2

3   **Stable isotopes and diet uncover trophic-niche divergence and ecological**

4   **diversification processes of endemic reptiles on Socotra Island**

5

6   Natalia Martín[a,b], Sergi Martínez[a], Eudald Pujol-Buxó[a], Amador Viñolas[c], Gustavo A.

7   Llorente[a], Carola Sanpera[a], Raquel Vasconcelos[d,e], Salvador Carranza[e], Xavier Santos[d,*]

8

9   [a] Departament de Biologia Animal, and Institut de Recerca de la Biodiversitat (IRBio),

10   Universitat de Barcelona, Barcelona, Spain.

11   [b] Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional.

12   (CIIDIR Oaxaca), Instituto Politécnico Nacional (IPN). Hornos 1003, Col. Nochebuena,

13   Santa Cruz Xoxocotlán, 71230, Oaxaca, México.

14   [c] Museu de Ciències Naturals de Barcelona. C/ Passeig Picasso s/n. 08003 Barcelona,

15   Spain.

16   [d] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO

17   Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, R. Padre

18   Armando Quintas 7, 4485-661 Vairão, Portugal.

19   [e] Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra). Passeig Marítim

20   de la Barceloneta 37-49, E-08003 Barcelona, Spain.

21

22   [*] Corresponding author: Xavier Santos. E-mail: xsantossantiro@gmail.com

23

Abstract: Ecological diversification on islands typically results in divergence of ecological niches. As diet is a major component of species niches, we hypothesize that sister species within island monophyletic groups diversify in their dietary preferences. We have examined this hypothesis in two *Haemodracon* and four *Hemidactylus* species endemic reptiles of from Socotra Island (Yemen), corresponding to two independent colonization events. Convergence i.e., similar dietary patterns of phylogenetically unrelated species, was also examined. Trophic niches were studied by the analysis of carbon and nitrogen stable isotopes combined with faecal samples. We collected tail tips (for isotopes) and faecal pellets during two visits in 2013 and 2014 to Socotra. Specific trophic niche widths inferred from stable isotopes were estimated from ellipse-based metrics, whereas interspecific differences were compared by linear mixed models and examined in a phylogenetic framework. From faecal samples, diet variation among species was quantified by the Bray-Curtis index. Isotope and dietary interspecific divergence was compared with Mantel tests. For both isotopes, models detected interspecific differences between sister species i.e., trophic niche divergence and also interspecific similarities of distant lineages that use similar microhabitats i.e., ecological convergence. We did not find any phylogenetic signal neither in the interspecific differences in δ^{13}C nor in δ^{15}N isotopic values; thus species phylogenetically more closely related did not have more similar isotopic niches. The Mantel test demonstrated similar interspecific divergence using isotopes and faecal samples. In a phylogenetic context, trophic-niche interspecific comparisons highlight some mechanisms that are driving ecological diversification and speciation of Socotra Island.

Key words: ecological diversification, endemism, reptile, Socotra, stable isotopes, trophic niche.

1. Introduction

Islands have long been recognized as natural laboratories to study the patterns of species diversification (Parent and Crespi, 2006; Grant and Grant, 2008; Losos and Ricklefs, 2009; Algar et al., 2013). Colonization of islands represents the opportunity for colonizers to find new resources unconstrained by mainland biota, then facilitating diversification in novel directions (Losos and Ricklefs, 2009). The degree of such a diversification can be mediated by inherent islands characteristics such as geological history, geographic location, size, and isolation time (MacArthur and Wilson, 1967; Del Arco et al., 2006; Fernández-Palacios et al., 2011). The absence of top predators, low species richness and short trophic chains are common rules on islands (MacArthur and Wilson, 1967; Losos and Ricklefs, 2009) that ultimately reduce antagonistic interactions and may facilitate ecological diversification. Ecological diversification and speciation on islands typically results in divergence of ecological niches (Nosil, 2012). Defined as the ways in which organisms obtain resources and interact with the environment, the ecological-niche concept has multiple components being diet and habitat use two major axes (Schoener, 1989). Thus, description of the realized niche (i.e. the subset of fundamental niche where species are restricted due to their interspecific interactions; Soberón and Nakamura, 2009) among phylogenetically related species may illustrate which are the drivers of ecological divergence and increase our understanding of mechanisms that govern intra-island speciation (Diamond, 1986; Losos, 2010). Independent lineages in islands (i.e. those resulted from independent colonization events) can develop similar diversification modes producing consistent patterns of eco-morphological convergence (Losos et al., 1998). This similarity among phylogenetically independent lineages could evidence similar evolutionary processes in response to

73   island environmental factors (Montaña and Winemiller, 2013), for example related to

74   exploitation of a limited set of available food and habitat resources.

75   In this study, we have described and compared the isotopic signature of six

76   reptile species inhabiting Socotra, by the quantification of carbon and nitrogen stable

77   isotope ratios. Stable isotope analysis (SIA) is a widespread tool in studies of diet

78   composition, trophic interactions, habitat use, and migration (Layman et al., 2007; Caut,

79   2013). SIA quantifies the ratio between any given element and its stable isotope.

80   Comparisons can then be made between isotopic ratios in tissues of different organisms

81   to make dietary or trophic level inferences. The most commonly used elements are

82   carbon (C) and nitrogen (N); the carbon isotope ratio ($\delta^{13}C$) changes minimally through

83   food webs (Rounick and Winterbourn, 1986), whereas the nitrogen isotope ratio ($\delta^{15}N$)

84   of a consumer enriched by ~3‰ relative to that in the diet (Minagawa and Wada, 1984).

85   Thus, $\delta^{13}C$ shows original carbon source of a consumer' nutrients (e.g. type of habitat),

86   and $\delta^{15}N$ estimates consumer relative trophic position (Post, 2002). SIA provides

87   insights into trophic relationships among organisms, and hence it has been an important

88   advance in food-web ecology dynamics (Layman et al., 2012). However, isotopic ratios

89   can vary according to a number of environmental and physiological factors, notably the

90   C3/C4 photosynthetic pathway of plant species (higher $\delta^{13}C$ values for C4 plants;

91   Rounick and Winterbourn, 1986) and precipitation rates (higher $\delta^{13}C$ values in more

92   arid zones; Kohn, 2010). SIA is an indirect characterization of organisms' diet, and

93   interpretation of isotope data is exposed to potential ambiguity (Layman et al., 2012).

94   Hence, environmental variation of sampling sites and additional data sets particularly

95   diet analysis are necessary to provide answers for questions regarding trophic ecology

96   of organism (Layman and Post, 2008). For this reason, we also examined faecal pellets

97   from a subsample of reptiles used in the isotope study. Isotope and diet studies in

98   parallel are adequate tools to examine dietary niche segregation (e. g. in cichlid fishes;

99   Genner et al., 1999; Hata et al., 2015) and convergence (cichlids and centrarchids;

100   Montaña and Winemiller, 2013).

101   This study was conducted in Socotra Island, the main island of an archipelago of

102   continental origin located in the northern part of the Indian Ocean and isolated from

103   Arabia in the Red Sea and Gulf of Aden around 30-17 Mya (Autin et al., 2013). The

104   island show an elevational / climatic gradient (arid in lowlands and more humid in

105   mountains), and two main lithologies, namely granitic and limestone (Fig. 1). Almost

106   all reptile species in Socotra are endemic (29 out 31; Razzetti et al., 2011; Sindaco et al.,

107   2012; Vasconcelos and Carranza, 2014), with phylogenetic studies demonstrating a

108   number of independent colonizers from the mainland that diversified on the island,

109   which then over time led to the current endemic species (Gómez-Díaz et al., 2012;

110   Badiane et al., 2014). Because of their low metabolic rate and resistance to dryness and,

111   in some groups, to salinity (e.g. geckos), reptiles are the second most capable vertebrate

112   group of colonizing islands after birds (Carranza et al. 2000). For this reason, they

113   represent a good model group to understand evolutionary patterns and processes of

114   island colonization and diversification (Losos and Ricklefs, 2009; Camargo et al.,

115   2010). The six gecko species studied, two species of the genus *Haemodracon* Bauer et

116   al., 1997 and four species of the genus *Hemidactylus* Oken, 1817, conform two

117   monophyletic lineages based on independent colonization events and further intra-island

118   diversification (Gómez-Díaz et al., 2012; Simó, 2012). *Haemodracon* is an endemic

119   Socotran genus and only these two species have been described. In contrast,

120   *Hemidactylus* is a widespread genus on the world with seven species occurring in the

121   island; from these species, only four were selected for this study according to their

122   phylogenetic relatedness within a single colonizer event (Gómez-Díaz et al., 2012).

123 Within an historical context, the description of their trophic niches is expected to

124 contribute to understand how the reptile ecological diversification occurred in Socotra.

125 Specifically we tested the hypothesis that there was trophic diversification between

126 phylogenetically related species, and eventual convergence between phylogenetically

127 unrelated ones.

128　　　To attain this general aim, the specific objectives and questions were: (i) to

129 describe the carbon and nitrogen isotopic ratios of two *Haemodracon* and four

130 *Hemidactylus* endemic geckos from Socotra Island; (ii) to examine whether isotopic

131 signatures are related to habitat selection (expectation of lower $\delta^{15}N$ ratios in vegetation

132 habitats for the foreseeable presence of more herbivorous arthropods which would be in

133 lower trophic levels; Layman et al., 2012), elevation (expectation of lower $\delta^{13}C$ values

134 at higher wetter altitudes; Kohn, 2010), and soil lithology (expectation of higher $\delta^{13}C$

135 values in limestone than igneous ground due to the rich carbon composition and sea

136 origin; Jardine et al., 1989), as sources of isotopic variation; (iii) within a phylogenetic

137 comparative framework, to examine the phylogenetic signal of the trophic niche

138 diversification within the six species studied; and (iv) to compare whether isotope and

139 dietary interspecific differences are related.

140

141 **Material and methods**

142 *2.1. Study area*

143　　　The Socotra Archipelago is located in the northern part of the Indian Ocean, 230

144 km NE of the Horn of Africa and 350 km south of Ras Fartak, on the Arabian coast

145 (Fig. 1). It has a total area of 3,625 km^2, and it is composed of a large main island,

146 Socotra, and three islets, Samha, Dharsa, and Abd al Kuri. This archipelago is a

147 fragment of the Gondwana Supercontinent, isolated in the Indian Ocean around 17-30

6

148   Mya (Autin et al., 2013). In 2008, Socotra was recognized as a World Natural Heritage

149   site by the United Nations Educational, Scientific and Cultural Organization (UNESCO,

150   2014), because of its singularity and endemism rate of flora and fauna. For example,

151   there are about 825 species of vascular plants, 307 of which are regarded as endemic

152   (Miller and Morris, 2004). Similarly, there is a high level of endemism of fauna (Van

153   Damme, 2009; Batelka, 2012). The lithology of Socotra Island consists of igneous

154   stones basically located on the Haggar Mountains, and limestones occupying the rest of

155   the island (Scholte and De Geest, 2010). Overall, the climate corresponds to the

156   boundaries of the monsoonal precipitation regime with mean annual rainfall being 216

157   mm (Scholte and De Geest, 2010) and mean annual temperatures ranging between

158   17.9°C and 28°C (Batelka, 2012). However, there is climatic variation along the

159   altitudinal gradient with arid climate up to 1000 m elevation and semi-arid conditions

160   due to the presence of fog and mist brought by sea winds from 1000 m to the top

161   Haggar Mountains at 1500 m. Accordingly, Socotra has a remarkably diverse vegetation

162   cover, with 19 land-cover classes (Král and Pavlis, 2006) and homogeneous land units

163   (Attorre et al., 2014), arranged on a geo-altitudinal gradient (De Sanctis et al., 2013). In

164   summary, De Sanctis et al. (2013) identified four main vegetation zones each of them

165   including several types of woody, shrub and herbaceous vegetation types: 1) between 0

166   and 200 m altitude, an arid coastal plain on alluvial substrata with shrubland and

167   grassland communities; 2) between 200 and 400 m, a transition zone; 3) between 400

168   and 1000 m, an arid limestone zone interspersed with hills and plateaus; and 4) between

169   1000 and 1500 m, a semi-arid upper zone of the Haggar mountains on a granitic

170   substratum.

171

172   *2.2. The reptile community and species sampling*

173   There are 31 reptile species, 29 of those endemic to the archipelago (Razzetti et

174   al., 2011; Sindaco et al., 2012; Vasconcelos and Carranza, 2014). Phylogenetic studies

175   have fixed the historical relatedness of Socotran to Arabian and Malagasian reptiles

176   (Schätti and Utiger, 2001; Nagy et al., 2003; Sindaco et al., 2012; Gómez-Díaz et al.,

177   2012; Badiane et al., 2014). Recent phylogenic studies suggested old colonization

178   events from mainland and further intra-island speciation (Gómez-Díaz et al., 2012;

179   Badiane et al., 2014).

180   Stable isotopes and diet were described in two groups of phylogenetically related

181   endemic species, all of them with nocturnal activity. The first group is composed of two

182   species of the endemic Socotran gecko genus *Haemodracon* (*H. riebeckii* [Peters,

183   1882]; and *H. trachyrhinus* [Boulenger, 1899]; Supplementary Materials S1) which

184   diversified on the island (Simó, 2012). The second group is composed by four gecko

185   species of the globally distributed genus *Hemidactylus* (*H. dracaenacolus* Rösler and

186   Wranik, 1999; *H. granti* Boulenger, 1899; *H. inintellectus* Sindaco et al., 2009; and *H.*

187   *pumilio* Boulenger, 1903; Supplementary Materials S1). These *Hemidactylus* species

188   form a monophyletic lineage resulting from intra-island speciation with a common

189   ancestor that originated by vicariance from Arabian mainland taxa ca. 14 Mya (Gómez-

190   Díaz et al., 2012). Other independent *Hemidactylus* transmarine colonization events

191   arrived more recently to Socotra (e.g. *H. oxyrhinus* Boulenger, 1899; *H. forbesii*

192   Boulenger, 1899; and *H. homoeolepis* Blanford, 1881; Vasconcelos and Carranza,

193   2014); the lack of samples and their independent origin were the reason to exclude these

194   species from analyses.

195   Field sampling was conducted between March and April in 2013 and 2014. Two

196   to four researchers systematically visited 34 sites throughout the island (Fig. 1). Sites

197   were chosen randomly in order to cover an altitudinal gradient, different habitat types,

198 and the two main lithologies of the island. Reptiles were collected by hand or noosing,

199 and tail tips of 87 specimens of the six focal species were collected for isotopic

200 analyses. Each reptile specimen was identified to species level, sexed and measured

201 (SVL, snout-vent length, accuracy= 0.5 mm). These specimens were gently palpated in

202 the abdomen, and pellets were collected from 59 of them. Major microhabitat type (i. e.

203 cliff, ground and vegetation) and geographic coordinates of each individual were

204 registered for further analyses. Cliff was assigned to geckos found on vertical positions

205 of big rocks and stony walls, and ground to specimens found on the ground or under

206 stones. Vegetation was assigned to geckos found on tree trunk or branches tree and

207 shrub. We acknowledge that this is a broad microhabitat classification; however in

208 Socotra there is relatively little microhabitat specialization among lizards compared to

209 that found in the tropics. Given the more generalist nature of the lizards in Socotra,

210 these broader categories seemed more useful when trying to detect different nitrogen

211 ratios for geckos found on vegetation due to the particular consumption of herbivorous

212 prey. Tail tips and pellets were transported to the laboratory for further analyses at the

213 Department of Animal Biology of the Universitat de Barcelona. All specimens were

214 released to the exact place of capture.

215

216 *2.3. Laboratory procedures*

217 Tail tips were used for the analysis of carbon and nitrogen stable isotopes

218 (hereafter $\delta^{13}C$ and $\delta^{15}N$). Since the carbon isotope ratio $^{13}C/^{12}C$ (expressed in standard

219 delta notation as $\delta^{13}C$) changes minimally (circa 1‰) as carbon moves through food

220 webs (Rounick and Winterbourn, 1986), it is commonly used to identify the source of

221 carbon in the tested individuals and ultimately at the base of the food web. In contrast,

222 the nitrogen isotope ratio $^{15}N/^{14}N$ ($\delta^{15}N$) in consumer's tissues is typically considered to

223　be enriched by circa 3‰ relative to that in the diet (Minagawa and Wada, 1984). It is

224　thus commonly used to estimate trophic position along food chains with increase

225　between 2 - 6‰ per trophic level (Caut, 2013). Thus, $\delta^{13}C$ can be used to track the

226　original sources of consumer nutrients, and $\delta^{15}N$ can be used to estimate a consumer

227　relative trophic position, i.e. higher $\delta^{15}N$ indicates higher trophic position (Post, 2002).

228　The data have not been corrected for diet-tissue discrimination since all the samples

229　were from the same tissues (tail tip). We acknowledge that it can be intra- specific

230　(size/age-related) differences in the discrimination factor within a single tissue (Steinitz

231　et al., 2015). To minimize such issues, we excluded any lizards with regrown tails from

232　the study.

233　　　　In the laboratory, tail tips were cleaned, dried and cut to very small pieces.

234　Subsamples were weighed to the nearest μg (0.25-0.5 μg) and placed into tin capsules

235　for $\delta^{13}C$ and $\delta^{15}N$ analyses. Analyses were carried out at the Serveis Científico-Tècnics

236　(Universitat de Barcelona, Spain) by means of a Thermo-Finnigan Flash 1112 (CE

237　Elantech, Lakewood, NJ, USA) elemental analyzer coupled to a Delta-C isotope ratio

238　mass spectrometer via a CONFLOIII interface (Thermo Finnigan MAT, Breman,

239　Germany). Stable isotope ratios were expressed in conventional notation as parts per

240　thousand (‰), using: $\delta X = ((Rsample/Rstandard) - 1) * 1000$, where X is ^{15}N, ^{13}C and

241　R is the corresponding ratio $^{15}N{:}^{14}N$, $^{13}C{:}^{12}C$. Reference materials from the International

242　Atomic Energy Agency (IAEA CH6, IAEA CH7 and USGS 24 for C, and IAEA N1,

243　IAEA N2 and IAEA NO3 for N) were inserted every 12 samples to calibrate the system

244　and compensate for any drift over time. $\delta^{15}N$ values are expressed relative to

245　atmospheric nitrogen (VAIR) and $\delta^{13}C$ values are expressed relative to Pee Dee

246　Belemnite (VPDB). Replicate assays of standards indicated analytical measurement

247　errors of ±0.1‰ and ±0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. For animals, there is a

248   strong effect of lipid content on δ^{13}C, resulting in lipid-rich tissues showing lower

249   carbon isotope ratios (Post et al., 2007). These authors suggest that C:N ratios higher

250   than 4 for terrestrial animals indicate high lipid content on the tissues analysed; in these

251   cases, lipid extraction would have little influence on the δ^{13}C values. In the Socotran

252   geckos examined, C:N ratios were similar among species and never exceeded 3.5 (Table

253   1), indicating low lipid content of tail tip samples.

254   In order to find the maximum differences between the six gecko species and to

255   correlate them with differences in isotopic signatures among species, diet remains from

256   pellets were photographed with an Olympus SZX10 stereoscope and identified at least

257   to the Order level. The examination of Coleopteran elytra allowed these items to be

258   identified at Family level. Some Hymenoptera items were classified to Family level by

259   distinguishing between ants (Fam. Formicidae) and other Hymenoptera. Unfortunately,

260   other arthropods could not be identified to a lower taxonomic level due to the

261   exoskeleton fragmentation. The maximum lengths of Coleopteran elytra were measured

262   with the program cellSens Standard 1.6. (2011). Samples were deposited in scientific

263   collections at the Universitat de Barcelona (UB) and the Natural Science Museum of

264   Barcelona (MCNB).

265

266   *2.4. Data analysis for isotopes*

267   The trophic niche width of each species was assessed by calculating several metrics

268   (Layman et al., 2007): the convex hull area (TA) occupied by all individuals of each

269   group in the δ^{15}N - δ^{13}C biplot, and the mean distance to the δ^{15}N and δ^{13}C centroid

270   (CD). The latter is the average Euclidean distance of each sample to the ellipse centroid,

271   and provides a measure of the average degree of trophic diversity within a particular

272   species. The application of these metrics can be biased according to sampling size and

273   the existence of extreme values; for this reason, Jackson et al. (2011) proposed the

274   calculation of the standard ellipse areas (SEA) with a correction for small sample sizes

275   (SEAc). This method applies a Bayesian approach that takes into account uncertainty of

276   the data, and allows at comparing isotopic community metrics between groups (Jackson

277   et al., 2011). For each species, the ellipse centroid is the mean δ^{13}C and δ^{15}N values

278   among the samples. Euclidean distances between ellipse centroids for the six species

279   studied (i.e. difference in centroid location) were assessed following Turner et al.

280   (2010). Two centroids occupied different locations (i.e. different trophic niches) if the

281   Euclidean distance between them is significantly greater than zero. We also calculated

282   the eccentricity (E; Turner et al., 2010) that gives insights into differences of the

283   distribution of δ^{13}C and δ^{15}N values within a particular species (i.e. a measure of the

284   covariation between both isotopes); thus, E = 0 means a circular ellipse and E = 1

285   describes a perfect relationship between both isotope values. Interspecific comparisons

286   of these metrics were based on analysis of nested linear models and residual

287   permutation procedures (RPP) implemented by Turner et al. (2010). SEAs were

288   calculated following Jackson et al. (2011) implemented in the R package SIBER

289   (Parnell and Jackson, 2013).

290   Sampling individuals at different locations can mask the identification of intra-

291   population niche variation (Araújo et al., 2007), and may inflate variation in isotope

292   values when sources vary spatially (Layman et al., 2012). Our aim was to examine

293   variation in isotopic signatures of six reptile species within a phylogenetic comparative

294   framework. Accordingly, knowledge of organisms' natural history can aid in the

295   interpretation of isotope data (Layman et al., 2012). Moreover, several sources of

296   isotope variation, i. e. lithology, altitude, microhabitat, and locality of capture, were

297   considered on statistical analyses. For example, species can segregate spatially by the

soil lithology since the island is mainly composed by two main soil lithologies, namely limestone of marine origin and igneous rocks (Scholte and De Geest, 2010). Isotope values (especially $\delta^{13}C$) can be very sensitive to differences between terrains of marine and terrestrial origin (Harding and Reynolds, 2014). Altitude and microhabitat were animals were collected was considered since some of the species considered segregate spatially according to these factors (Razzetti et al., 2011).

Plant photosynthetic pathways, i.e. C3 and C4 plants, are also source of carbon and nitrogen isotope variation (e.g. C4 species have enriched carbon isotope ratios relative to C3 species; Rounick and Winterbourn, 1986). How C3 / C4 plants are distributed along the geo-altitudinal gradient in Socotra could contribute to better understand the causes of isotope variation in the six reptile species studied. Unfortunately, C3 / C4 plant distribution in Socotra is unknown; likewise, the proportion in which arthropods (the main geckos' prey) are feeding on plants with different isotopic ratio is also unknown. This makes very difficult the predictability of isotopic variation with altitude. In contrast, there is general evidence that $\delta^{13}C$ values increase at smaller precipitation rates within C3 and C4 plants (Weiguo et al., 2005; Kohn, 2010). Accordingly, the potential isotopic variation in lizards placed at different altitudes can be explained by the climatic and altitudinal gradient observed in Socotra.

A complete barcoding analysis of reptile species from Socotra recently demonstrated high levels of cryptic diversity (Vasconcelos et al., 2016). Although we do not know potential ecological or morphological differences between cryptic species, for those species involved in our study, we only used specimens from the more widespread clade.

Differences in $\delta^{13}C$ and $\delta^{15}N$ values among the six species studied were examined by fitting Linear Mixed Models (LMMs) with the package nlme (Pinheiro et

323   al., 2014). LMMs were conducted separately for $\delta^{13}C$ and $\delta^{15}N$ as both values refers to

324   different trophic and habitat information. As potential fixed effects we included taxa,

325   altitude, soil lithology and microhabitat. Altitude of localities was included as a

326   continuous variable in the models as a potential covariable. The factor lithology was

327   included as a predictor variable with two levels: limestone and igneous. Microhabitat

328   where each reptile was collected was also considered as a categorical predictor with

329   three main types namely cliff, vegetation and ground, given that it could influence

330   isotopic signatures of specimens (Clementz and Koch, 2001). Locality was always

331   included as a random effect in order to account for lack of independence of isotopic

332   signatures of reptiles collected in the same localities. Sex were excluded as a factor

333   from the analysis as a preliminary MANOVA test demonstrated no sexual differences

334   within the six species studied ($F_{2,69} = 2.3$, $P = 0.06$).

335   In a first step, we fitted a full LMM with all taxa and all potential predictors

336   using maximum likelihood (ML) to subsequently evaluate each fixed effect using

337   likelihood ratio tests (LRTs). Therefore, we dropped from the model only the predictor

338   of interest in each case, obtaining AIC values for the full and simplified models, plus a

339   LRT and a p-value of the simplified model tested against the full model in each case. In

340   a second step, we examined particular effects and their interactions (e. g. the effect of

341   microhabitat on isotope ratios among species located on limestone sites). To conduct

342   these analyses, some species were removed (e. g. *H. pumilio* as it is only present in

343   ground microhabitats and *H. granti* only found in igneous lithologies) before refitting

344   and testing the terms of the model using the same procedures. In all cases we did

345   residual analysis of the models to discard geographic or non-random patterns in the

346   residuals, that is, patterns in the data that would not be explained by the models.

347   Snout-vent length (SVL) is a potentially interesting variable to be included in

348   LMM analyses since many reptile species show ontogenetic dietary shift, and this can

349   be reflected in variation of $\delta^{13}C$ and $\delta^{15}N$ signatures according to body size. A recent

350   study has demonstrated that for *Hemidactylus* and *Haemodracon* species from Socotra,

351   intra-island diversification resulted in great differences in body size (García-Porta et al.,

352   2016). Within the samples used in our study, the biggest individuals of some species

353   were smaller that the smallest individuals of others (Table 1). In parallel to this

354   morphological differentiation, the studied species experienced habitat segregation

355   (Supplementary Materials S2). For example, within the six species studied, the soil

356   specialists *H. pumilio* were the smallest species, vegetation species had intermediate

357   size, and a cliff species were the largest ones (*H. riebecki*). In order to avoid a collinear

358   effect between SVL and the habitat where species inhabit, we did not consider lizards

359   SVL in the LMM analyses. Analyses of isotopic data were done using R software (R

360   Core Team, 2014).

361

362   *2.5. A comparative analysis of intraspecific isotopic differences*

363   We examined the phylogenetic signal of the isotopic differences between the six

364   species studied. To conduct this analysis we first inferred an ultrametric tree using

365   Bayesian Inference with the software BEAST v.1.8.0 (Drummond and Rambaut, 2007)

366   (Fig. 2). The dataset included 371 base pairs of the 12S rRNA mitochondrial gene for

367   one representative of each one of the six species of geckos included in this study. Three

368   individual runs of 5×10^7 generations were carried out, sampling at intervals of 10000

369   generations. Models and prior specifications applied were as follows (otherwise by

370   default): model of sequence evolution for the 12S gene GTR+G (inferred with

371   jModeltest v.0.1.1; Guindon and Gascuel, 2003; Darriba et al., 2012); Yule process tree

372   prior; random starting tree; base substitution prior Uniform (0,100); alpha prior Uniform

373   (0,10). Posterior trace plots and effective sample sizes (ESS) of the runs were monitored

374   in Tracer v1.5 (Rambaut and Drummond, 2007) to ensure convergence. The results of

375   the individual runs were combined in LogCombiner discarding 10% of the samples and

376   the maximum clade credibility (MCC) ultrametric tree was produced with

377   TreeAnnotator (both provided with the BEAST package). The ultrametric tree was

378   loaded into R (R core team, 2015) using the functions from the package ape (Paradis et

379   al., 2004). Since the tests for phylogenetic signal are poor with a small number of

380   species, we tested for phylogenetic signal using two different indices. We estimated and

381   tested the significance of Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al.,

382   2003) indices using *phylosig* from the *phytools* package (Revell, 2012), which

383   incorporates individual variation (following Ives et al., 2007). We used the implemented

384   randomization tests (5000 iterations) to determine the significance level of both indices.

385

386   *2.6. Comparisons of diet, stable isotopes and genetic distances of gecko species*

387   From the abundance matrix of the taxonomic prey groups identified in the 59

388   pellets analyzed, dietary similarities between pairs of individuals were calculated with

389   the Bray-Curtis similarity index. An ANOSIM analysis was further performed based on

390   the Bray-Curtis similarity scores, using 999 random permutations. This test compares

391   how similar diets are among species, by giving a general R-value and further pairwise

392   comparisons between species. A Cluster Analyses was performed to visualize which

393   species have more similar diets.

394   To evaluate the completeness of the sampling, diversity accumulation curves

395   were calculated for the six species studied. Curves were computed with EstimateS

396   (Colwell, 2013), in order to eliminate the effect of the order in which the data is

397 included in the analysis (Moreno and Halffter, 2000). Diversity accumulation was

398 calculated by the Chao1 metric (Chao, 1984) which estimates taxa richness identified

399 from pellet analysis. Correlation between predator (reptiles) size (snout-vent length,

400 SVL) and prey sizes (maximum length of coleopteran elytra) was inferred from 33

401 elytra measured in the laboratory from pellets of four species: *H. riebeckii* (n = 4), *H.*

402 *dracaenacolus* (n = 13), *H. granti* (n = 3) and *H. inintellectus* (n = 13). We used

403 maximum length of coleopteran elytra as surrogate of coleopteran body length. Based

404 on data from elytra and body size measured from species of the same Families found in

405 pellets, the relative elytra length (and range) averaged 63.58% of the coleopteran size

406 (range 58,41% - 69,36%; A. Viñolas, unpublished data). We used coleopteran elytra as

407 this is the commonest prey type among the six geckos examined (see Results). Due to

408 the low sample size of some species, we pooled all the data in a single correlation in

409 order to get exclusively a general trend of the predator-size vs prey-size relationship.

410   Diet description is based on the pellets collected from specimens used for SIA.

411 We acknowledge that this subsample is not enough to describe the diet of the six target

412 species, but it is a useful approach to independently corroborate the reliability of

413 intraspecific differences in isotopes. The correlation between diet and stable isotope

414 values of the six gecko species analyzed was performed by Partial Mantel tests using

415 the genetic distance between species as a covariate. To run Mantel test, first similarity

416 matrices between pairs of species in stable isotopes (ISOT), diet (DIET), and genetic

417 distance (GENET) were performed. ISOT was calculated from the individual $\delta^{13}C$ and

418 $\delta^{15}N$ values of geckos using Euclidean Distances between pairs of species. DIET was

419 calculated from the matrix of relative abundances of prey types consumed by gecko

420 species using the Bray-Curtis index. Finally, GENET was calculated as the evolutionary

421 divergence over 37 published sequence pairs of the 12S mitochondrial gene among the

422   six studied species (Gómez-Díaz et al., 2012; Simó, 2012), and represented the average

423   number of base differences per site among species. There were a total of 376 base pairs

424   in the final dataset. This analysis was conducted in MEGA5 (Tamura et al., 2011). The

425   Partial Mantel test correlation of ISOT and DIET was performed with Passage 2

426   (Rosenberg and Anderson, 2011). To take into account the phylogenetic relations

427   among species, DIET and ISOT matrices were compared keeping GENET matrix

428   constant.

429

430   **2. Results**

431   *3.1. SVL and microhabitat of the target species*

432   Based on our own data set, the six species varied greatly in body size (see body-

433   size range in Table 1): *H. pumilio* and *H. trachyrhinus* were the smallest species,

434   individuals of *H. inintellectus*, *H. dracaenacolus*, and *H. granti* had intermediate sizes,

435   and *H. riebeckii* was the largest species (Supplementary Materials S2). In terms of

436   habitat preference, *H. pumilio* was a ground-dwelling specialist, *H. trachyrhinus* and *H.

437   dracaenacolus* were mostly or exclusively found on vegetation (i. e. *Cissus* bushes*,

438   Dracaena cinnabari* Balf. f. trees; respectively), and the rest of species largely occupied

439   vegetation or cliff habitats (Supplementary Materials S3). The six species also differed

440   in terms of altitudinal range (Supplementary Materials S4): *H. dracaenacolus* and

441   especially *H. granti* were highland species whereas the rest of species occur on

442   medium-high to lowlands (Razzetti et al., 2011).

443

444   *3.2. Stable isotope differences*

445   SEAc varied among the six species studied, being *H. trachyrhinus* and *H.

446   pumilio* the species with the largest and *H. dracaenacolus* and *H. granti* the smallest

447   areas (Table 2; Fig. 3). *Hemidactylus granti* showed the most different SEAc with no

448   overlap with the rest of species. *Haemodracon trachyrhinus* and *H. pumilio* partially

449   diverged with respect to *H. riebeckii*, *H. dracaenacolus* and *H. inintellectus* that almost

450   completely overlapped (Fig. 3). The distance between ellipse centroids was significantly

451   different of 0 for *H. granti* and *H. pumilio* with respect to the rest of species

452   (Supplementary Materials S5).

453   We also found interspecific differences in MDC and E. Thus, *H. trachyrhinus*

454   and *H. pumilio* had significantly higher MDC values than the rest of species ($p < 0.05$ in

455   all the comparisons), suggesting larger ellipses (Fig. 3). *Haemodracon riebeckii* differed

456   in E respect to *H. trachyrhinus*, *H. granti* and *H. dracaenacolus*, and *H. granti* and *H.*

457   *inintellectus* also differed ($P < 0.05$ in all the comparisons).

458   Likelihood ratio tests on LMMs showed that the only significant factor

459   explaining differences for $\delta^{13}C$ was Lithology (LRT = 18.96, $P < 0.0001$), whereas

460   Taxa, Habitat and Elevation were not significant ($P > 0.4$; Supplementary Materials S6).

461   Reptile samples collected on limestone had higher $\delta^{13}C$ values than those collected on

462   igneous localities. On a second step, we repeated LMMs for sites located in limestone

463   (*H. granti* excluded) and igneous soil (*H. riebeckii* and *H. dracaenacolus* excluded)

464   separately. In these new LMMs, we found interspecific differences both in limestone

465   (LRT = 11.53, $P = 0.02$) and igneous localities (LRT = 9.78, $P = 0.02$; Table 1). On

466   limestone localities, differences among taxa were motivated by high *H. trachyrhinus*

467   and *H. pumilio* $\delta^{13}C$ values (Fig. 4a), whereas on igneous localities by low *H. granti*

468     $\delta^{13}C$ values (Fig. 4a).

469   The LMM for $\delta^{15}N$ showed that microhabitat and elevation were influential

470   factors (LRT = 5.56, $P = 0.06$; LRT = 4.45, $P = 0.03$ respectively), whereas taxa and

471   lithology were not significant ($P > 0.1$; Supplementary Materials S6). Thus, we repeated

472   the LMMs excluding lithology and removing *H. granti*, because it was a species with

473   clear altitudinal segregation from the rest (Supplementary Materials S4), and *H.*

474   *pumilio*, because it was a species almost exclusively found on ground microhabitat

475   (Supplementary Materials S3). In this model, microhabitat maintained a significant

476   effect (Table 1, LRT = 5.66, P = 0.02) whereas elevation and taxa did not (P > 0.4).

477   Finally, in the LMM conducted with *H. inintellectus* and *H. riebeckii*, the only geckos

478   that were consistently found in two different microhabitats (cliff and vegetation), the

479   only significant effect was Habitat (LRT = 4.38, P = 0.04); whereas Taxa, Elevation and

480   the interaction Habitat x Taxa were not significant (P > 0.2). For both species,

481   individuals collected on cliff had higher $\delta^{15}N$ values than those collected on vegetation

482   (Fig. 4b).

483   We did not find any phylogenetic signal either in the interspecific differences in

484   $\delta^{13}C$ isotopic values (K = 0.256, p = 0.8; λ = 0, P = 1.0) or in $\delta^{15}N$ isotopic values (K=

485   0.191, P = 0.8; λ = 0, P = 1.0). In other words, phylogenetically closer species did not

486   have more similar isotopic niches.

487

488   *3.3. Diet description and isotope-diet correlation*

489   In total, 160 prey from 10 different arthropod orders were found as prey in gecko

490   pellets: Araneae, Pseudoscorpionida, Chilopoda, Hymenoptera, Heteroptera, Orthoptera,

491   Neuroptera, Homoptera, Blattodea and Coleoptera. The order Coleoptera was the

492   commonest group found in pellets (71 prey, 44.4%), and was represented by seven

493   families (Table 3). *Haemodracon riebeckii, H. dracaenacolus* and *H. inintellectus* were

494   the species with a greatest number of orders represented in their pellets (seven Orders

495   found in the diet within each these three species), while *H. granti* showed the lowest

496   number of groups in its diet (Table 3). *Hemidactylus granti* had the most different diet

497   since it was the only species that foraged on Cleridae and Histeridae beetles, and did not

498   present Araneae and Chilopoda on its diet (Table 3).

499   Accumulative curves of diversity for the six species studied showed different

500   shapes (Supplementary Materials S7). For some species, the number of pellets was too

501   low to account for a complete diet (e.g. *H. trachyrhinus*, *H. granti* and *H. pumilio*).

502   Accordingly, more samples would be required to have a complete view of the diet of

503   these geckos. Those species with a bigger sample size, *H. dracaenacolus* and *H.*

504   *riebeckii* showed low prey diversity; the asymptotic shape of the curve for these two

505   species suggested that the sample size was enough to describe their diet. In contrast, *H.*

506   *inintellectus* showed the highest diversity in the diet, although the shape of the curve

507   suggested that more pellets were needed to know the complete prey spectrum of this

508   species (Supplementary Materials S7).

509   The ANOSIM indicated significant interspecific differences in diet (r = 0.081, *P*

510   = 0.02). Pairwise comparisons indicated that pairs with the highest differences were: *H.*

511   *trachyrhinus - H. pumilio* (*r* = 0.333, *P* = 0.04), *H. riebeckii - H. granti* (r = 0.322, *P* =

512   0.003), *H. trachyrhinus - H. granti* (r = 0.550, *P* = 0.008) and *H. granti - H.*

513   *dracaenacolus* (r = 0.268, *P* = 0.001). The cluster tree showed four groups of species

514   according to their diet (Fig. 5)*: (1) H. granti*, (2) *H. pumilio*, (3) *H. trachyrhinus* and

515   finally (4) a group composed by the three biggest reptiles that commonly used vertical

516   environments (*H. riebeckii*, *H. dracaenacolus* and *H. inintellectus*).

517   The size of elytra ranged between 1-7 mm. As expected, smaller reptile

518   individuals foraged on smaller beetles, whereas the largest individuals foraged generally

519   on bigger prey. The correlation between predator size and prey size was significant (all

520   predators and prey pooled; r = 0.414, *P* < 0.0001). The individual that consumed the

521   largest prey was not *H. riebeckii* but *H. dracaenacolus*. Large individuals also

522   consumed small prey, this fact meaning that there was some potential competition

523   between species for small prey items.

524   The Partial Mantel test showed a correlation between DIET and ISOT matrices

525   with GENET matrix keeping constant (R = 0.49, P = 0.07, 999 permutations). This

526   means that the isotopic differences among species most probably reflected variation of

527   diet among the six gecko species examined in Socotra.

528

529   **3. Discussion**

530   *4.1. Intraspecific variation in isotope ratios and diets*

531   This study describes for the first time the trophic niche of six endemic lizard

532   species from Socotra using in tandem stable isotope and pellet analyses. The analysis of

533   carbon and nitrogen stable isotopes described a scenario of contrasted trophic niches for

534   some species and considerable overlap for others. The contrast is motivated by the soil

535   lithology of sampling localities (δ^{13}C values) but also by the microhabitat where

536   samples were collected (δ^{15}N values). When the lithology factor was controlled, some

537   species also diverged in their δ^{13}C values suggesting that isotope analyses may

538   contribute to identify interspecific trophic niche variation for Socotran reptiles.

539   We acknowledge that the isotopic signature of the six reptiles alone may not be

540   sufficient to infer their trophic position and carbon source without an appropriate

541   isotopic baseline, i. e. the isotopic signature of the food resources (Post, 2002).

542   Moreover, the time scale information for tail tip isotopes (the entire life of a gecko for

543   an original tail) versus faecal pellets (the last few days of an individual's diet) is

544   different. Despite these limitations, pellet analyses showed that the six species studied

545   were exclusively anthropophagous. And more importantly, the Mantel test demonstrated

546   that diet similarities between pairs of species were correlated to isotope similarities; this

547　last result showed parallelism between isotopes and diet despite the time scale

548　differences between both methods. The number of pellets used in this study was

549　unfortunately small in some species (e. g. *H. pumilio*), and diversity accumulation

550　curves suggest that more samples would be needed to know the complete dietary

551　spectrum of the six analyzed species. The diet description was not the objective of this

552　study since examination of pellets has a potential bias of information on reptile dietary

553　studies (Francesco et al., 1997; Pérez-Mellado et al., 2011). However, the pellets

554　examined were enough to identify some dietary differences that in turn were correlated

555　with the isotopic signatures. *Hemidactylus pumilio* and *H. granti* had the most different

556　diets probably related to the contrasted microhabitats (*H. pumilio* is the only typical

557　ground-dwelling species), and altitudinal range (*H. granti* is typically a highland

558　species) occupied by these species. The combination of pellet and stable-isotope

559　analyses showed differences in trophic niche position among the six Socotran geckos

560　studied.

561　　　　Why *H. granti* showed the most divergent isotopic values? After controlling for

562　lithology, the most likely explanation is that this species only occupies Socotran

563　highlands. According to Schmiedl and Mackensen (2006), $\delta^{13}C$ can vary depending on

564　the microhabitat occupied by the prey consumed by predators following environmental

565　aridity gradients. This seems observed both in C3 and C4 plants (Weiguo et al., 2005;

566　Kohn, 2010). Moreover, $\delta^{13}C$ ratio is higher in arid environments where C_4 plants

567　(higher $\delta^{13}C$ values; O'Leary, 1988; Farquhar et al., 1989) are more abundant as they are

568　more adapted to dry conditions than C_3 plants (lower $\delta^{13}C$ values). Although Socotra

569　shows variation in vegetation types according to a geo-altitudinal gradient (De Sanctis

570　et al., 2013), the distribution of C4/C3 plants and also which plant resources are

571　consumed by gecko's prey are unknown. However, lower $\delta^{13}C$ ratios for plants living in

more humid environments seem a general trend (Kohn, 2010), and moving up to the

food web, reptiles that live in more humid habitats are expected to have a lower δ^{13}C

ratio. Taking into account the marked precipitation (rainfall and mist) increase in

Socotra with altitude (Batelka, 2012), the lowest δ^{13}C values for *H. granti* matched the

distribution of this gecko at the highest (and more humid) sites of Socotra.

Interestingly, we found a significant effect of δ^{15}N according to the

microhabitats were species were primarily found. These differences accounted for

reptiles on cliffs and vegetation (higher values on reptiles collected on cliffs), and this

pattern persisted at the intraspecific level (e.g. between *H. riebeckii* and *H. inintellectus*

individuals collected on these microhabitats). We acknowledge that plant resources

could have disparate nitrogen tissue ratios, which then propagate up the food chain from

herbivorous arthropods to geckos. Although we now have information on arthropods

found in the diet of the gecko species from this study, we lack information of the plant

species fed upon by these various arthropods. δ^{15}N values consistently differ between

trophic levels (Minagawa and Wada, 1984). For this reason, differences at a

microhabitat level observed within our study species could indicate consumption of

prey types from different trophic position, perhaps related to prey type availability at

each microhabitat (e.g. more predatory arthropods in cliffs and more herbivorous

arthropods in vegetation). Indeed, our results would indicate that δ^{15}N values are

sensitive enough to detect interspecific differences in microhabitat use among Socotran

geckos.

Interspecific differences in microhabitat use and altitudinal segregation has

promoted several *Haemodracon* and *Hemidactylus* species to present different isotopic

niches. This argument is valid for *H. granti* (altitudinal segregation), *H. pumilio*

(ground-dwelling specialist) and *H. trachyrhinus* (small size and vegetation specialist).

597 The other three species, *H. dracaenacolus*, *H. inintellectus* and *H. riebeckii* have more

598 similar trophic niches. However, the examination of ellipse metrics gives new insights:

599 *H. dracaenacolus* has the smallest ellipse area (surrogate of trophic niche width) that

600 matches its ecological specialization. This gecko is listed as Critically Endangered

601 (IUCN, 2015) as only occurs on a reduced part of the island and lives exclusively on

602 *Dracaena cinnabari* trees (Razzetti et al., 2011). Extensive sampling on *Dracaena* trees

603 across the island indicated that *H. dracaenacolus* and the couple *H. inintellectus*/*H.*

604 *riebeckii* are not syntopic (authors, unpublished data). Thus, small ellipse area of *H.*

605 *dracaenacolus* would reflect microhabitat extreme specialization that in turn may be

606 related to ecological segregation among Socotran reptiles in face of evolutionary

607 diversification.

608

609 *4.2. Divergent trophic niches in a phylogenetic framework*

610   The analysis of isotope quantification and faecal samples for the six Socotran

611 geckos support some degree of trophic niche divergence. According to Losos and

612 Ricklefs (2009), sympatry and high population densities reached by island reptile

613 species induce competition for resources; in this scenario, selection may favor

614 adaptations that reduce competition between species, including morphological

615 divergence and resource segregation. Our results support this statement since within the

616 six species studied, we found trophic divergence linked to microhabitat and also

617 altitudinal (vicariance) segregation. For example, *H. dracaenacolus* and *H. granti*, two

618 species with contrasting trophic niches, have parapatric distributions possibly linked to

619 a vicariance process that occurred on the island approximately 2.3 Mya (Gómez-Díaz et

620 al., 2012).

621   We did not find a phylogenetic signal in the isotopic differences among the six

622   species studied. Thus, isotopic niche similarity between species of different genera

623   suggests that diet diversification is largely uncoupled from the phylogenetic

624   background. Although our sample is small (six species), this conclusion agrees with

625   those regarding the cichlid fish community at the Lake Tanganyika (Muschick et al.,

626   2012). The lack of phylogenetic signal seems a common pattern in evolutionary studies

627   of islands (Losos, 2008) because of the high rates of evolutionary diversification early

628   in the history of the new colonizers (Schluter, 2000). In contrast, phylogenetically

629   unrelated species like *H. riebeckii* and *H. inintellectus* have the more similar trophic

630   niches. They have rather comparable body sizes and were found in vertical

631   microhabitats (cliff and vegetation); this correspondence could suggest evolutionary

632   convergence that explains similarities between these species without having a common

633   phylogenetic origin. Convergent evolution in reptiles has been largely studied in

634   Caribbean *Anolis* lizards (Harmon et al., 2005) for which independent diversification at

635   each island produced a set of convergent (specialist) lizard forms. Patterns of ecological

636   convergence in independent lineages also have provided evidence for adaptation

637   involving morphological feeding traits in fish communities (Montaña and Winemiller,

638   2012). Futures studies with the whole reptile community in Socotra will examine

639   convergence within independent lineages that colonized the archipelago linking habitat

640   selection, diet and morphology.

641   Isotopic-niche comparisons of the six gecko species in a phylogenetic

642   framework (Gómez-Díaz et al., 2012; Simó, 2012) uncovered some diversification

643   mechanisms occurring in Socotra during intra-island speciation. Microhabitat,

644   altitudinal and body-size segregation have promoted Socotra to be an island with an

645   amazing and very rich endemic reptile community (29 species; Razzetti et al., 2011;

646   Sindaco et al., 2012; Vasconcelos and Carranza, 2014) despite its rather small surface

647   area (3,625 km^2) and aridity (Kier et al., 2009). This fact has promoted Socotra to be

648   considered the Galapagos of the Indian Ocean (Van Damme and Banfield, 2011; Hájek

649   and Bezděk, 2012). This study is the first attempt aimed at uncovering the ecological-

650   based mechanisms that have promoted reptile diversification in Socotra.

651

652   **Acknowledgments**

665

666   **References**

667   Algar, A.C., Luke, MD, Glor, RE, Losos, JB, 2013. Niche incumbency, dispersal

668   limitation and climate shape geographical distributions in a species-rich island

669   adaptive radiation. Global Ecol. Biogeogr. 22, 291-402.

670 Araújo, M.S., Bolnick, D.I., Machado, G., Giaretta, A.A., dos Reis, S.F., 2007. Using

671   delta C-13 stable isotopes to quantify individual-level diet variation. Oecologia

672   152, 643-654.

673 Attorre, F., Issa, A., Malatesta L., Adeeb, A., De Sanctis, M., Vitale, M., Farcomeni A.,

674   2014. Analysing the relationship between land units and plant communities: the

675   case of Socotra Island (Yemen). Plant Biosystems 148, 529–539.

676 Autin, J., Bellahsen, N., Leroy, S., Husson, L., Beslier, M., d'Acremont, E., 2013. The

677   role of structural inheritance in oblique rifting: Insights from analogue models

678   and application to the Gulf of Aden. Tectonophysics 607, 51-64.

679 Badiane, A., Garcia-Porta, J., Cervenka, J., Kratochvíl, L., Sindaco, R., Robinson,

680   M.D., Carranza, S., 2014. Phylogenetic relationships of Semaphore geckos

681   (Squamata: Sphaerodactylidae: Pristurus) with an assessment of the taxonomy of

682   *Pristurus rupestris*. Zootaxa 3835, 33-58.

683 Batelka, J., 2012. Socotra Archipelago a lifeboat in the sea of changes: advancement in

684   Socotra insect biodiversity survey. in: Hájek, J., Besděk, J. (Eds.), Insect

685   biodiversity of the Socotra Archipelago. Acta Entomol. Musei Nationalis Pragae

686   52, pp. 1-26.

687 Bauer, A.M., Good, D.A., Branch, W.R., 1997). The taxonomy of the southern African

688   leaf-toed geckos (Squamata: Gekkonidae), with a review of Old World

689   *Phyllodactylus* and the description of five new genera. Proc. California Acad.

690   Sci. 49, 447–497.

691 Blanford, W.T., 1881. Notes on the lizards collected in Socotra by Prof. I. Bayley

692   Balfour. *Proc. Zool. Soc. London* 1881, 464–469.

693 Blomberg, S.P., Garland, Jr T., Ives, A.R., 2003. Testing for phylogenetic signal in

694   comparative data: Behavioral traits are more labile. Evolution 57, 717-745.

695   Boulenger, G.A., 1899. The expedition to Sokotra. II. Descriptions of new species of

696   reptiles. Bulletin of the Liverpool Museums 2, 4–7.

697   Boulenger, G.A., 1903. Reptiles, in: Forbes, H.O. (Ed), The natural history of Sokotra

698   and Abd-el-Kuri. Liverpool- the free public Museum Henry Young & Sons

699   publ., London, pp. 75–104.

700   Camargo, A., Sinervo, B., Sites, J.W., 2010. Lizards as model organisms for linking

701   phylogeographic and speciation studies. Mol. Ecol. 19, 3250–3270.

702   Carranza, S., Arnold, E.N., Mateo, J.A., López-Jurado, L.F., 2000. Long-distance

703   colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia:

704   Gekkonidae), revealed by mitochondrial DNA sequences. Proc. R. Soc. London

705   Ser. B. 267, 637–649.

706   Caut, S., 2013. Isotope incorporation in broad-snouted caimans (crocodilians). Biol.

707   Open 2, 629-634.

708   Chao, A., 1984. Non-parametric estimation of the number of classes in a population.

709   Scandinavian J. Stat. 11, 265–270.

710   Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging

711   ecology with stable isotopes in tooth enamel. Oecologia 129, 461-472.

712   Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared

713   species from samples. Version 9. Persistent URL <purl.ocic.org/estimates>.

714   Darriba, D., Taboada, G.L., Doallo., R., Posada., D., 2012. jModelTest 2: more models,

715   new heuristics and parallel computing. Nat. Methods 9, 772-772.

716   De Sanctis, M., Adeeb, A., Farcomeni, A., Patriarca, C., Saed, A., Attorre, F., 2013.

717   Classification and distribution patterns of plant communities on Socotra Island,

718   Yemen. Appl. Veg. Sci. 16, 148–165.

719 DeNiro, M.J., Epstein., S., 1981. Influence of diet on the distribution of nitrogen

720   isotopes in animals. Geochimica Cosmochimica Acta 45, 341–351.

721 Del Arco, M., Pérez de Paz, P.L., Acebes, J.R., González-Mancebo, J.M., Reyes-

722   Betancort, J.A., Bermejo, J.A., De Armas, S., González, R., 2006.

723   Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands).

724   Ann. Botanici Fennici 43, 167-192.

725 Diamond, J.M., 1986. Evolution of ecological segregation in the New Guinea montane

726   avifauna, in: Diamond, J.M., Case, T.J. (Eds.), Community ecology. Harper &

727   Row, New York, pp. 98–125.

728 Drummond, A., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by

729   sampling trees. BMC Evol. Biol. 7, 214.

730 Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and

731   photosynthesis. Ann. Rev. Plant Physiol. & Plant Mol. Biol. 40, 503-537.

732 Fernández-Palacios, J.M., De Nascimiento, L., Otto, R., Delgado, J.D., García-Del Rey,

733   E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-

734   Macaronesia, with particular reference to the long-term biogeography of the

735   Atlantic island laurel forest. J. Biogeog. 38, 226-246.

736 Francesco, M.A., Luiselli, L., Rugiero, L., 1997. Food habits of the green lizard,

737   *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis.

738   Italian J. Zool. 64, 267-272.

739 Garcia-Porta, J., Morales, H.E., Gómez-Díaz, E,. Sindaco, R., Carranza, S. 2016.

740   Patterns of diversification in islands: A comparative study across three gecko

741   genera in the Socotra Archipelago. Mol. Phil. Evol. 98, 288-299.

742   Genner, M.J., Turner, G.F., Barker, S., Hawkins, S.J., 1999. Niche segregation among

743   Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecol. Let.

744   2, 185-190.

745   Gómez-Díaz, E., Sindaco, R., Pupin, F., Fasola, M., Carranza, S., 2012. Origin and in

746   situ diversification in *Hemidactylus* geckos of the Socotra Archipelago. Mol.

747   Ecol. 21, 4074-4092.

748   Grant, P.R., Grant, B.R., 2008. How and why species multiply: The radiation of

749   Darwin´s fiches. Princeton Univ. Press.

750   Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large

751   phylogenies by maximum likelihood. Syst. Biol. 52, 696-704.

752   Hájek, J., Bezděk, J., 2012. Insect biodiversity of the Socotra Archipelago. Acta

753   Entomol. Musei Nationalis Pragae 52, 1-557.

754   Hammerschlag-Peyer, C.M., Yeager, L.A., Araújo, M.S., Layman, C.A., 2011. A

755   hypothesis-testing framework for studies investigating ontogenetic niche shifts

756   using stable isotope ratios. PloS ONE 6, e27104.

757   Handley, L.L., Austin, A.T., Stewart, G.R., Robinson, D., Scrimgeour, C.M., Raven,

758   J.A., Heaton, T.H.E., Schmidt, S., 1999. The ^{15}N natural abundance (δ^{15}N) of

759   ecosystem samples reflects measures of water availability. Austral J. Plant

760   Physiol. 26, 185–199.

761   Harding, J.M.S., Reynolds, J.D., 2014. From earth and ocean: investigating the

762   importance of cross-ecosystem resource linkages to a mobile estuarine

763   consumer. Ecosphere 5(5), art 54.

764   Harmon, L.J., Kolbe, J.J., Cheverud, J.M., Losos, J.B., 2005. Convergence and the

765   multidimensional niche. Evolution 59, 409–421.

766 Hata, H., Shibata, J., Omori, K., Kohda, M., Hori, M., 2015. Depth segregation and diet

767   disparity revealed by stable isotope analyses in sympatric herbivorous cichlids in

768   Lake Tanganyika. Zool. Let. 1, 15.

769 Hopkins, III J.B., Ferguson, J.M., 2012. Estimating the diets of animals using Stable

770   isotopes and a comprehensive Bayesian mixing model. PLoS ONE 7, e28478.

771 IUCN, 2015. Categorías y Criterios de la Lista Roja de la IUCN. Versión 3.1. Comisión

772   de Supervivencia de Especies de la IUCN. IUCN, Gland, Switzerland &

773   Cambridge, UK.

774 Ives, A.R., Midford, P.E., Garland Jr, T., 2007. Within-species variation and

775   measurement error in phylogenetic comparative biology. System. Biol. 56, 252-

776   270.

777 Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche

778   widths among and within communities: SIBER - Stable Isotope Bayesian

779   Ellipses in R. J. Animal Ecol. 80, 595-602.

780 Jardine, P.M., Weber, N.L., Mccarthy, J.F., 1989. Mechanisms of dissolved organic

781   carbon adsorption on soil. Soil Sci. Soc. Am. 53, 1378–1385.

782 Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott,

783   W., 2009. A global assessment of endemism and species richness across island

784   and mainland regions. Proc. Natl. Acad. Sci. USA 106, 9322-9327.

785 Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of

786   (paleo)ecology and (paleo)climate. Proc. Natl. Acad. Sci. USA 107, 19691-

787   19695.

788 Král, K., Pavlis, J., 2006. The first detailed land-cover map of Socotra Island by

789   Landsat/ETM+data. Int. J. Remote Sensing 27, 3239-3250.

790 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope

791   ratios provide for community-wide measures of trophic structure? Ecology 88,

792   42-48.

793 Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E.,

794   Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M.,

795   Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an

796   overview of analytical tools. Biol. Rev. 87, 545-562.

797 Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the

798   relationship between phylogenetic relatedness and ecological similarity among

799   species. Ecol. Let. 11, 995–1007.

800 Losos, J.B., 2010. Adaptive radiation, ecological opportunity, and evolutionary

801   determinism. Am. Nat. 175, 623-639.

802 Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K., Rodriguez-Schettino, L., 1998.

803   Historical contingency and determinism in replicated adaptive radiations of

804   island lizards. Science 279, 2115–2118.

805 Losos, J.B., Ricklefs, R.E., 2009. Adaptation and diversification on islands. Nature 457,

806   830-836.

807 MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton

808   Univ Press.

809 McKechnie, A.E., 2004. Stable isotopes: powerful new tools for animal

810   ecologists. South Afr. J. Science 100, 131-134.

811 Miller, A.G., Morris, M., 2004. Ethnoflora of the Soqotra Archipelago. Royal Botanic

812   Garden, Edinburgh.

813   Minagawa, M., Wada, E., 1984. Stepwise enrichment of δ^{15}N along food chains: further

814   evidence and the relation between δ^{15}N and animal age. Geochimica

815   Cosmochimica Acta 48, 1135-1140.

816   Montaña, C.G., Winemiller, K.O., 2013. Evolutionary convergence in Neotropical

817   cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable

818   isotope analysis. Biol. J. Linn. Soc. 109, 146–164.

819   Moreno, C.E., Halffter, G., 2000. Assessing the completeness of bat biodiversity

820   inventories using species accumulation curves. J. Appl. Ecol. 37, 149-158.

821   Muschick, M., Indermaur, A., Salzburger, W., 2012. Convergent evolution within an

822   adaptive radiation of cichlid fishes. Current Biol. 22, 2362–2368.

823   Nagy, Z.T., Joger, U., Wink, M., Glaw, F., Vences, M., 2003. Multiple colonization of

824   Madagascar and Socotra by colubrid snakes: evidence from nuclear and

825   mitochondrial gene phylogenies. Proc. Royal. Soc. London B 270, 2613-2621.

826   Nosil, P., 2012. Ecological Speciation. Oxford Series in Ecology and Evolution. Oxford

827   University Press, New York.

828   O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. BioScience 38, 328–336.

829   Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401,

830   877-884.

831   Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and

832   evolution in R language. Bioinformatics 20, 289-290.

833   Parent, C.E., Crespi, B.J., 2006. Sequential colonization and diversification of

834   Galapagos endemic land snail genus *Bulimulus* (Gastropoda, Stylommatophora).

835   Evolution 60, 2311–2328.

836   Parnell, A., Jackson, A., 2013. SIAR: Stable Isotope Analysis in R. R package version

837   4.2. http://CRAN.R-project.org/package=siar.

838   Pérez-Mellado, V., Pérez-Cembranos, A., Garrido, M., Luiselli., L, Corti., C, 2011.

839   Using faecal samples in lizard dietary studies. Amph.-Rept. 32, 1-7.

840   Peters, W.C.H., 1882. Die von Herrn Dr. E. Riebeck auf Socotra gesammelten

841   Reptilien. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin

842   1882, 42–46.

843   Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2014. nlme: Linear and

844   nonlinear mixed effects models. R package version 3.1-118, URL:

845   http://CRAN.R-project.org/package=nlme.

846   Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods,

847   and assumptions. Ecology 83, 703-718.

848   Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña,

849   C.G., 2007. Getting to the fat of the matter: models, methods and assumptions

850   for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

851   PRIMER, 2001. Primer 5 for Windows version 5.2. PRIMER-E ltd.

852   R Core Team, 2015. R: A language and environment for statistical computing. R

853   Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-

854   project.org/.

855   Rambaut, A., Drummond, A., 2007. Tracer v1.4. Available from:

856   http://beast.bio.ed.ac.uk/Tracer.

857   Razzetti, E., Sindaco, R., Griego, C., Pella, F., Ziliani, U., Pupin, F., Riservato, E.,

858   Pelliteri-Rosa, D., Butikofer, L., Saeed, S.A., Awadh, A.B., Carugati, C.,

859   Boncompagni, E., Fasola, M., 2011. Annotated checklist and distribution of the

860   Socotran Archipelago Herpetofauna (Reptilia). Zootaxa 2826, 1-44.

861   Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and

862   other things). Methods Ecol. Evol. 3, 217-223.

863   Rosenberg, M.S., Anderson, C.D., 2011. PASSaGE: Pattern Analysis, Spatial Statistics
864   and Geographic Exegesis. Version 2. Methods Ecol. Evol. 2, 229-232.

865   Rosenblatt, A., Heithaus, M., 2013. Slow isotope turnover rates and low discrimination
866   values in the American alligator: implications for interpretation of ectotherm
867   stable isotope data. Physiol. Biochem. Zool. 86, 137-148.

868   Rösler, H., Wranik, W., 1999. Beiträge zur Herpetologie der Republik Jemen. 5. Drei
869   neue Gecko-Arten vom Sokotra-Archipel (Reptilia: Sauria: Gekkonidae).
870   Zoologische Abhandlungen Staatliches Museum für Tierkunde, Dresden 50,
871   249–265.

872   Rounick, J.S., Winterbourn, M.J., 1986. Stable carbon isotopes and carbon flow in
873   ecosystems. BioScience 36, 171–177.

874   Schätti, B., Utiger, U., 2001. *Hemerophis*, a new genus for *Zamenis socotrae* Günther,
875   and a contribution to the phylogeny of Old World racers, whip snakes, and
876   related genera (Reptilia: Squamata: Colubrinae). Rev. Suisse Zool. 108, 919–
877   948.

878   Schluter, D., 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

879   Schmiedl, G., Mackensen, A., 2006. Multispecies stable isotopes of benthic
880   foraminifers reveal past changes of organic matter decomposition and deepwater
881   oxygenation in the Arabian Sea. Paleoceanography 21, PA4213.

882   Schoener, T.W., 1989. The ecological niche, in: Cherrett, J.M. (Ed.), Ecological
883   concepts. Blackwell Scientific Publications, Oxford, pp. 79-113.

884   Scholte, P, De Geest, P, 2010. The climate of Socotra Island (Yemen): A first-time
885   assessment of the timing of the monsoon wind reversal and its influence on
886   precipitation and vegetation patterns. J. Arid Environ. 74, 1507-1515.

887   Simó, M., 2012. Diversificació intra-illa del gènere *Haemodracon* (Gekkota,

888   Phyllodactylidae) a l'arxipèlag de Socotra: una aproximació filogenètica,

889   ecològica i morfomètrica. Màster en Biodiversitat, Universitat de Barcelona,

890   Barcelona.

891   Sindaco, R., Metallinou, M., Pupin, F., Fasola, M., Carranza, S., 2012. Forgotten in the

892   ocean: systematics, biogeography and evolution of the *Trachylepis* skinks of the

893   Socotra Archipelago. Zool. Scripta 41, 346–362.

894   Sindaco, R., Ziliani, U., Razzetti, E., Carugati, C., Grieco, C., Pupin, F., Pella, F.,

895   Fasola, M., 2009. A misunderstood new gecko of the genus *Hemidactylus* from

896   Socotra Island, Yemen (Reptilia: Squamata: Gekkonidae). Acta Herpetologica 4,

897   83–98.

898   Soberón, J., Nakamura, M., 2009. Niches and distributional areas: Concepts, methods,

899   and assumptions. Proc. Natl. Acad. Sci. U S A 106, 19644-19650.

900   Steinitz, R., Lemm, J.M., Pasachnik, S.A., Kurle, C.M. 2016. Diet-tissue stable isotope

901   (Δ13C and Δ15N) discrimination factors for multiple tissues from terrestrial

902   reptiles. Rapid Communications in Mass Spectrometry 30, 9-21.

903   Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5:

904   Molecular Evolutionary Genetics Analysis using Maximum Likelihood,

905   Evolutionary Distance, and Maximum Parsimony Methods. Mol. Biol. Evol. 28,

906   2731-2739.

907   Turner, T.F., Collyer, M.L., Krabbenhoft, T.J., 2010. A general hypothesis-testing

908   framework for stable isotope ratios in ecological studies. Ecology 91, 2227–

909   2233.

910   UNESCO, 2014. http://whc.unesco.org/en/list/1263.

911   Van Damme, K., Banfield, L., 2011. Past and present human impacts on the

912   biodiversity of Socotra Island (Yemen): implications for future conservation.

913   Zool. Middle East. 54, 31-88.

914   Van Damme, K., 2009. Socotra Archipelago. Encyclopedia of Islands, pp. 846-851.

915   Vasconcelos, R., Carranza, S., 2014. Systematics and biogeography of *Hemidactylus*

916   *homoeolepis* Blanford, 1881 (Squamata: Gekkonidae), with the description of a

917   new species from Arabia. Zootaxa 3835, 501-527.

918   Vasconcelos, R., Montero-Mendieta, S., Simó-Riudalbas, M., Sindaco, R., Santos, X.,

919   Fasola, M., Llorente, G., Razzetti, E., Carranza, S., 2016. Unexpectedly high

920   levels of cryptic diversity uncovered by a complete DNA barcoding of reptiles

921   of the Socotra Archipelago. PLoS ONE 11(3): e0149985.

922   Weiguo, L., Xiahong, F., Youfeng, N., Qingle, Z., Yunning, C., Sheng, Z. 2005. δ^{13}C

923   variation of C3 and C4 plants across an Asian monsoon rainfall gradient in arid

924   northwestern China. Global Change Biol. 11, 1094–1100.

925 **Table 1:** SVL range (in mm), C/N proportion, and total isotopic mean values and standard error (SE) of $\delta^{13}C$ and $\delta^{15}N$ for the six Socotran

926 lizards examined and grouped by microhabitats where individuals were observed. Sample sizes (n) are also given.

	SVL range (mm)	C:N	Total $\delta^{13}C \pm SE$	n	Cliff $\delta^{13}C \pm SE$	n	Vegetation $\delta^{13}C \pm SE$	n	Ground $\delta^{13}C \pm SE$	n
Haemodracon riebeckii	66-118	2.92±0.05	-20.86±0.37	12	-20.35±0.54	7	-21.56±0.80	5		
Haemodracon trachyrhinus	23-42	2.99±0.03	-19.56±0.78	13			-19.56±0.50	13		
Hemidactylus dracaenacolus	31-75	2.95±0.02	-20.65±0.18	14			-20.65±0.48	14		
Hemidactylus granti	54-74	3.07±0.01	-23.23±0.28	6	-22.77±0.83	4	-23.47±1.27	2		
Hemidactylus inintellectus	35-64	3.09±0.03	-20.64±0.27	27	-20.63±0.32	22	-20.67±0.80	5		
Hemidactylus pumilio	21-33	3.06±0.02	-19.72±0.57	15					-19.72±0.57	15
			$\delta^{15}N \pm SE$	n	$\delta^{15}N \pm SE$	n	$\delta^{15}N \pm SE$	n	$\delta^{15}N \pm SE$	n
Haemodracon riebeckii			11.11±0.37	12	11.69±0.59	7	10.31±0.57	5		
Haemodracon trachyrhinus			11.46±0.37	13			11.46±0.35	13		
Hemidactylus dracaenacolus			11.01±0.28	14			11.01±0.34	14		
Hemidactylus granti			5.87±0.59	6	6.71±0.9	4	4.61±0.90	2		
Hemidactylus inintellectus			11.72±0.33	27	12.01±0.35	22	10.98±0.57	5		
Hemidactylus pumilio			9.97±0.48	15					9.97±0.48	15

927

928

929   **Table 2:** Total area (TA), Standard ellipse areas (SEA), standard ellipse areas corrected

930   for small sample size (SEAc), standard deviation (SD), and ellipse centroids as the $\delta^{13}C$

931   and $\delta^{15}N$ average values for the six gecko species examined.

932

					Centroids	
	TA	SEA	SEAc	SD	$\delta^{13}C$	$\delta^{15}N$
Haemodracon riebeckii	9.68	5.248	5.549	1.599	-20.858	11.125
Haemodracon trachyrhinus	22.045	11.397	12.647	3.276	-19.562	11.454
Hemidactylus dracaenacolus	4.33	2.331	1.872	0.645	-20.664	11.007
Hemidactylus granti	1.67	3.486	2.261	1.680	-23.040	5.880
Hemidactylus inintellectus	24.655	7.451	7.743	1.465	-20.633	11.715
Hemidactylus pumilio	25.945	12.035	13.371	3.187	-19.720	9.980

Table 3. Number (n) and abundance (%) of prey items per taxa for each studied species. * Coleoptera families; + Hymenoptera family; ° Hymenoptera infraorder. Total number of faecal samples examined is given between brackets.

| Taxa arthropods | Haemodracon | | | | | | Hemidactylus | | | | | |
| | H. riebeckii (n = 19) | | H. trachyrhinus (n = 5) | | H. dracaenacolus (n = 14) | | H. granti (n = 5) | | H. inintellectus (n = 13) | | H. pumilio (n = 3) | |
	n	%	n	%	n	%	n	%	n	%	n	%
Araneae	11	29.7	4	50.0	8	16.3	−		6	15.8	2	14.3
Pseudoscorpionida	−		−		−		−				7	50.0
Chilopoda	3	8.1	1	12.5	5	10.2	−		1	2.6	1	7.1
Hymnenoptera (total)	4	10.8	−		9	18.4	−		7	18.4	−	
Formicidae +	2		−		8		−		5		−	
Aculeata °	2		−		−		−		−		−	
Other Hymenoptera	−		−		1		−		2		−	
Heteroptera	−		−		−		3	21.4	1	2.6	−	
Orthoptera	2	5.4	1	12.5	1	2.0	−		1	2.6	−	
Neuroptera	2	5.4	−		−		−		1	2.6	−	
Homoptera	−		1	12.5	1	2.0	−		−		−	
Blattodea	1	2.7	−		3	6.1	2	14.3	−		−	
Coleoptera (total)	14	37.8	1	12.5	22	44.9	9	64.3	21	55.3	4	28.6
Curculionidae *	4		1		7		−		13		−	
Tenebrionidae *	5		−	−	1		−		1		1	
Sylvanidae *	1		−	−	4		2		2		−	
Chrysomelidae *	−		−	−	2		−		−		−	
Ptinidae *	−		−	−	3		−		−		−	
Cleridae *	−		−	−	−		1		−		−	
Histeridae *	−		−	−	−		2		−		−	

Other Coleoptera	4	–	–	5	4	5	3
TOTAL PREY	37	8		49	14	38	14

937 **Legend of Figures**

938 **Figure 1.** Location of the Socotra Archipelago, and locations where pellets (faecal

939 analysis) and tail (isotopic analysis) samples were collected from each of the six reptile

940 species studied. The elevations and soil types on Socotra are also depicted.

941 **Figure 2.** Phylogeny of the six Socotra gecko species included in the present study

942 based on sequences of the 12S rRNA mitochondrial gene (see Material and methods).

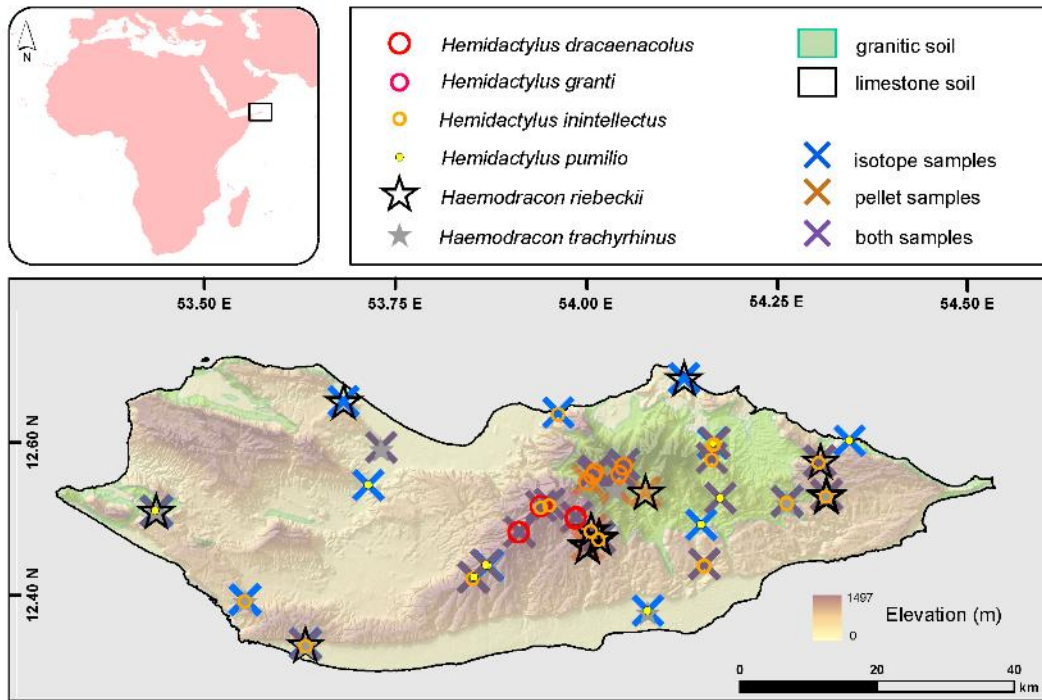943 Black points in nodes indicate posterior probability values > 0.95.

944 **Figure 3.** Standard ellipse areas based on δ^{13}C and δ^{15}N ratios of the six reptile species

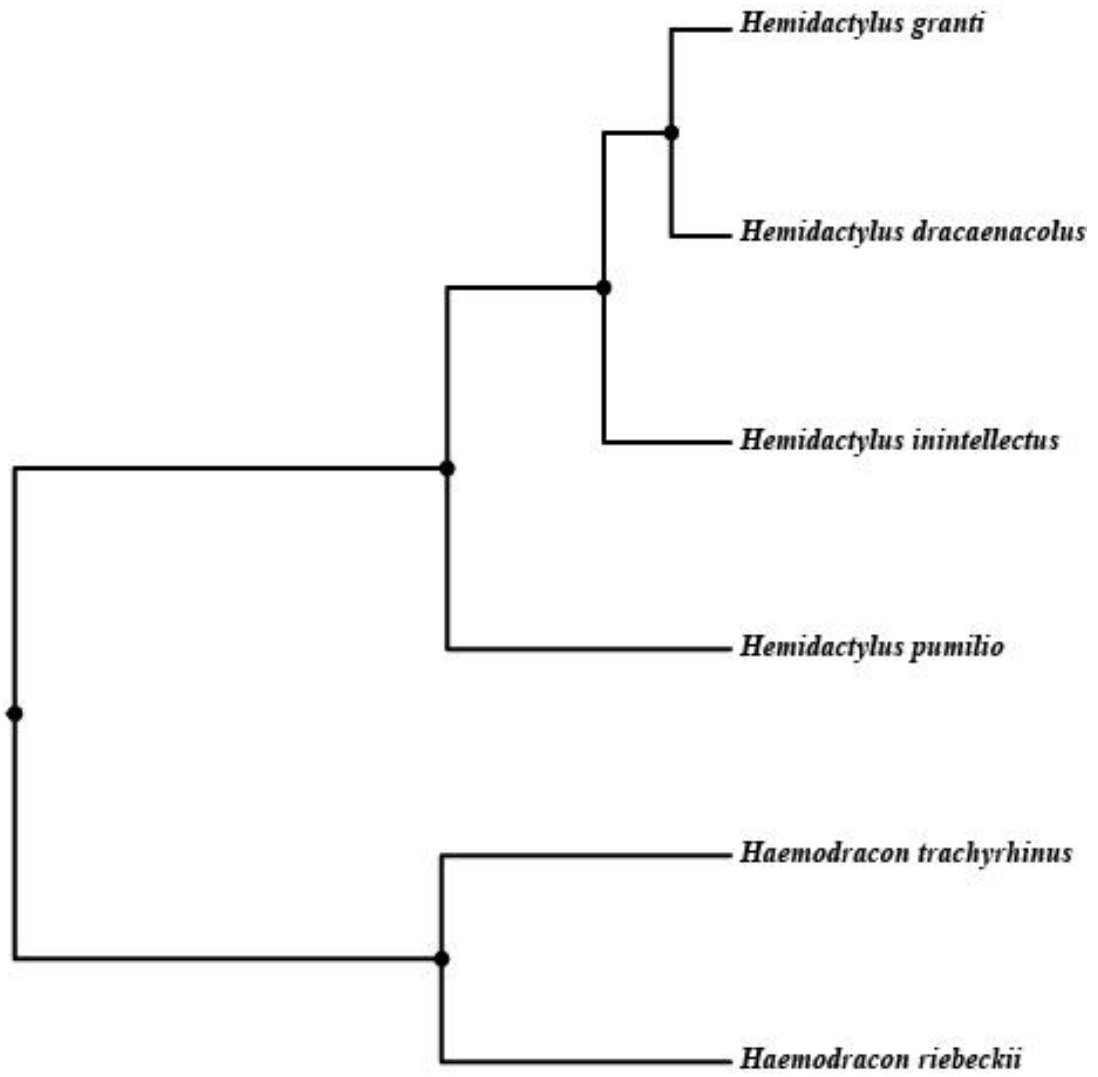945 studied in Socotra. Each point represents the isotopic values of a sample.

946 **Figure 4:** (A) Mean (point) and standard error (box) δ^{13}C values for animals collected

947 on limestone (grey boxes) and igneous (open boxes) ground. Note that some species

948 were only collected on one or the other substrate. (B) δ^{15}N values for *Haemodracon*

949 *riebeckii* and *Hemidactylus inintellectus* as the only species for which specimens were
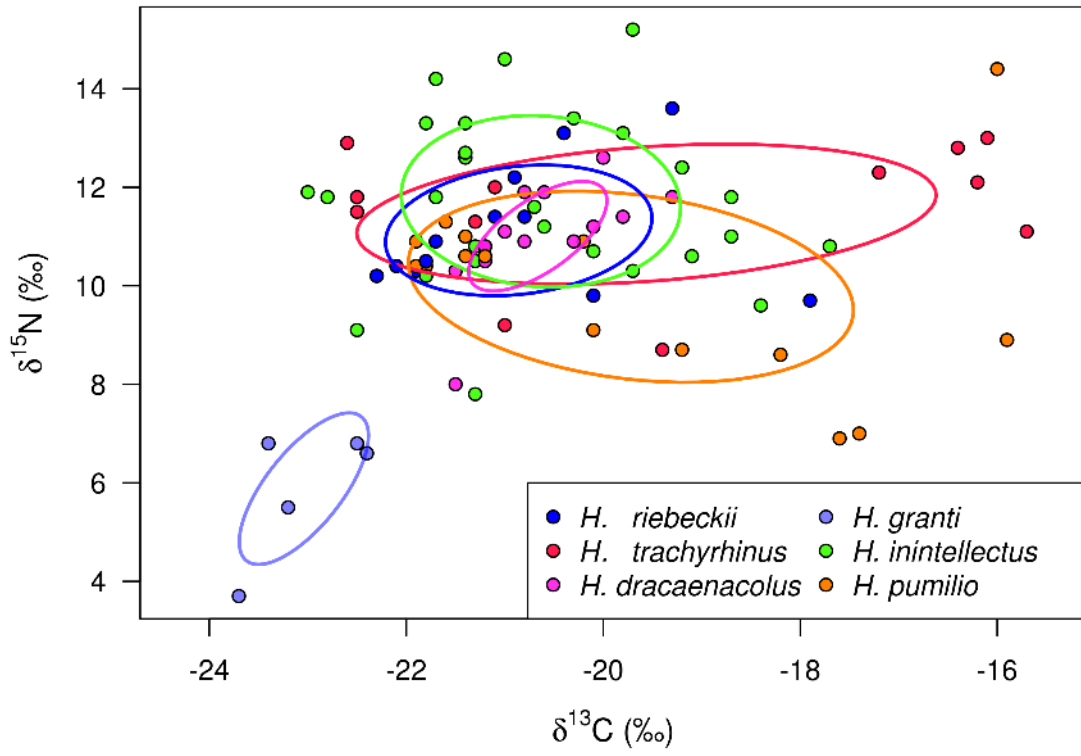
950 collected on vegetation and cliff microhabitats.

951 **Figure 5**. Cluster dendrogram based on Bray-Curtis diet similarities among six gecko

952 species of Socotra Island. Split points in the cluster indicate the dietary similarity

953 between pairs of species: for example, *Haemodracon dracaenacolus* and *Hemidactylus*

954 *initellectus* had the more similar diets with a mean similarity index around 70%.

955 Pictures are scaled for the body size of each species.

956

957   Fig 1

958

959   Fig 2

Hemidactylus granti

Hemidactylus dracaenacolus

Hemidactylus inintellectus

Hemidactylus pumilio

Haemodracon trachyrhinus

Haemodracon riebeckii

960

961 Fig 3

962

963

964   Fig 4

965

966   Fig 5