



Stable isotope analysis reveals variation in trophic niche depending on altitude in an endemic alpine gecko

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Abstract

Interspecific competition is considered a major determinant of ecological niche. It is hypothesized that increased competition should reduce niche breadth. However, there are scarce field tests on this hypothesis. Here, we test this central hypothesis in ecology by using the Atlas day gecko *Quedenfeldtia trachyblepharus*. This alpine gecko faces fewer competitors as altitude increases, and thereby, we predict that this species should increase niche breadth and relevant fitness parameters with altitude. We tested this prediction by analysing the isotopic signature of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Our results reveal that specimens from higher altitudes showed higher values for both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, had better body condition and a greater isotopic breadth when compared to specimens from lower altitudes. Altitudinal variation in carbon values was not explained by variation in isotopic concentration in the baseline of the trophic chain. Therefore, our findings support the prediction that relaxed interspecific competition favours increased trophic niche breadth. These results also suggest that global warming may represent an important threat for this species, as it may provoke the ascent in altitude of competitors, with negative consequences for the conservation of this endemism.

Zusammenfassung

Interspezifische Konkurrenz wird als ein bedeutender Steuerungsfaktor für die ökologische Nische angesehen. Es wird angenommen, dass zunehmende Konkurrenz die Nischenbreite verringern sollte. Indessen gibt es aus dem Freiland nur wenige Überprüfungen dieser Hypothese. Hier testen wir diese zentrale Hypothese der Ökologie am Beispiel des Atlas-Taggeckos, *Quedenfeldtia trachyblepharus*. Dieser alpine Gecko ist in größeren Höhen mit weniger Konkurrenten konfrontiert, und deshalb postulieren wir, dass diese Art ihre Nischenbreite und relevante Fitnessparameter mit der Höhe steigern sollte. Wir überprüften diese Vorhersagen anhand von Analysen zu den stabilen Isotopen von Kohlenstoff ($\delta^{13}\text{C}$) und Stickstoff ($\delta^{15}\text{N}$). Individuen aus

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größeren Höhen wiesen höhere Signaturen für Kohlenstoff ($\delta^{13}\text{C}$) und Stickstoff ($\delta^{15}\text{N}$) auf, hatten eine bessere Konstitution und zeigten ein breiteres Isotopenspektrum als Individuen aus geringerer Höhe. Die mit der Höhe assoziierte Variation der C-Signaturen konnte nicht mit der Variation der Isotopenkonzentrationen an der Basis der Nahrungskette (Pflanzen) erklärt werden. Deshalb unterstützen unsere Befunde die Vorhersage, dass nachlassende interspezifische Konkurrenz eine erweiterte Nahrungsnische begünstigt. Diese Ergebnisse legen außerdem nahe, dass die globale Erwärmung eine wichtige Bedrohung für diese Art darstellen könnte, da Konkurrenten in größere Höhen aufsteigen könnten - mit negativen Folgen für den endemischen Atlas-Taggecko.

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Introduction

The concept of the ecological niche is a cornerstone of Ecology (Chase & Leibold 2003). The ecological niche occupied by one species has important implications, not only for the ecology of that species, but also for the ecology of sympatric species (Schoener 1974). This is because the fundamental niche of a given species is predicted to be limited by competition with sympatric species, and species may be forced to occupy a smaller niche (the realized niche; e.g., Pianka 1974). Consequently, interspecific competition is considered a major factor determining the ecological niche breadth of sympatric species (May & MacArthur 1972). Increased competition for food, in fact, can cause a decrease in trophic niche breadth, growth rate and/or body condition (Jones & Barmuta 1998; Gómez-Mestre & Tejedo 2002; Benard & Maher 2011). Therefore, in a gradient of decreasing competition, niche breadth should increase. Because of this, species inhabiting islands or alpine environments may occupy a wider trophic niche due to a lower presence of competitors (MacArthur, Diamond, & Karr 1972).

In mountain habitats there is a gradual turnover in species composition with altitude (Jankowski, Ciecka, Meyer, & Rabenold 2009). As a general pattern, species richness decreases with altitude or has a peak at middle elevations, which depends mainly on the gradient of temperature and moisture (Van Rensburg, Chown, & Gaston 2002). Those spatial changes in species composition with altitude (e.g. Fig. 1) imply changes in the number of competitors: at higher altitudes there is an ecological release in competition, and consequently, an expansion of trophic niche space is expected (Nimmo, James, Kelly, Watson, & Bennett 2011).

High mountains present harsh environmental conditions for life, as low temperatures imply reduced primary productivity, which is moreover concentrated in a small window of time. For this reason, this type of environment presents lower species richness, although it shows elevated rates of endemism (Terborgh 1977). In order to complete their life cycles, endemic alpine species display adaptations to the special environmental conditions under which they live (Arribas & Galán 2005). However, generalist species may occur in mountain communities, where they exploit these

environments with lower competition, predation and, consequently, higher resource availability for a short period of time (Luiselli, Filippi, & Di Lena 2007). Nonetheless, the gradual constraints on the distributions of generalist species with altitude imply that alpine specialists have greater access to resources at high elevations, which in turn may increase population density (Díaz 1997).

In this study, we test the prediction that alpine species should increase their trophic niche breadth with altitude, as a consequence of reduced competition. We also expect that species inhabiting communities with fewer competitors will exhibit better body condition. We analysed these predictions by exploring variations with altitude in the trophic niche breadth of an endemic alpine gecko, the Atlas day gecko *Quedenfeldtia trachyblepharus*, using a stable isotope approach. It is endemic to the mountain range of the High Atlas and occurs from 1400 m altitude, reaching up to 4000 m (Bons & Geniez 1996; Schleich, Kästle, & Kabish 1996; Fig. 1); it is the only alpine gecko of the Mediterranean region. The Atlas day gecko is the dominant species in lizard communities from the alpine stage in our study area, although it becomes scarcer as altitude decreases, coinciding with an increase in the number of competitors (Fig. 1). When different species coexist, competition may result in reduced abundance, fecundity and growth (e.g., Eccard & Ylönen 2002). Therefore, if competition is higher at low altitude, we predict that this gecko's trophic niche should be narrower and that its body condition should worsen with decreasing altitude.

We investigated the trophic niche of the Atlas day gecko by using stable isotope analysis. Given that the frequency of isotopes varies throughout the trophic levels, the isotopic composition of animal tissues reflects dietary signatures of the consumed resources, as well as its position in the trophic chain (Fry 2006). This approach provides a more stable signal over time than those obtained from stomach contents or faeces (Seminoff, Jones, Eguchi, Jones, & Dutton 2006; Warne, Gilman, & Wolf 2010; Rosenblatt & Heithaus 2013). Then, stable isotope analysis became a powerful tool to overcome some of the limitations of conventional dietary studies, such as differential digestibility of prey items or their inability to reflect longer-term diet. Therefore, stable isotope analysis allows the evaluation of the trophic niche breadth of

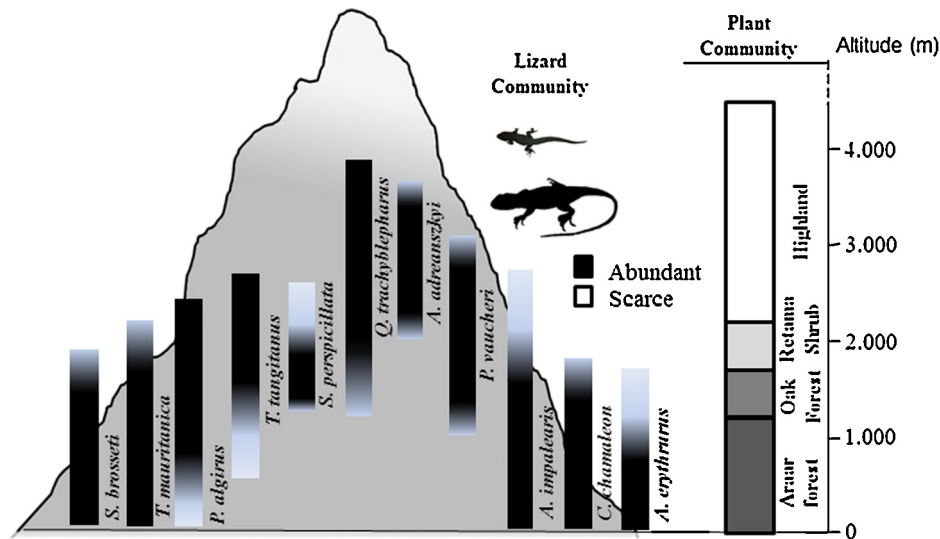


Fig. 1. Altitudinal distribution of lizard community inhabiting Oukaïmeden, High Atlas (Bons & Geniez 1996; Schleich et al. 1996).

a species (Bearhop, Adams, Waldron, Fuller, & Macleod 2004; Newsome, Del Rio, Bearhop, & Phillips 2007). For our study, we used stable carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) isotopes, the most frequently used isotopes for studying trophic relationships (Kelly 2000). The large dietary diversity within reptiles suggests that stable isotope analysis (SIA) can be broadly applied for studying ecological questions in this group (for example, Willson, Winne, Pilgrim, Romanek, & Gibbons 2010; Brischoux, Bonnet, Cherel, & Shine 2011; Murray & Wolf 2013).

Material and methods

Study area

The study zone is Oukaïmedene Plateau in the High Atlas of Morocco (31.21°N , 7.83°W). The climate is Mediterranean, with precipitation values around 400–500 mm per year. Average temperatures range from 23.5°C in the warmest month to -2.7°C in the coldest month, with 82–139 days of frost per year (Aloui Haroni, Alifriqui, & Simonneaux 2009). The vegetation consists of dry and wet grasslands at the plateau of Oukaïmedene with richer vegetal communities at lower altitudes (Mediterranean shrubs of *Retama* spp. and Atlas Cedars *Cedrus atlantica* plantations).

In this region, endemic alpine reptile species co-occur with other species with broader ranges, including species from Eurasia together with species of Mediterranean and Ibero-Maghrebian range (Bons & Geniez 1996; Schleich et al. 1996; Fig. 1). Above 2500 m.a.s.l., the Atlas day gecko shares its habitat mainly with the lizard *Atlantolacerta andreanszkyi* (Bons & Geniez 1996). Nevertheless, populations below 2500 m.a.s.l. must share the habitat with an increasing diversity of other species of scansorial lizards with similar or

slightly higher mass (*Podarcis vaucheri*, *Scelarcis perspicillata*, *Tarentola mauritanica*) and ground-dwelling species as *Psammotromus algirus*, but also species of larger size such as *Timon tangitanus* and *Agama impalearis* (Bons & Geniez 1996; Schleich et al. 1996). Also, there is a replacement of saurophagous snakes with altitude, with *Malpolon monspessulanus* at low altitudes and *Vipera monticola* at higher altitudes (Schleich et al. 1996).

Sampling

Sampling was carried out in September 2010. The specimens of Atlas day gecko were captured by hand and after manipulation were released at the capture site. No specimen suffered permanent damage as a consequence of this study. A total of 42 adult males, 38 females and 11 immatures were captured from different altitudes (ranging from 2096 m.a.s.l. to 2755 m.a.s.l.) at six different sample points. We obtained muscle tissue samples from individual tails, which were stored immediately in vials containing 1.5 mL of 70% ethanol for posterior stable isotope determination (Hobson, Gibbs, & Gloutney 1997). There were no significant differences in isotopic proportions in geckos with complete or regenerated tail (MANOVA test; Lambda de Wilks = 0.98, $F_{(2, 88)} = 0.98$, $P = 0.38$). In addition, we took the following biometrics: snout-vent length (SVL), measured from the tip of the snout to the posterior border of the vent; head length (HL), from the tip of the snout to the posterior border of the collar; and head width (HW), at the broadest point of the head (to the nearest 0.1 mm). Weight was measured using a precision balance (Denver Instrument Company Model 100A; accuracy 0.1 g). Body condition was estimated as residuals from the body length-body weight linear regression (Green 2001). Moreover, we collected samples from the more

representative plant species in high and low altitude, which were used to estimate the signature baseline.

Stable isotopic analyses

To reduce isotopic variability due to differential content of lipids, these were extracted with several rinses of chloroform-methanol (2:1, v/v) (Logan et al. 2008). Once lipids were extracted, each sample of muscle was dried to constant mass powdered and homogenized and aliquots of 0.3 mg were placed into tin capsules and crimped for combustion. Isotope analyses were carried out at the Scientific Services of the Barcelona University by means of elemental analysis-isotope ratio mass spectrometry using a Thermo Finnigan Flash 1112 (CE Elantech, Lakewood, NJ, USA) elemental analyser, coupled to a delta isotope ratio mass spectrometer via a CONFLOIII interface (Thermo Finnigan MAT, Bremen, Germany). Stable-isotope ratios are expressed in δ notation as parts per thousand (‰) deviations from the international standards (Pee Dee Belemnite marine limestone for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$; Fry 2006), according to the equation: $\delta X = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$, where X is ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Based on several hundred replicates of laboratory standards, we estimated laboratory measurement error to be $\pm 0.1\%$ for carbon and $\pm 0.2\%$ for nitrogen.

Data analysis

The covariation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and body condition, with altitude was analysed through Linear Models (LM) of Ordinal Least Squares (OLS) with sum of squares type III. Statistical models were performed using the packages “vegan” (Oksanen et al. 2013) and “car” (Fox & Weisberg 2009) in R (R Development Core Team 2012). Specimens were classified by sex (immature, which not present adult colouration [Blouin-Demers et al. 2013], were

not included in the analyses) and assigned to two altitude intervals (above and below 2500 m). This altitudinal threshold coincides approximately with the described altitudinal limits for generalist species such as *P. vaucheri* and *S. perspicillata* (Bons & Geniez 1996). Sexual dimorphism was tested by including sex as a factor in the models. Differences in head size (width and length) were tested with ANCOVA, with altitude and sex as categorical factors and SVL as continuous variable to control for allometric relationships. The assumptions of normality and homoscedasticity of the residuals were checked with the Shapiro–Wilk’s test and Levene’s tests, respectively.

In order to analyse differences in isotopic niche breadth with altitude and considering sample sizes differed between altitudes ($n = 59$ specimens for high altitude and $n = 21$ specimens for low altitude), we used a randomly extracted sub-sample of high altitude specimens, thus comparing similar sample sizes ($n = 21$ specimens for each altitude range). Differences in isotopic niche breadth between high and low lands were statistically tested by using *F*-ratio tests (Bearhop et al. 2004). Isotopic niche breadth was measured as the variance of carbon and nitrogen isotopic ratios. Spearman correlations were performed to test correlations among average isotopic variables and body condition with values of altitude of each sampling point. Pearson correlations were used to examine correlations between morphological variables and isotopic niche. Mann Whitney *U*-test was performed for testing differences in isotopic ratios in plants between altitudes, and an *F*-ratio test was done to test for differences in the variance of isotopic ratios with altitude in plants.

Results

The concentrations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significantly higher in high altitude populations (Table 1; Fig. 2). At the same time, body condition also increased with altitude

Table 1. Stable carbon ($\delta^{13}\text{C}$), nitrogen isotope ($\delta^{15}\text{N}$) concentrations (mean ‰) of lipid-extracted tail muscle tissues, body condition (residuals), SVL (mm), body mass (g), head length and head width (mm) in the Atlas day gecko at two altitudes by sex (raw data, mean \pm SE). Sample size is indicated (n). The effect of altitude and sex (*F*-values, $df = 1, 77$) is shown. Note that for head length and head width, SVL was included as covariate, and therefore $df = 1, 76$ for these variables. Non-significant effects are indicated by “ns”, $^{\S}0.10 > P > 0.05$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. The interactions altitude \times sex interaction were non-significant in every case and were not included in final models.

Variable	Lowland (<2500 m)		Highland (>2500 m)		Altitude $F_{1,77}$	Sex $F_{1,77}$
	Females ($n = 11$)	Males ($n = 10$)	Females ($n = 27$)	Males ($n = 32$)		
$\delta^{13}\text{C}$ (‰)	-24.1 ± 0.17	-23.9 ± 0.18	-22.9 ± 0.11	-22.9 ± 0.10	57.50***	0.00 ^{ns}
$\delta^{15}\text{N}$ (‰)	7.80 ± 0.37	7.96 ± 0.39	9.94 ± 0.24	9.62 ± 0.22	37.33***	0.51 ^{ns}
Body condition	-0.05 ± 0.03	-0.05 ± 0.03	-0.01 ± 0.02	0.04 ± 0.02	9.11**	3.19 [§]
SVL (mm)	42.6 ± 0.71	46.2 ± 0.74	43.0 ± 0.45	45.1 ± 0.42	0.30 ^{ns}	21.93***
Mass (g)	2.20 ± 0.11	2.69 ± 0.12	2.37 ± 0.07	2.78 ± 0.07	1.82 ^{ns}	25.00***
Head length (mm)	10.79 ± 0.21	11.91 ± 0.23	10.78 ± 0.14	11.63 ± 0.13	0.48 ^{ns}	18.49***
Head width (mm)	7.54 ± 0.15	8.29 ± 0.16	7.86 ± 0.10	8.33 ± 0.09	3.35 [§]	7.27**

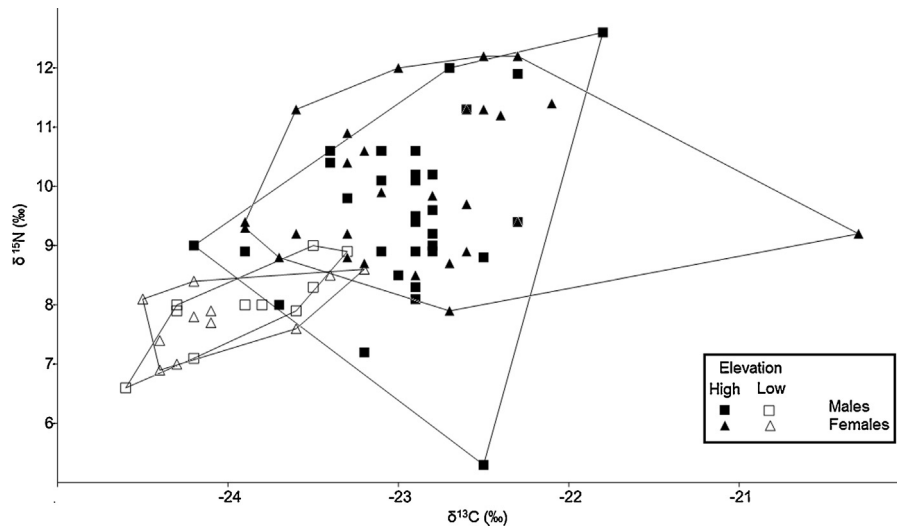


Fig. 2. Bivariate plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the Atlas day gecko (*Quedenfeldtia trachyblepharus*). Lines represent the “Convex Hull Polygon” proposed by Layman, Arrington, Montaña, & Post (2007). Black figures indicate high altitude and empty figures represent low altitude data. Squares are males, triangles are females.

(Table 1). These variables did not show significant differences between sexes or for the sex \times altitude interaction (Table 1), which implies that males and females overlap in their trophic niche (Fig. 2). Similarly, Spearman correlations showed an increase of average isotopic ratios with altitude for both nitrogen ($r_s = 0.94$, $P = 0.0048$) and carbon ($r_s = 1$, $n = 6$ sampling points), while average body condition tended to increase with altitude ($r_s = 0.77$, $P = 0.072$).

Isotopic variability of the Atlas day gecko increased with altitude for both $\delta^{13}\text{C}$ (F -ratio = 2.96, $P = 0.02$) and $\delta^{15}\text{N}$ (F -ratio = 3.22, $P = 0.01$; Fig. 2). We found a higher isotopic niche breadth in $\delta^{13}\text{C}$ for females than for males at high altitude (F -ratio = 2.17, $P = 0.04$; variance for females: 0.70, for males: 0.48). Females and males showed similar isotopic niche breadth for $\delta^{15}\text{N}$ at high altitude (F -ratio = 1.62, $P = 0.21$; variance for females: 1.18, for males: 1.50). At low altitude, females and males did not differ in their niche breadth for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (respective variances: 0.59 vs. 0.71 and 0.43 vs. 0.45, F -ratios = 1.42 and 1.07, $P = 0.59$ and 0.91).

We examined whether differences found in trophic niche and niche breadth may be a consequence of differences in morphology. In spite of niche overlap between sexes, males showed larger snout-vent length, mass and head size (length and width, controlled for body size) than females (Table 1). In contrast, altitudinal variation in trophic niche and trophic niche breadth could not be explained by differences in morphology, as we found no differences in SVL, body mass or head morphology between altitudes (Table 1). Nevertheless, head width tended to increase with altitude ($P = 0.071$; Table 1). We found no significant correlation among morphological variables and isotopic niche of geckos (always $P > 0.10$).

The isotopic signature of plants in the environment did not differ significantly between altitudes, neither for nitrogen

(mean \pm SD at high altitude: $4.93 \pm 2.99\text{‰}$, at low altitude $1.86 \pm 0.81\text{‰}$; $z = 1.47$, $P = 0.142$), nor for carbon (high altitude: $-28.78 \pm 0.42\text{‰}$; low altitude: $-26.82 \pm 1.46\text{‰}$; $z = -1.72$, $P = 0.086$; Appendix A: Fig. S1). Plant nitrogen variance tended to increase with altitude (Appendix A: Fig. S1), but not significantly (high altitude: 8.942, low altitude: 0.662; F -ratio = 13.52, $P = 0.058$). However, plant carbon variance significantly decreased with altitude (high altitude: 0.174, low altitude: 2.118; F -ratio = 12.14, $P = 0.0035$).

Discussion

Niche width

The Atlas day gecko showed significant isotopic variability depending on altitude. This isotopic variability was greater in populations located above 2500 m, for both carbon and nitrogen isotopes. Greater isotopic variability at higher altitude suggests that niche breadth of the Atlas day gecko is greater as altitude increases (Bearhop et al. 2004). Consequently, the Atlas day gecko, as predicted, presented an expanded trophic niche where fewer competitor species co-occur.

Increased amplitude in geckos nitrogen ratios with altitude could be explained by increased variance in baseline nitrogen isotopes with altitude, given that we found that $\delta^{15}\text{N}$ variance in vegetation trend to increase with altitude. This explanation, nonetheless, may be discarded for the increase in carbon isotopic variance. That is, the increase in carbon isotope amplitude with altitude detected in the geckos cannot be explained by an increased variance in carbon isotopes in plants with altitude, as the variance in carbon isotopes in plants in fact decreased with altitude. Moreover, variation in trophic niche amplitude with altitude cannot be explained by differences in body size or head morphology, although we

found a non-significant trend for geckos at high altitude to have wider heads.

Therefore, our findings suggest that the Atlas day gecko modifies its trophic breadth as altitude increases, possibly as a consequence of reduced competition. At high altitudes the only abundant lizard species that appears in syntopy with Atlas day gecko (a scansorial lizard) is *A. andreaszkyi*, a ground-dwelling lacertid species. Below 2500 m, the Atlas day gecko shares trophic resources with a larger number of competitors with similar scansorial habitats such as *P. vaucheri*, *S. perspicillata* and *T. mauritanica* (Carretero, Perera, Harris, Batista, & Pinho 2006). The presence of competing species is expected to restrict niche breadth (Bolnick, Svanbäck, Araújo, & Persson 2007).

Trophic position

We found greater isotopic values for both carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) at higher altitude in the Atlas day gecko. This implies that at high altitude, gecko tissues contain a higher proportion of the heavy isotope for both C and N (Fry 2006). Stable carbon and nitrogen isotopes values are correlated with the trophic position in the trophic chain (Bearhop, Waldron, Votier, & Furness 2002; Fry 2006; Newsome et al. 2007). This is especially relevant for the nitrogen stable isotope, given that $\delta^{15}\text{N}$ values in the predator tissues tend to be between 2.5‰ and 5‰ greater than those of their prey (Post 2002). Therefore, greater values suggest a higher trophic position for populations living at higher altitudes. Carbon stable isotope ratio also increases with trophic level, but to a much lesser degree than nitrogen (about 1‰; Inger & Bearhop 2008).

The fact that isotopic niche is different at higher altitude could reflect different isotopic concentration with altitude in the available prey (Matthews & Mazumder 2004). For example, changes found in $\delta^{13}\text{C}$ with altitude might reflect changes in C isotope in the primary producers (Warne, Pershall, & Wolf 2010). Regarding $\delta^{15}\text{N}$, previous studies found that this element is relatively constant with altitude (Graves, Romanek, & Navarro 2002; Hobson et al. 2003), or even that $\delta^{15}\text{N}$ decreases with altitude (Bai et al. 2009). Nevertheless, our findings suggest that differences in trophic niche with altitude cannot be explained by isotopic variation in the baseline, given that average isotopic signature in representative plants of the ecosystem did not vary with altitude. $\delta^{15}\text{N}$ tended to increase with altitude (not significantly), but $\delta^{13}\text{C}$, in fact, tended to decrease with altitude, a pattern opposite to that found in geckos. Therefore, our findings suggest that the Atlas day gecko also modifies its diet as altitude increases, seeming to change to a higher trophic position as consequence of decreased presence of competitors.

The analysis of the isotopic signal revealed an overlap in the trophic niche occupied by both sexes. Trophic overlap between sexes has been also observed by analysing the diet by conventional methods (Carretero et al. 2006). Differences

have been found in trophic niches occupied by males and females in other species, especially if the sexual dimorphism is marked (Perry 1996). In the Atlas day gecko, sexual dimorphism for body size and head morphology is pronounced (males have larger body size and head size), but this sexual dimorphism did not translate into sexual differences in trophic niche, which is consistent with other studies (Costa, Vitt, Pianka, Mesquita, & Colli 2008). In the Atlas day gecko, morphological differences between sexes could be explained by different sexual roles, such as greater aggressiveness of males, as it occurs in other species of lizards (Lailvaux & Irschick 2007).

Body condition

The Atlas day gecko showed a significant loss of physical condition as the number of competitors increased – at low altitude. This loss of body condition may be due to competition for food at lower altitudes, where trophic resources have to be partitioned within a richer community. This fact could also explain the decrease in density of the populations at lower altitudes (see Eccard & Ylönen 2002). However, we cannot rule out that better body condition in highland geckos is a consequence of increased fat storing for hibernation (Warne, Gilman, Garcia & Wolf 2012).

Potential effects of global change

Global change is causing changes in species distribution and abundance (review in Parmesan 2006; for reptiles see Sinervo et al. 2010; Moreno-Rueda, Pleguezuelos, Pizarro, & Montori 2012). Moreover, organisms restricted to alpine habitat suffer particularly from global warming (Raxworthy et al. 2008; Dubey & Shine 2010), and because the distribution of the Atlas day gecko is strictly limited to alpine areas, it may be particularly vulnerable (Thomas, Franco, & Hill 2006). Our study shows how niche width changes with altitude and suggests that the Atlas day gecko is affected by interspecific competition. Therefore, we conclude that the Atlas day gecko might be potentially vulnerable to climate warming by upslope displacement of distributions of competing species. Species with narrower niches are at greater risk of extinction (Williams et al. 2009). Because the Atlas day gecko shows a narrower niche where there are more competitors, upslope displacement of generalist species may form an important potential extinction threat for this species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2014.05.005>.

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