

Short Note

Cabo Verde giant gecko: how many units for conservation?

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Abstract. *Tarentola gigas* (Bocage, 1875) is the largest gecko living in the Cabo Verde Archipelago. It is subdivided into two subspecies, one confined to the Branco Islet, *Tarentola gigas brancoensis* (Schleich, 1984), and another to the Raso Islet, *Tarentola gigas gigas* (Bocage, 1875). These islets were classified as Integral Natural Reserves and further studies on the species are needed to outline more assertive conservation measures. Thus, this study aims to integrate for the first time genetic, morphometric and meristic data to test if there are significant differences between these two taxonomical groups that would support the subspecific designation. The results indicated that they are two closely related subspecies, with some visible differences in size and shape, possibly related to diet, habitat conditions or drift. Given the conservation status of the species, this should be further investigated, aiming an adequate management of these two evolutionarily significant units.

Keywords: Desertas Islands, geckonids, genetics, morphology.

After the disappearance of the Cabo Verde giant skink *Chioninia coctei* (Duméril & Bibron, 1839), the Cabo Verde giant gecko *Tarentola gigas* (Bocage, 1875) is the most charismatic extant reptile of this archipelago. It has the largest size compared to the other gecko species in the country. In this archipelago, all *Tarentola* geckos are descended from Canary geckos, estimated to have reached Cabo Verde 7.7 million years ago, Ma (Vasconcelos et al., 2010). Slow differentiation, conditioned by habitat or genetic drift, resulted in the emergence of new species, such as *T. gigas* that emerged circa 3 Ma.

The first studies with *T. gigas* were based only on morphological data (e.g., Schleich, 1980, 1984; Joger, 1984). The results indicated the existence of two subspecies, *Tarentola gigas brancoensis* Schleich, 1984 on Branco Islet and *Tarentola gigas gigas* (Bocage, 1875) on Raso Islet. This species also stands out for having a lightened longitudinal line on the back, with five markings on greyish olive background, dark spots on the labial scales making an alternating light-dark pattern, and a dark grey iris with typical light bars at the back side of the orbits (Vasconcelos et al., 2012). Additionally, it differs from other related species, such as *Tarentola protogigas*, genetically, ecologically, behaviourally, and in its wider geographical distribution in the past (Vasconcelos et al., 2012, 2013).

Tarentola g. brancoensis has a lower body size and weight than *T. g. gigas*, a higher width/length ratio of the fourth finger and a shorter snout (Joger, 1984; Schleich, 1984). It was also mentioned that the first subspecies can sometimes show a more slender than wider head and a longer tail in comparison to snout-vent length (Schleich, 1984), lower number of scales

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around the midbody, and more often a vertebral stripe than the latter (Joger, 1984). The first lives under sandstone blocks, at low altitudes near the rocky coast, in pits and fissures of volcanic rocks, and in the sandy ravines of gravel and shells, along the south coast of Branco (Schleich, 1980). The latter inhabits the low altitudes and shoreline areas on Raso, mainly in the southern part of the islet, and in cliff holes occupied by seabirds (Vasconcelos, 2015). The division of the subspecies seems to have little molecular support according to phylogeographic studies, which included a few samples of these taxa (Caranza et al., 2000; Jesus et al., 2002; Vasconcelos et al., 2010, 2012). According to the Cabo Verde Red List, both are classified as Endangered (Schleich, 1996). According to the IUCN Red List, the species is classified as Endangered, threatened by natural disasters such as drought, climate change, human disturbance, and introduction of exotic predators (Vasconcelos, 2013). For these reasons, it is necessary to clarify the need of developing protection measures for the species on each islet. Studying the genetics and morphology of *T. gigas* to test if it has one or two evolutionary units provides a more solid foundation for the management measures to be implemented in those protected areas.

We sampled 30 individuals from each subspecies on Raso and Branco from May 6-11 and September 18-20 2017, respectively. We recorded the following morphometric variables following Vasconcelos et al. (2012): snout-vent length (SVL); head length from the rear of cranium to the snout and maximum head width (HL and HW); eye-ear and snout-eye distance (E-E and E-S), from posterior margin of the eye to anterior margin of the ear and from snout to anterior margin of the eye, respectively; and maximum ear width and length (EW and EL). We have excluded tail-related variables as many individuals presented it regenerated. All individuals were photographed for counting: the digital lamellae from the fingertip to the base of the fingers, from the 1st to the 5th, of the

right (RF1-5) and left front limbs (LF1-5) and of the right (RH1-5) and left (LH1-5) hindlimbs; the number of dorsal tubercles found in the left (LT) and right (RT) rows along the spine; and the average number of supralabial (SLS) and infralabial (ILS) scales to the level of the mid-eye. We have not taken colouration into account, as it is extremely variable. We sexed the geckos by the presence of hemipenes or more developed cloacal pouches in males (Barbadillo et al., 1999). We removed a tail portion of 10 individuals from each islet and stored it in 96% ethanol for genetic studies, resealing all individuals at the same site they were collected afterwards. We have deposited all photographs in MorphoBank: P3783 (M693453-M693673) and genetic sequences in GenBank (MW756998-MW757013; MW762618-MW762637).

We used PAST3 software (Hammer et al., 2001) to perform exploratory data analysis (boxplots) and statistical analyses (MANOVA) to test for differences between the meristic and morphometric variables of the two subspecies, considering all individuals and each sex separately. As morphometric variables are correlated with body size, we also used SVL-corrected variables for these analyses, by dividing the raw values per SVL. We performed the Cochran C-test to verify the homogeneity of the data.

Total genomic DNA was extracted using the ammonium acetate saline extraction method reported in Vasconcelos et al. (2012), followed by the amplification of cytochrome *b* (*cyt b*) and 12s rRNA mitochondrial (mtDNA) genes. The PCR primers used in amplification and sequencing were 12Sa and 12Sb for the 12S rRNA, and *cyt b*1 and *cyt b*2 for the *cyt b* (Kocher et al., 1989; Palumbi, 1996) and conditions described in Delgado (2019). Sequencing was performed on an automated Sanger sequencer and results were compared with sequences available in GenBank using Geneious (<https://www.geneious.com/>).

A network of non-rooted haplotypes based on the 95% parsimony method was constructed in TCS1.21 (Clement et al., 2000) with the final

manipulation in tcsBU (Múrias dos Santos et al., 2015). Genetic differentiation and population analyses were done using DnaSP5 (Rozas et al., 2003).

The morphometric data showed that *T. g. gigas* (*Tgg*) is larger than *T. g. brancoensis* (*Tgb*) and that males of both subspecies presented longer SVL than females (males: *Tgg* = 112.47 ± 9.17 mm; *Tgb* = 101.40 ± 0.75 mm; females: *Tgg* = 98.47 ± 6.15 mm; *Tgb* = 88.20 ± 0.79 mm; table 1, fig. 1A, supplementary table S1). We also found significant differences between taxa ($F_{1,56} = 30.231$; $P = 0.000$) and sexes in the SVL-corrected variables ($F_{1,56} = 49.144$; $P = 0.000$), but not when the two factors interacted. *A posteriori* tests revealed that *Tgg* specimens have, proportionally to SVL, higher values of HW, and lower values of E-E and E-S than *Tgb* specimens, whereas this latter ratio is higher in males than in females.

Regarding the results of the meristic variables, there were no significant differences in the labials or lamellae between subspecies or sexes. However, *Tgg* had a significantly higher number of tubercles than *Tgb* (LT $F_{1,56} = 49.65$; $P = 0.000$; RT $F_{1,55} = 45.68$; $P = 0.000$; fig. 1A, supplementary table S2).

The haplotype networks for both molecular markers showed a linear distribution and some haplotype sharing between subspecies (fig. 1B). For *cyt b*, we have recovered three haplotypes for each taxa. For the 12S we have recovered four haplotypes for *Tgb*, representing the first and the fourth unique haplotypes for this islet, and two haplotypes for *Tgg* (fig. 1B).

The population analyses showed that the differences in haplotypic and nucleotide diversity, number of mutations and unique variable site levels are substantially small, and more visible for the 12S. However, the nucleotide difference between taxa is greater and higher for *Tgb* than *Tgg* in 12S, but the inverse in *cyt b*. The Tajima's and Fu's test were not significant ($P > 0.10$), so we cannot infer about demographic expansions, linkage or selective sweeps.

Meristic variables showed that subspecies have few differences, although *T. g. gigas* is significantly larger than *T. g. brancoensis*, as described by Bocage (1875) and Schleich (1984). Consequently, as expected, *T. g. gigas* has more dorsal tubercles. Additionally, other morphometric variables, such as larger head width, as previously suggested by Schleich (1984), and lower eye-ear and snout-eye distances clearly distinguish the subspecies into two different groups. Those characters, together with some unique mitochondrial haplotypes, provide an updated diagnosis of the two *T. gigas* subspecies.

Maybe the conditions found in the habitat of each population can explain some of these differences. Raso has a larger flat area, so better mobility conditions for these geckos than on Branco, as the species prefers to move on flat surfaces or non-steep slopes (Schleich, 1984) and larger sizes and weights may be disadvantageous on steeper terrain such as those on Branco. Alternatively, drift may explain these differences if larger individuals from Branco colonized Raso by chance, leading to increased body sizes and relative increase in head posterior and lengths widths, as well as in the number of tubercles. Based on the molecular dating of the species and geological age of the islands, it is unclear if individuals arriving at the much younger islet of Raso had rafted directly from São Nicolau or Santa Luzia Island or by stepping-stone on Branco (Carranza et al., 2000; Ancochea et al., 2015). The ancestor of the species may have even first reached one of these islets, depending on the ocean currents of the past. As no DNA samples or morphological data of *T. gigas* extinct populations from Santa Luzia or São Vicente are available, neither gecko fossil records from São Nicolau, it is hard to support any of these alternative hypotheses. In addition, as Santa Luzia, Branco and Raso were later connected during Pleistocene sea level falls (Ancochea et al., 2015), what could have promoted increased drift effects and/ or gene flow

Table 1. Descriptive statistics (average, range and respective standard errors, SD) of the morphometric and meristic variables for females, males and all individuals of *T. g. gigas* and *T. g. brancoensis*: Check the text for details on the variables.

Code	<i>Tarentola gigas brancoensis</i> (Branco Islet)						<i>Tarentola gigas gigas</i> (Raso Islet)					
	Females		Males		All		Females		Males		All	
	mean ± SD	Range	mean ± SD	Range	mean ± SD	Range	mean ± SD	Range	mean ± SD	Range	mean ± SD	Range
SVL	88.20 ± 1.26	76.00–105.00	101.40 ± 1.37	87.00–114.00	94.80 ± 1.79	76.00–114.00	98.47 ± 1.12	89.00–108.00	112.47 ± 1.67	97.00–122.00	105.47 ± 1.91	89.00–122.00
HL	26.17 ± 0.33	24.24–31.11	29.41 ± 0.36	25.52–32.80	27.80 ± 0.44	24.24–32.80	27.65 ± 0.63	21.90–32.80	28.40 ± 0.46	27.10–36.50	29.79 ± 0.68	21.90–36.50
HW	15.59 ± 0.34	12.62–19.22	18.07 ± 0.42	13.40–21.17	16.67 ± 0.24	12.62–21.17	20.35 ± 0.40	17.40–24.30	20.96 ± 0.49	19.40–29.40	22.01 ± 0.54	17.40–29.40
E-E	09.15 ± 0.15	08.08–11.10	10.50 ± 0.18	08.47–12.45	09.83 ± 0.21	08.08–12.45	09.39 ± 0.11	08.10–10.20	09.86 ± 0.25	08.40–13.90	10.26 ± 0.25	08.10–13.90
E-S	24.19 ± 0.24	22.33–26.93	26.74 ± 0.31	23.71–29.86	25.47 ± 0.36	22.33–29.86	11.67 ± 0.19	09.60–12.90	11.45 ± 0.29	09.60–14.90	12.12 ± 0.25	09.60–14.90
EH	03.54 ± 0.13	02.25–04.92	03.89 ± 0.07	03.35–04.70	03.72 ± 0.11	02.25–04.92	03.63 ± 0.14	02.00–04.60	03.73 ± 0.10	03.30–04.90	03.88 ± 0.13	02.00–04.90
EW	01.68 ± 0.05	01.14–02.30	01.79 ± 0.12	01.38–02.99	01.74 ± 0.09	01.38–02.99	01.97 ± 0.11	01.00–02.90	01.90 ± 0.11	01.20–03.00	02.00 ± 0.11	01.20–03.90
SLS	17.50 ± 0.18	16–18	17.00 ± 0.28	16–20	17.18 ± 0.25	16–20	17.07 ± 0.19	15–19	16.26 ± 0.26	15–20	17.33 ± 0.22	15–20
ILS	14.75 ± 0.27	14–17	14.00 ± 0.18	12–15	14.27 ± 0.23	12–17	13.47 ± 0.17	12–15	12.45 ± 0.17	12–15	13.30 ± 0.17	12–15
LT	17.15 ± 0.46	14–23	18.70 ± 0.53	13–24	18.00 ± 0.52	13–24	23.27 ± 0.63	16–29	22.32 ± 0.40	19–27	23.23 ± 0.52	16–29
RT	16.54 ± 0.47	14–23	18.10 ± 0.51	12–22	17.33 ± 0.51	12–23	22.53 ± 0.69	16–29	21.95 ± 0.47	19–29	22.67 ± 0.58	16–29
RF1	16.23 ± 0.29	14–19	16.15 ± 0.27	14–19	16.19 ± 0.27	14–19	15.43 ± 0.17	14–17	14.68 ± 0.20	14–18	15.75 ± 0.19	14–18
RF2	16.36 ± 0.28	14–18	16.33 ± 0.32	14–20	16.35 ± 0.30	14–20	16.13 ± 0.19	14–17	15.01 ± 0.19	14–17	16.13 ± 0.19	14–17
RF3	15.93 ± 0.27	14–18	16.14 ± 0.17	15–18	16.03 ± 0.23	14–18	15.53 ± 1.26	13–19	14.36 ± 0.18	13–17	15.27 ± 0.22	13–19
RF4	16.36 ± 0.15	15–18	16.36 ± 0.15	15–18	16.38 ± 0.15	15–18	15.87 ± 0.17	14–17	15.04 ± 0.13	15–18	16.10 ± 0.15	14–18
RF5	16.40 ± 0.23	14–18	16.14 ± 0.21	15–19	16.28 ± 0.22	14–19	16.67 ± 0.32	12–19	15.44 ± 0.21	15–18	16.57 ± 0.27	12–19
LF1	15.73 ± 0.32	13–19	16.13 ± 0.34	13–20	15.93 ± 0.33	13–20	16.60 ± 0.19	15–19	15.11 ± 0.16	14–17	16.20 ± 0.19	14–19
LF2	16.13 ± 0.25	14–18	16.79 ± 0.26	14–19	16.44 ± 0.26	14–19	16.67 ± 0.20	15–18	15.36 ± 0.25	14–19	16.43 ± 0.22	14–19
LF3	16.00 ± 0.22	14–18	16.21 ± 0.13	15–17	16.10 ± 0.18	14–18	15.33 ± 0.16	14–18	14.59 ± 0.19	14–17	15.50 ± 0.18	14–18
LF4	16.33 ± 0.27	14–18	16.13 ± 0.19	15–18	16.23 ± 0.24	14–18	16.20 ± 0.16	15–17	15.05 ± 0.20	14–18	16.23 ± 0.18	14–18
LF5	16.13 ± 0.23	14–18	16.13 ± 0.26	13–18	16.13 ± 0.24	13–18	16.40 ± 0.22	15–18	15.37 ± 0.26	14–19	16.47 ± 0.23	14–19
RHP1	15.80 ± 0.27	13–18	15.92 ± 0.16	14–17	16.86 ± 0.21	13–18	16.40 ± 0.18	15–18	15.49 ± 0.20	15–19	16.53 ± 0.19	15–19
RHP2	16.13 ± 0.28	13–18	16.53 ± 0.18	15–19	16.33 ± 0.24	13–19	16.13 ± 0.22	15–19	14.98 ± 0.21	14–18	16.07 ± 0.21	14–19
RHP3	16.50 ± 0.27	14–19	16.21 ± 0.11	15–17	16.36 ± 0.20	14–19	15.33 ± 0.30	12–18	14.40 ± 0.18	14–18	15.47 ± 0.24	12–18
RHP4	16.13 ± 0.30	13–18	16.40 ± 0.20	15–19	16.24 ± 0.26	13–19	14.93 ± 0.22	13–18	14.39 ± 0.22	13–18	15.27 ± 0.22	13–18
RHP5	16.14 ± 0.26	14–18	16.07 ± 0.25	12–18	16.10 ± 0.25	12–18	15.93 ± 0.29	13–19	15.03 ± 0.27	14–19	16.03 ± 0.28	13–19
LHP1	16.13 ± 0.28	14–19	15.85 ± 0.31	13–18	16.00 ± 0.30	13–19	16.27 ± 0.19	15–18	14.69 ± 0.54	16–18	16.03 ± 0.40	06–18
LHP2	16.07 ± 0.21	14–18	16.47 ± 0.34	12–19	16.27 ± 0.28	12–19	15.87 ± 0.14	15–17	14.73 ± 0.45	18–18	15.93 ± 0.32	08–18
LHP3	16.27 ± 0.24	14–18	16.90 ± 0.18	14–18	16.28 ± 0.22	14–18	15.27 ± 0.15	15–17	14.72 ± 0.16	14–18	15.70 ± 0.15	14–18
LHP4	16.33 ± 0.23	14–18	16.00 ± 0.14	15–17	16.19 ± 0.20	14–18	15.27 ± 0.36	11–17	14.38 ± 0.18	14–17	15.50 ± 0.28	11–17
LHP5	15.93 ± 0.23	14–18	16.08 ± 0.29	14–19	16.00 ± 0.26	14–19	15.60 ± 0.18	13–17	14.63 ± 0.14	15–17	15.73 ± 0.16	13–17

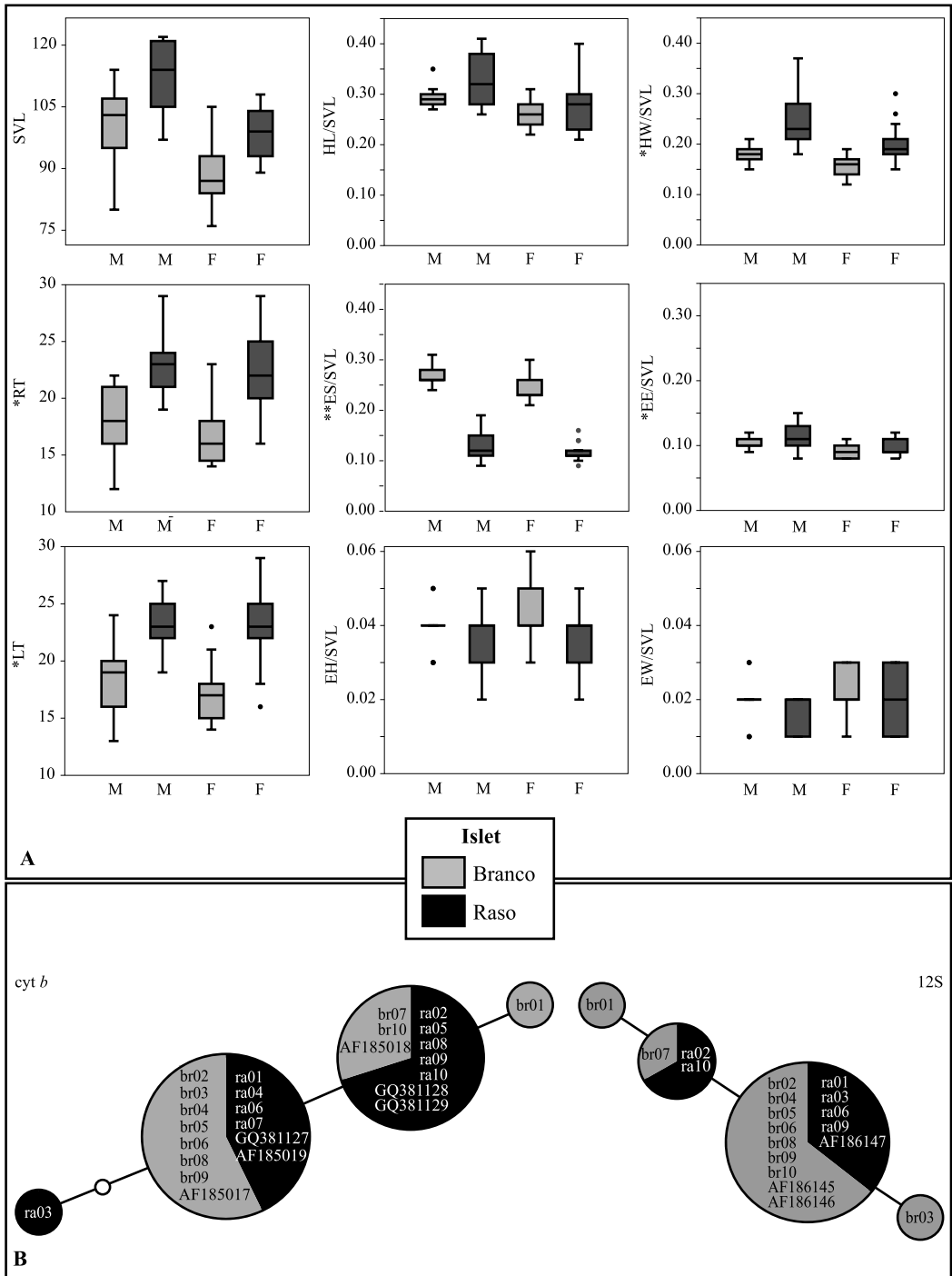


Figure 1. Results of the morphological and genetic analyses for individuals of *T. gigas* from Branco (in light grey) and Raso (in dark grey). **A**) Boxplots analyses results for morphometric and meristic variables (M, male; F, female; one asterisk marks the statistical significance between islets and two the statistical significance between islets and sexes). For correspondence with the variable codes, check table 1. **B**) Haplotype networks for the *cyt b* (left) and 12S (right) mitochondrial markers. Lines represent mutational steps and circles haplotypes. The size of circles is proportional to the number of individuals.

among populations, acting in opposite direction to divergent selection, it is even harder to clarify this. Hence, during either selective or random processes, these populations acquired mutations that resulted in the emergence of the observed differences between subspecies. Size differences could also be due to richer food supply or older age structure of Raso population, although empirical evidence (similar species richness and proportion of *T. gigas* juveniles of both islets) do not support those hypotheses.

According to the results obtained by Pinho et al. (2018), this species has a wide diet, ranging from plants, invertebrates to birds and fishes. In these bare and dry islets, survival is a huge challenge, which may explain the wide trophic niche of these geckos. In recent years, rainfall is more irregular and decreasing, that is, the availability of food is decreasing as well, affecting all species in this chain (Lopes et al., 2019). Notably, *T. g. gigas* developed a significantly larger head than *T. g. brancoensis*, which in contrast has a longer snout. This difference may be related to the type of food available in each habitat, or to another unknown reason. Raso is drier than Branco due to the lack of an altitudinal gradient that allows the retention of moisture from the clouds and the creation of niches with shade and/or wind protection (Freitas et al., 2015). Thus, it is reasonable to assume that Raso individuals may have been selected to eat harder, drier foods such as chitinous invertebrates or plants that are more fibrous, better adapted to arid environments. If so, then a wider head would allow a larger bite force that would ease preying on these diet items (Sagonas et al., 2014). The relationship between bite force and head width was already demonstrated for other species of the same genus (Massetti et al., 2017). The size and behaviour of available prey may also had driven changes in the size and shape of the head, as seen in other taxa (Walmsley et al., 2013).

Sex differences, in addition to size, are also related to the shape of the head, more specifically to the longer length of the snout of males,

even when excluding the effect of size. This result is interesting and may point to the existence of a different trophic niche between sexes, providing males with greater ability to prey larger or harder preys, as observed by other authors in other reptile groups (Walmsley et al., 2013) and Raso larks occupying the same habitat as *T. gigas* (Donald et al., 2003). It may also be related to other factors such as sexual selection (higher bite force of males for holding females for copulation or for deeper and louder vocalizations for calling females; Böhme et al., 1985; Sagonas et al., 2014) or natural selection between males (higher bite force for territorial fights; Sagonas et al., 2014).

At the genetic level, haplotype networks showed that Raso and Branco populations are of the same species, as they share haplotypes due to retention of ancestral polymorphisms (Vasconcelos et al., 2012). We thus proved that the subspecies are closely related, corroborating the results of Carranza et al. (2000), Jesus et al. (2002) and Vasconcelos et al. (2010, 2012) reported in previous phylogenetic and integrative taxonomy works. Therefore, this work supports the classification of these two evolutionary units as two *Tarentola gigas* subspecies following the integrative taxonomy framework, which claims that splits supported by only one line of evidence, morphology in this case, within infraspecific allopatric populations should be considered as different subspecies (Vasconcelos et al., 2012). The differences expressed in the phenotype arose from the need to adapt to the somewhat different habitat of each islet or due to genetic drift effects. Therefore, we recommend the use of microsatellites as well as other nuclear markers to confirm that the two taxa only recently diverged.

The population tests indicated that the difference in polymorphisms is very low. Considering that sampling of *T. g. gigas* was better spatially distributed than of *T. g. brancoensis* due to the flatter orography on Raso, it is possible to speculate that *T. g. brancoensis* presents a greater genetic diversity than Raso population.

While genetic results and based on meristic variables support some degree of overlap expected for not fully separated species, some linear measurements completely separate the specimens into two distinct groups. The Cabo Verde giant gecko is classified as an Endangered species according to national and international criteria; therefore, we recommend these geckos to be treated as two separate conservation units in the management and conservation plans of the Marine Protected Area of Santa Luzia, Raso and Branco. Moreover, we consider that it is crucial to investigate its spatial and ecological preferences, behaviour and life style, especially on Branco where the species was less studied.

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