and Chelazzi, 1991; Golubović et al., 2013; Longepierre et al., 2001). Individuals from populations in lowland plains and other less rugged habitats may be at a disadvantage if confronted with the opposite as Golubović et al. (2013) have demonstrated. Therefore, it is interesting that Miguel Castro and David Cavagnaro (in Pritchard, 2007), noted high mortality in (now extinct) Pinta Island Galápagos Giant Tortoises (mainly males) presumably resulting from falls into upland ravines. They suggested that grazing competition from introduced goats at lower altitudes had forced the tortoises to forage at higher altitudes in more rugged habitats where fatal falls into ravines would be more likely due to their lack of experience in coping with such obstacles in their movements. Despite their possible reticence in negotiating uneven, fractured terrain, the requirements for finding food, mates, etc., may have forced displaced lowland forms to take risks they would have declined in more normal times and habitats. Pritchard (2007) discounted their hypothesis, but Golubović et al. (2013) might have predicted such results if lowland populations shifted into higher altitudes, and more rugged habitats to which they were poorly adapted behaviorally. Pritchard (2007) argued that the upland tortoises were just the last remaining individuals of a once continuous population extending from the southern lowlands into the uplands. The lowland dwellers were the first to be decimated by collectors because of the greater ease in acquiring them there. The upland tortoises were able to survive a bit longer because the rugged uplands made collecting more difficult. The explanation for the demise of the last upland Pinta Tortoises may never be fully known.

Although the ravines in question did not lead into subterranean caverns, the likelihood of similar behaviors which could lead to cave entrapment seem plausible. Other factors could influence tortoise falls also. Male tortoises are often more active (Lagarde et al., 2002; Lagarde et al., 1999) and more agile than females (Bonnet et al., 2001), although Golubović et al. (2013) observed no significant difference in jumping ability between males and females from the populations tested in their study. Male Galápagos Giant Tortoises are known to chase females (Pritchard, 2007) and these higher male activity levels, and perhaps the distractions inherent in intersexual premating behavior (e.g., perhaps with females running into pitfalls to escape males, pursuing males entering the pitfalls, etc.) and intraspecific male combat, might increase their likelihood of stumbling into a pitfall trap. The overwhelming male bias in mortality in the Pinta ravines examined by Pritchard (2007) suggests greater male activity levels may be a factor, but the male-biased sex ratio observed in this dwindling population before its total demise (Pritchard, 2007) masks the significance of this factor. Many "surviving intact caves are well concealed with small, often precarious entrances" (Hume, 2014). These may increase their likelihood of remaining undetected by wandering tortoises, especially if partially concealed by bushes (e.g., Hume, 2014;

Steadman, 1986; Townsend, 1928). Individuals could also potentially seek an interior cave water supply, seek out potential mates inside, or seek shelter from the conditions experienced outside the cave. John B. Iverson (pers. obs.) has observed Red-Footed Tortoises (*Chelonoidis carbonarius*) using "borrowed" armadillo burrows for shelter and Branch (2012) has recorded the use of animal burrows as shelters by Cape tortoises (*Homopus areolatus* and *H. femoralis*). A tortoise which misjudged the depth of a "presumed" burrow and tumbled into a cave below could be interred permanently as a result. Giant Galápagos tortoise remains have been observed in deep crevasses formed by collapsed lava tubes (Hennessy, 2019). It is also possible that some tortoises could have been trapped in lava tubes by simply walking across their roofs, causing them to collapse. Some parts of their roofs are very thin and unstable because the rocks which form them are only held together by pressure exerted against each other. A giant tortoise could be heavy enough to initiate such a collapse (T. Banik, pers. com.).

Despite the accumulated direct evidence from living tortoises, and indirect evidence suggested by the subfossil remains from caves discussed in the Mascarene Islands (mainly), there are evidently researchers that have not considered voluntary cave ingress and use as a mechanism to explain the presence of fossil, subfossil, and/or recent remains in caves such as the Post Office lava tube (inferior) of Floreana Island. It is interesting that Bour et al. (2014) and Hume (2014), in the chapters in Gerlach (2014) that mainly deal with Mascarene Islands Tortoise cave remains, never mention the possibility of voluntary entry with the exception of the historical account by Bellanger de Lespinay (1671) quoted earlier. Even the presence of the intact or nearly intact remains of the La Réunion Island caves are attributed to falls or water transport (Hume, 2014). Uncertainty will always be an issue when attempting to reconstruct the past, but it can never be completely avoided in paleoecological research. Decisions must be based upon the best available evidence, and in this case the data suggest that some of the remains in these caves could have resulted from voluntary ingress and subsequent entrapment, in addition to, or instead of, accidental falls.

CONCLUSIONS

Water-, predator-, and human-mediated transport, accidental falls, and voluntary entry and subsequent entrapment are possible mechanisms resulting in the accumulation of tortoise remains in caves. Voluntary entry followed by entrapment appears to best explain the presence of some of the subfossil tortoise fauna of the Post Office lava tube (inferior). In order to determine which is the most likely explanation for the majority of the remains discovered in a particular location, the following suggestions are offered: 1) The condition and abundance of the shells should be scrutinized. The presence of many intact or nearly intact carapaces, plastrons, and delicate skeletal elements in a cave, especially those characterized by particularly thin shells and less sturdy skeletal elements (e.g., the Mascarene Rodrigues *Cylindraspis* [Hume, 2014] and the Pinta Island Galápagos Tortoises [Pritchard, 2007]) may suggest voluntary entry. 2) The geological and chronological history of the caves themselves should be considered in as much detail as possible to determine when and where travel in and out of the caves might have been feasible or not. The lava tube caves like Floreana's Post Office lava tubes would often have been likely to allow tortoise entry soon (geologically speaking) after their lava drained out through relatively horizontal or downslope openings described and portrayed by Carlquist (1980) and Greeley (1971a, b). Subsequent blockage by roof collapse and/or landslides would have obstructed such movement and entrapped tortoises within, while pitfall openings in the ceiling would allow only one-way entry from above in the future. Sophisticated dating techniques should be employed to pinpoint the timing of those phenomena and to evaluate the resulting tortoise mortality patterns. For example, the presence of large numbers of subfossil tortoises of the same geological age within a cave might suggest voluntary entries, and subsequent entrapment within (or perhaps a mass mortality event followed by interment). Accidental entry by falls and other types of misjudgment may be suggested by the presence of subfossil tortoises of various age periods, perhaps in different strata on the cave floor. 3) Preferably, the cave floor remains should be undisturbed by animal and/or human intrusion and excavation until investigations of the above phenomena are initiated. Analysis of the tortoises' stratification patterns on and within the cave floor, and the opportunity to apply appropriate dating techniques upon the remains for comparison with the timing of critical geological phenomena would be particularly informative. Finally, 4) The exploration of new, untouched, cave systems to accumulate more relevant data (as suggested by Hume [2014] on Rodrigues) would provide more data for comparison with previously available material.

Few or no caves would be expected to provide all of the necessary criteria to establish a completely certain explanation for the origins of its fossil or subfossil tortoise fauna. The more criteria evaluated, as described above, that suggest the likelihood of one explanation over another would be extremely valuable in contributing to a consensus viewpoint concerning the cave faunas' origins. This approach would surely be better than automatically assuming that all the tortoises within result solely from accidental entrapment by pitfall or other involuntary means. Voluntary cave use by extant tortoises is too prevalent and widespread to be excluded from consideration in paleoecological research designed to elucidate use patterns of the past.

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