# IS *HYALOSAURUS KOELLIKERI* A TRUE FOREST LIZARD?

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*Abstract.*—**Hyalosaurus koellikeri is the only member of the family Anguidae found on the African continent. It has been suggested that its distribution is dependent on forest habitats. Here, we investigated habitat selection of this secretive species in Morocco, at a fine spatial resolution. We examined the association between the presence of *H. koellikeri* and vegetation cover, substrate, topography, and climate. We then compared the habitat selection of this species and that of other lizards in the same region. Our results indicate that the proportion of tree crown cover is the variable that best explains the occurrence of this species, and to lesser extents, the climatic, substrate, and topographic conditions. However, this species is not associated with a particular class of forest and is present in both dry assemblages of evergreen oaks and junipers and in humid deciduous forests. *Hyalosaurus koellikeri* occupies forests more frequently than other genera of lizards, though it coexists with several generalist species in these habitats. This association with forest/woodland habitats could explain the sparse distribution of this species in Morocco and suggests that some isolated populations, like those of the Atlantic Plain, are vulnerable to extinction.**

*Key Words.*—Anguidae; conservation; Morocco; secretive species

## INTRODUCTION

The anguids are a group of lizards typically found in the mesic environments of Eurasia and America (Campden-Main 1970; Stebbins 1985; Valakos et al. 2008). *Hyalosaurus koellikeri* (Fig. 1) is the only species present on the African continent, and is the product of a basal split within the family (Macey et al. 1999). This species is endemic to northwest Africa, and is found in central Morocco and extreme northwestern Algeria (Sindaco and Jeremĉenko 2008). In Morocco, it is a secretive and sparsely distributed species, apparently limited to herbaceous and forest habitats with humid conditions (Bons and Geniez 1996; Schleich et al. 1996; de Pous et al. 2011; Escoriza and Comas 2011). However, to date, no habitat selection studies have been undertaken at a fine spatial resolution. Knowledge of the habitat preference of the species is essential to its conservation, particularly considering the increasing land-use changes in the region (Nafaa and Watfeh 2000) and the known impact of habitat loss on anguid populations (e.g., *Pseudopus apodus* in Bulgaria; Beshkov and Nanev 2006).

In this study, we characterized the habitats in which *H. koellikeri* occurs in Morocco. We measured various forest features related to stand maturity and structural complexity, both of which determine the composition of faunal assemblages in these habitats (Schonberg et al. 2004; Guénette and Villard 2005). The characteristics of the forest habitats were assessed at several scales, each describing different ecological aspects of low-dispersal vertebrates, ranging from habitat use (smaller scale) to metapopulation stability (larger scale; Hanski 1991; Gamble et al. 2007). We also examined the substrate properties, given that soil is a component of the anguid habitat (Gregory 1980) and determines habitat suitability for several species of lizards (Kuhnz et al. 2005; Disi 2011). Finally, we evaluated the effect of topography and climate, because the occurrence of ectothermic vertebrates is explained by these variables, especially in warm and semiarid environments (Monger and Bestelmeyer 2006).

The habitat selected by *H. koellikeri* was compared with that of other lizard genera inhabiting the same region. In central Morocco, lizards are particularly diverse and include lineages of very distinct biogeographical origins (Bons and Geniez 1996). They occupy most Moroccan ecoregions, from subtropical scrub to temperate montane grasslands (Schleich et al. 1996). However, forests are not favourable environments for many species of lizards because they are heliothermic (Huey 1974; Vitt et al. 1997). If *H. koellikeri* is a forest species, its association with this type of habitat should be greater than those of other groups of lizards. In this article, we report the habitat use by a little-known anguid species endemic to northwestern Africa. Our hypotheses were that the lizard is a forest species and is therefore more strongly associated with this type of habitat than are other lizards,

**FIGURE 1.** Adult *Hyalosaurus koellikeri,* Forêt de la Maâmora, Atlantic Plain of Morocco. (Photographed by Daniel Escoriza).

and that the sparse distribution of the species could be attributable to changes in land use to agriculture.

### MATERIALS AND METHODS

*Study area.*—The study area covered most of northern Morocco, between Essaouira to the south, Debdou to the east, and the Tingitana Peninsula to the north (Fig. 2). The region falls within the dry-summer subtropical climate belt (Köppen classification), and the high-altitude mountain ranges generate an important climatic gradient that allows the growth of very heterogeneous plant communities, combining Mediterranean, Tethyan, and Sahelian elements (Charco 2001).
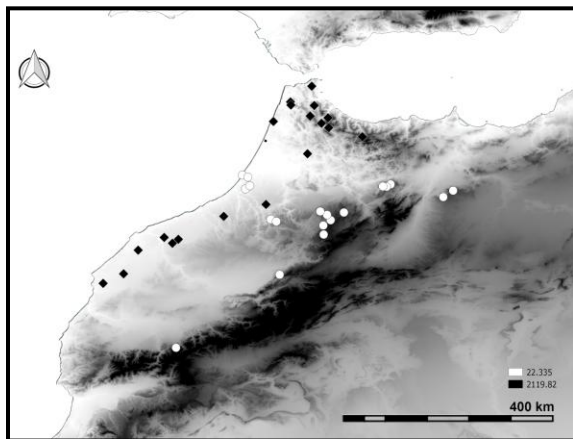


**FIGURE 2**. The study region in Morocco (northwestern Africa). White circles: presence localities of *Hyalosaurus koellikeri*. Black diamonds: localities of absence.

*Survey protocol and habitat characterization.*—We conducted several surveys from March to April and October to November during 2008–2013, as part of a study of north-African amphibian and reptile species (Escoriza 2010; Comas et al. 2014; Escoriza and Ben Hassine 2014, 2015). We selected survey sites to cover most of the range of the species (rather than selection by habitat condition) to avoid biases related to the expectations of the researchers. We conducted sampling between 1100 and 1700 (local time) on sunny days (cloudiness <30%), and involved turning over stones and small logs. Rock/log flipping and visual surveys are techniques commonly used in qualitative sampling of squamates (Lovich 2012). It also proved to be useful in surveys of other groups of ectothermic vertebrates that inhabit forest habitats (Crawford and Semlitsch 2007). The fieldwork was restricted to two person-hours in 2.5 ha, and ended when the selected portion of land was completely sampled, the time limit was reached, or a specimen of *H. koellikeri* was found. We also recorded other species of lizards and amphisbaenians found during the surveys. We defined absence using two criteria: no confirmed observation of *H. koellikeri* during the surveys or the absence of previous records in the area (10 km radius).

For habitat characterization, we used the Food and Agriculture Organization (FAO) definition of forest: a land in which tree crown cover exceeds 10% of coverage, totalling a minimum of 0.5 ha and where trees reach a minimum height of 5 m at maturity (FAO. 2000. Available at http://www.fao.org/docrep/ [Accessed 20 March 2014]). Habitats composed of smaller dwarf and/or stunted trees are categorized as wooded land. We

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delimited an area of 100 m$^2$ around each point at which a specimen of *H. koellikeri* was found. Within this perimeter, we counted (n) all living trees (woody plants with a trunk diameter > 5 cm and height > 1.37 m; McKenny et al. 2006), and we measured the diameter at breast height (in cm, DBH; at 1.4 m). We calculated the tree density (ρ = n/100) and then, using DBH, estimated the tree basal area (BA = 0.00007854 * DBH²) in m², which is the portion of land surface occupied (Grove 2002). In the analyses, we used the ratio of summed BA to total ground surface (ΣBA/100). We also measured the height of every living tree (as defined above) using a clinometer. Three transects (50 × 2 m) were established, running from the specimen location and oriented north, southwest, and southeast (Guénette and Villard 2005). Along these transects, we counted all species of trees and shrubs (woody plants < 1.37 m tall) and classified them to species level according to Charco (2001). We used the counts of trees and shrubs to compute three indices of diversity (Keylock 2005): dominance, the Shannon-Wiener index (H), and the variation in Shannon-Wiener index (Hvar), an estimate of the spatial heterogeneity in plant composition. We calculated Hvar using a bootstrapped estimation (after 1000 replications) of the variation in the Shannon index when the north and the southwest transects were compared. For sites at which no *H. koellikeri* were found, we followed the same protocol so that the same number of sites was processed for both the presence and unconfirmed presence groups. We calculated diversity indices using the package PRIMER-E (PRIMER-E Ltd., Plymouth, UK).

***Geographic Information System (GIS) and remote sensing data.***—We obtained site-specific data summarizing the climate, topography, substrate, and proportion of vegetation cover from GIS layers. We described the climatic conditions using two key variables that explain the composition of vertebrate assemblages in the Palaearctic ecozone (Escoriza and Ruhí 2014): the aridity index (mean annual precipitation /mean annual potential evapotranspiration) and the mean annual temperature (Hijmans et al. 2005; Consortium for Spatial Information. 2009. Available at http://www.cgiar-csi.org/ [Accessed 8 September 2013]). We measured topography with an index of terrain ruggedness (Riley et al. 1999). This index describes the variation in altitude within a 3 × 3 pixel grid and ranges between 0 (level terrain) and 959 (extremely rugged terrain). We examined substrate characteristics at the first standard depth (0–5 cm): bulk density (soil compactation; t/m$^3$), cation exchange capacity (soil fertility; cmol/kg), soil organic carbon (g/kg), pH, sand (grain size 50–2000 μm) content, silt (grain size 2–50 μm) content, and clay (grain size < 2 μm) content (International Soil Reference and Information Centre. 2015. Available at

http://www.isric.org/content/ data [Accessed 9 January 2015]). Loose soils have a bulk density lower than 1.3 t/m$^3$, whereas medium compacted soils have a bulk density of 1.45 t/m$^3$ (Chesworth 2008). We examined vegetation cover (percentage coverage per km²) for four classes: forest, shrubs, herbaceous vegetation, and cultivated vegetation, as provided by Global 1-km Consensus Land Cover (Tuanmu and Jetz. 2014. Available at http://www.earthenv.org/landcover. html [Accessed 15 September 2014]). These data were extracted with a spatial resolution of 30 arc-seconds (1 km) using the package QGIS vs 2.6.1 (Quantum-GIS Development Core Team. 2015. Available at http://qgis.osgeo.org [Accessed 10 January 2015]). We also examined vegetation cover at a higher spatial resolution from satellite and aerial photographs (Google Earth 2014). This approach allowed us to determine the proportion of tree crown cover in a ground surface of 0.0625 km$^2$. We calculated the multispectral range based on a supervised classification routine implemented in the package MultiSpec vs.3.4 (Purdue Research Foundation 2014).

***Data analyses.***—A Principal Coordinate Analysis (PCO) was used to generate an ordination plot of the presence and absence (or unconfirmed presence) data. First, we constructed a Euclidean distance matrix based on the variables obtained from the characterization of forest, climate, topography, and substrate. We then tested for differences between both groups using permutational multivariate analysis of variance (PERMANOVA), assessing the significance after 9,999 unrestricted permutations. The explanatory capacity of the environmental parameters was determined with a distance-based linear model, using a presence/absence matrix (constructed with Sørensen's coefficient) as the dependent variable. To determine the variables that contributed most to the presence of *H. koellikeri*, we generated an optimal model using sequential tests, with the variables fitted as covariates (Anderson et al. 2008). We constructed the model using a step-wise procedure, using the Akaike Information Criterion (corrected for finite sample sizes; AIC$_c$) to select the best model (Burham and Anderson 2002). We determined significance with 99,999 permutations of the normalized predictor data. This analysis was performed using the package PRIMER-E (PRIMER-E Ltd., Plymouth, UK).

We also investigated whether the distribution pattern of *H. koellikeri* could be explained by land-use changes. To do this, an ecological niche model was run, with 75% of the locations allocated to training and a regularization value of one, enabling linear, quadratic, and hinge features based on the number of presence data for the species (Anderson and Gonzalez 2011). This ecological

**TABLE 1.** Forest and climate class (UNEP 1997) for presence localities of *Hyalosaurus koellikeri*

| Latitude | Longitude | Elevation (m) | Dominant species | Forest class | Climate class |
|---|---|---|---|---|---|
| 34.25 | -6.66 | 8 | *Juniperus phoenicia* | Evergreen needleleaved | Semi-arid |
| 34.21 | -6.57 | 60 | *Quercus suber* | Evergreen broadleaved | Semi-arid |
| 34.09 | -4.09 | 1,381 | *Quercus ilex* | Evergreen broadleaved | Semi-arid |
| 34.06 | -6.54 | 163 | *Quercus suber* | Evergreen broadleaved | Semi-arid |
| 34.05 | -4.23 | 1,149 | *Quercus suber* | Evergreen broadleaved | Semi-arid |
| 34.05 | -4.16 | 1,531 | *Quercus ilex* | Evergreen broadleaved | Semi-arid |
| 34.01 | -6.61 | 169 | *Quercus suber* | Evergreen broadleaved | Semi-arid |
| 33.98 | -3.01 | 1,286 | *Juniperus oxycedrus* | Evergreen needleleaved | Semi-arid |
| 33.87 | -3.18 | 1,218 | *Quercus ilex* | Evergreen broadleaved | Semi-arid |
| 33.62 | -5.31 | 1,279 | *Quercus ilex* | Evergreen broadleaved | Dry sub-humid |
| 33.60 | -4.90 | 1,525 | *Quercus ilex* | Evergreen broadleaved | Semi-arid |
| 33.56 | -5.20 | 1,517 | *Quercus canariensis* | Deciduous broadleaved | Humid |
| 33.48 | -6.17 | 940 | *Quercus ilex* | Evergreen broadleaved | Semi-arid |
| 33.47 | -5.13 | 1,605 | *Fraxinus dimorpha* | Deciduous broadleaved | Humid |
| 33.44 | -6.07 | 1,072 | *Quercus suber* | Evergreen broadleaved | Dry sub-humid |
| 33.37 | -5.26 | 1,625 | *Quercus ilex* | Evergreen broadleaved | Humid |
| 33.22 | -5.25 | 1,936 | *Quercus ilex* | Evergreen broadleaved | Humid |
| 32.52 | -6.02 | 1,347 | *Tetraclinis articulata* | Evergreen needleleaved | Semi-arid |
| 31.26 | -7.81 | 1,624 | *Juniperus oxycedrus* | Evergreen needleleaved | Semi-arid |

niche model included two climatic variables (aridity index, mean annual temperature) and four classes of vegetation cover (forest, shrubs, herbaceous, and cultivated vegetation). We calculated model accuracy based on the area under the receiver operating characteristic curve (AUC). This analysis was performed using the package MaxEnt 3.3.3k (Phillips et al. 2006).

Finally, we examined whether this species is associated with forest habitats more frequently than are other species of lizards occurring in the same region. To do this, we compared the habitat characteristics based on the records that we collected during the surveys. We defined habitats by the four classes of vegetation cover (forest, shrubs, herbaceous, and cultivated vegetation). We compared the observed associations with those obtained under the null distribution (after 99,999 iterations) using an equiprobable constraint to randomize the occurrences. If the length of the longest run is greater than that obtained under the null distribution, the occurrences are aggregated (Gotelli and Entsminger 2009). We performed this analysis using the Runs tests provided in the package Ecosim 7.72 (Gotelli and Entsminger 2009). The contribution of the four classes of vegetation to lizard occurrence in the region was examined with PCO and a similarity percentage (SIMPER) analysis, based on a standardized matrix of Bray-Curtis distances (Clarke and Gorley 2006). These analyses were carried out by the package PRIMER-E (PRIMER-E Ltd., Plymouth, UK).

### RESULTS

We found *H. koellikeri* at 19 sites (Fig. 2) and obtained 154 records for 17 genera and 28 species of lizards. Most of the *H. koellikeri* specimens were found in March and April, all under a rock or log. Site characterization revealed that *H. koellikeri* was present in forest and/or woodland (66% average tree crown cover per 0.0625 km$^2$; Appendix 1), mainly composed of evergreen oaks (*Quercus ilex* and *Q. suber*; 68.43%) and junipers (*Juniperus oxycedrus, J. phoenicia,* and *Tetraclinis articulata*; 21.05%), whereas deciduous forests (*Q. canariensis* and *Fraxinus dimorpha*) together accounted for no more than 10.52% of the sites containing *H. koellikeri* (Table 1). These forests and woodlands contained trees of variable sizes, and were usually dominated by a few plant species (Appendix 1). The substrate was loosely compacted, slightly acidic, and contained abundant organic matter (Appendix 1). The topographic and climatic conditions varied widely among these sites (Table 1 and Appendix 1).

The PCO ordination plot indicated that the two groups (sites at which *H. koellikeri* was present, those from which its presence was not confirmed) were distributed unevenly in ecological space (Fig. 3). PERMANOVA confirmed the significant differences between these groups (*pseudo-F$_{1,36}$* = 6.773, *P* < 0.001). Sequential tests indicated that the most important variable explaining the occurrence of *H. koellikeri* was the proportion of tree crown cover, and this variable alone explained 40% of the observed variance. The best model to explain the occurrence of *H. koellikeri* (75% of the observed variance) included the proportion of tree crown cover, climate (aridity and mean temperature), substrate (organic soil and pH), terrain ruggedness, and tree/shrub diversity (Table 2).

The ecological niche model produced an AUC of 0.941, indicating a very high predictive value. This model indicates that the populations of *H. koellikeri* can be divided into three main clusters (Atlantic Plain, Middle and High Atlas mountain ranges, and Tell Atlas
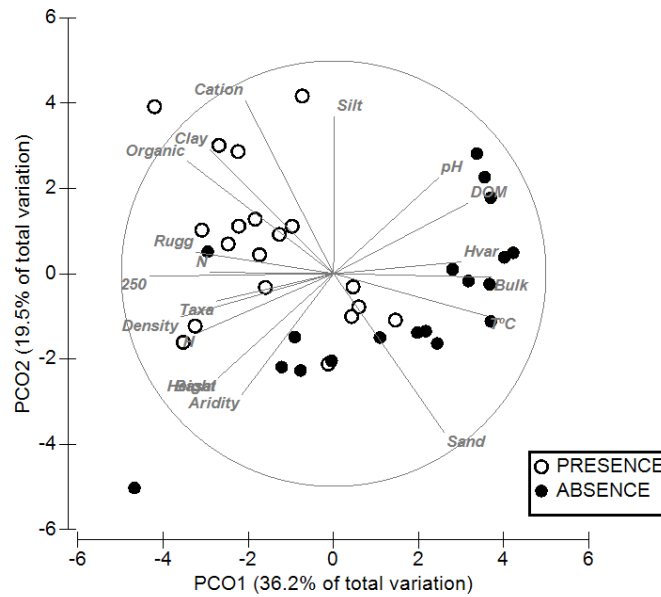
**FIGURE 3**. Principal coordinates ordination plot showing the distribution in the environmental space of presence/absence localities. 250: % of tree crown cover at 250 m resolution; Bulk: soil bulk density (t/m$^3$); Cation: soil cation exchange (cmol/kg); Organic: organic soil matter (g/kg); pH: soil pH; Sand, Silt and Clay: % in soil; Aridity: aridity index; T° C: mean annual temperature (° C); Rugg: terrain ruggedness; Basal: tree basal area (m$^2$) in 100 m$^2$; Height: tree average height (m) in 100 m$^2$; Density: tree density in 100 m$^2$; Taxa: number of species of trees/shrubs; N: total number of tree/shrubs. DOM: Dominance of tree/shrubs species; H: Shannon-Wiener index of tree/shrubs species; Hvar: variation in Shannon-Wiener index of tree/shrubs species.

mountains), isolated by broad areas of unsuitable habitat (Fig. 4). The ecological niche model also showed that the occurrence of *H. koellikeri* is mainly dependent on vegetation cover (Table 3). The analysis of null models indicated that the occurrence *H. koellikeri* is associated with forest more than would be expected if the distribution of the species were random (observed runs = 6, simulated runs = 2.15, $P < 0.001$). A SIMPER analysis showed that *H. koellikeri* appeared more

**TABLE 2**. Optimal model obtained by distance-based linear model sequential tests explaining the occurrence of *Hyalosaurus koellikeri*. The abbreviation Cumul. = cumulative proportion of explained variance.

|  | AIC$_c$ | *Pseudo–F* | *P* | Cumul. |
|---|---|---|---|---|
| Tree crown cover at 250 m | 198.68 | 24.12 | < 0.001 | 0.40 |
| +Aridity index | 190.85 | 10.76 | 0.002 | 0.54 |
| +Soil organic | 188.15 | 4.99 | 0.029 | 0.6 |
| +Soil pH | 186.04 | 4.41 | 0.043 | 0.65 |
| +Terrain ruggedness | 184.14 | 4.25 | 0.048 | 0.69 |
| +Tree/shrub diversity | 182.12 | 4.40 | 0.045 | 0.73 |
| +Mean annual temperature | 181.45 | 3.24 | 0.083 | 0.75 |

frequently in forest habitats than other lizard species (Table 4), although there was an important overlap with other genera, as shown on PCO first factorial plane (Appendix 2).

**DISCUSSION**

*Hyalosaurus koellikeri* is a remarkable lizard endemic to northwestern Africa, with a discontinuous distribution (Schleich et al. 1996). In this study, we investigated the habitat preferences of the species to clarify the factors underlying its distribution. The regional occurrence of lizards can be successfully described based on models that include climate, vegetation, and substrate descriptors, because these variables are related to the thermoregulatory efficiency of reptiles (Melville et al. 2001; Jácome-Flores et al. 2015). Our findings also indicate that the occurrence of *H. koellikeri* in central-western Morocco was mainly explained by the presence of forest/wooded land, and to a lesser extent by other abiotic factors, including substrate, topography, and climatic conditions. This anguid does not have a strong preference for a specific habitat composition and was found occupying both dry forests of junipers and evergreen oaks and humid deciduous forests. In contrast with the results obtained by de Pous et al. (2011), in our study the presence of *H. koellikeri* in closed deciduous forest was more marginal (10.52%).
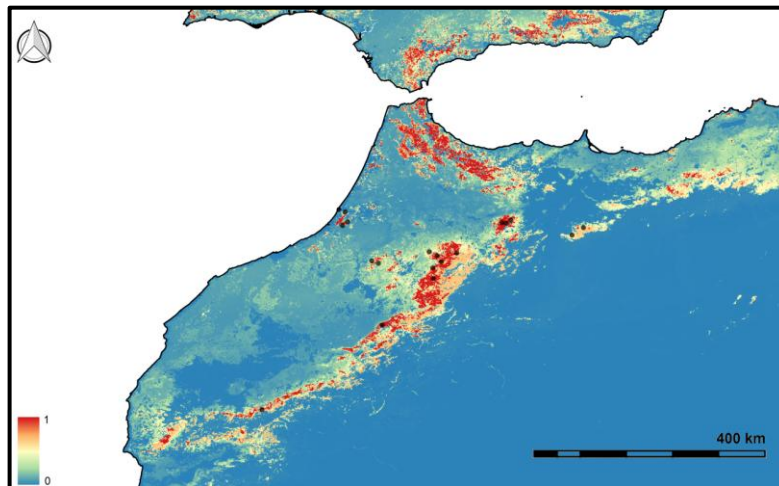
**FIGURE 4**. Ecological niche model obtained based on two climatic variables (aridity index and mean annual temperature) and four classes of vegetation cover (forest, shrubs, herbaceous, and cultivated vegetation). Black circles: presence localities of *Hyalosaurus koellikeri*.

These forests/woodlands can be composed of trees of variable heights that are spaced densely to very sparsely. These results indicate that *H. koellikeri* selects a habitat similar to that described for *Pseudopus apodus*, which inhabits open forests of pines and evergreen oaks (Rifai et al. 2005; Franzen et al. 2008; Valakos et al. 2008). *Hyalosaurus koellikeri* is not a substrate specialist, tolerating wide variations in the proportions of sand, silt, and clay. On the Atlantic Plain, it can occur in soils containing a high proportion of sand (82%), but in other regions, this proportion is lower, at around 47%. However, in most of the sites studied, the substrate was only slightly compacted (below 1.39 $t/m^3$), rich in organic matter and acidic, typical of forested areas (Islam and Weil 2000).

Compared with other genera of lizards, *H. koellikeri* was more frequently associated with forests, although other species of lizards also occur in this type of habitat. Both stenoecious species (e.g., *Chalcides lanzai*) and generalist species (e.g., *Agama bibronii, Tarentola mauritanica, Trogonophis wiegmanni*) occur sympatrically with *H. koellikeri*. The presence of *H. koellikeri* in forested habitats is partly attributable to the ability of anguids to forage while their body

**TABLE 3.** Relative contributions of the environmental variables to the ecological niche model for *Hyalosaurus koellikeri* (see Fig. 4).

| Variables | Percentage contribution | Permutation importance |
|---|---|---|
| Forest | 51.5 | 9.7 |
| Cultivated vegetation | 29.0 | 44.5 |
| Annual temperature | 17.0 | 15.6 |
| Herbaceous vegetation | 2.1 | 27.7 |
| Shrubs | 0.3 | 2.5 |
| Aridity index | 0.1 | 0.1 |

temperatures are low (Avery 1982; Capula and Luiselli 1993). Like other lizards, *H. koellikeri* displays heliothermic behavior. Nevertheless, it is active at dawn, at dusk, and on rainy days (Schleich et al. 1996). Activity with relatively low body temperatures could be related to the lower vulnerability of anguids to predation than other lizards, because they have heavily armoured skins (Hailey 1984; Meek 1986).

The association between *H. koellikeri* and the presence of forest/woodlands means that this species is vulnerable to factors that regulate the extent of this biome. In the last 30,000 y, the area covered by northwestern African forests has undergone major contractions (Rodríguez-Sánchez and Arroyo 2008; Alba-Sánchez et al. 2015). These contractions reached the peak during the hyper-arid periods associated with glaciation, when the forests were reduced to the Atlas Mountains (Rhoujjati et al. 2010). The survival of *H. koellikeri* in a few refugia at that time would explain its relatively low haplotype diversity (de Pous et al. 2011), similar to that described for other mesophilic species occurring in the region (Recuero et al. 2007).

We believe that our results have important implications for the conservation of this species. The ecological niche model indicates that some populations located on the Atlantic Plain (forêt de Maâmora and Sidi Boughaba) are probably isolated from the core distribution of the species. The Atlantic Plain was covered by forests, woodland, and scrub before the onset of agriculture (United States Geological Survey. 2013. Available from http://www. rmgsc.cr.usgs.gov/ecosystems [Accessed 28 September 2014]), indicating the presence of suitable conditions for the species in most of this region until historical times. However this landscape transformation becomes very intense in the

**TABLE 4.** Comparison on the association between occurrence and vegetation cover between the genus *Hyalosaurus* and other lizard genera occurring in the region, obtained by similarity percentage routine.

| Cover Type | *H. koellikeri* | Other genus | Average dissimilarity | Contribution% |
|---|---|---|---|---|
| Forest | 31.18 | 19.81 | 15.26 | 32.88 |
| Cultivated | 42.44 | 40.42 | 14.00 | 30.18 |
| Shrubs | 24.82 | 33.54 | 13.56 | 29.21 |
| Herbaceous | 1.56 | 6.23 | 3.59 | 7.73 |

last hundred years (Emberger 1939; Mhirit and Blerot 1999), making these populations highly vulnerable to extinction. Other peripheral populations are already very rare and may even be extinct. In Essaouira, Morocco, this species has not been recorded since 1931(Bons and Geniez 1996). However, in the Middle and High Atlas Mountains, there are still vast areas with suitable conditions for the species, where *H. koellikeri* could maintain stable populations in the long term.

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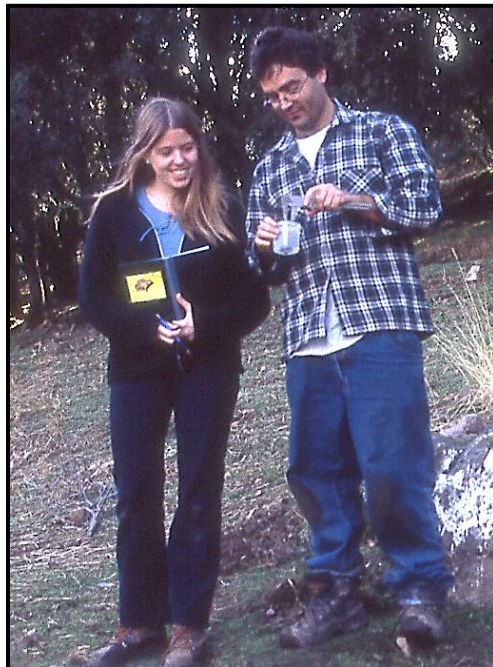
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and lizards along an altitudinal gradient in Sierra Nevada (Spain).
(Photographed by Daniel Escoriza).

**APPENDIX 1**. Comparison between the localities of presence/absence of *Hyalosaurus koellikeri* for several habitat dimensions: vegetation cover, substrate characteristics, climate, topography, and forest structure.

|  |  | Presence | Absence |
|---|---|---|---|
| Tree crown cover at | mean | 66 | 24 |
| 250 m | range | 33–99 | 0–93 |
| Soil bulk density | mean | 1.26 | 1.39 |
|  | range | 1.0–1.39 | 0.89–1.70 |
| Soil cation exchange | mean | 8.32 | 4.58 |
|  | range | 2.0–20.0 | 0–10.0 |
| Soil organic | mean | 11.79 | 7.11 |
|  | range | 6.0–23.0 | 5.0–11–0 |
| Soil pH | mean | 5.41 | 5.82 |
|  | range | 3.7–6.2 | 4.19–8.10 |
| Sand% | mean | 63.89 | 76.53 |
|  | range | 47–82 | 59–85 |
| Silt% | mean | 14.16 | 10.58 |
|  | range | 4–30 | 4–23 |
| Clay% | mean | 20.58 | 12.26 |
|  | range | 9–35 | 3–34 |
| Aridity index | mean | 0.47 | 0.52 |
|  | range | 0.24–0.72 | 0.27–0.94 |
| Mean annual | mean | 14.0 | 17.0 |
| temperature | range | 10.0–18.3 | 11.3–19.2 |
| Terrain ruggedness | mean | 240.5 | 148.9 |
|  | range | 31.1–651.1 | 4.0–510.9 |
| Tree $\Sigma BA/100$ | mean | 0.13 | 0.08 |
|  | range | 0.01–0.53 | 0.0–0.95 |
| Tree mean height | mean | 7.46 | 2.83 |
|  | range | 2.31–13.53 | 0.0–15.84 |
| Tree density | mean | 0.04 | 0.01 |
|  | range | 0.01–0.06 | 0.0–0.09 |
| Tree/shrub $N_{taxa}$ | mean | 4.6 | 3.4 |
|  | range | 2.0–15.0 | 1.0–14.0 |
| Tree/shrub $N$ | mean | 68.2 | 33.3 |
|  | range | 21–155 | 1–131 |
| Tree/shrub | mean | 0.49 | 0.66 |
| Dominance | range | 0.14–0.88 | 0.17–1.0 |
| Tree/shrub | mean | 0.96 | 0.64 |
| Shannon-Wiener index | range | 0.23–2.27 | 0.0–2.05 |
| Tree/shrub | mean | 0.45 | 0.72 |
| variation in Shannon-Wiener | range | 0.001–0.85 | 0.04–1.0 |
| index |  |  |  |
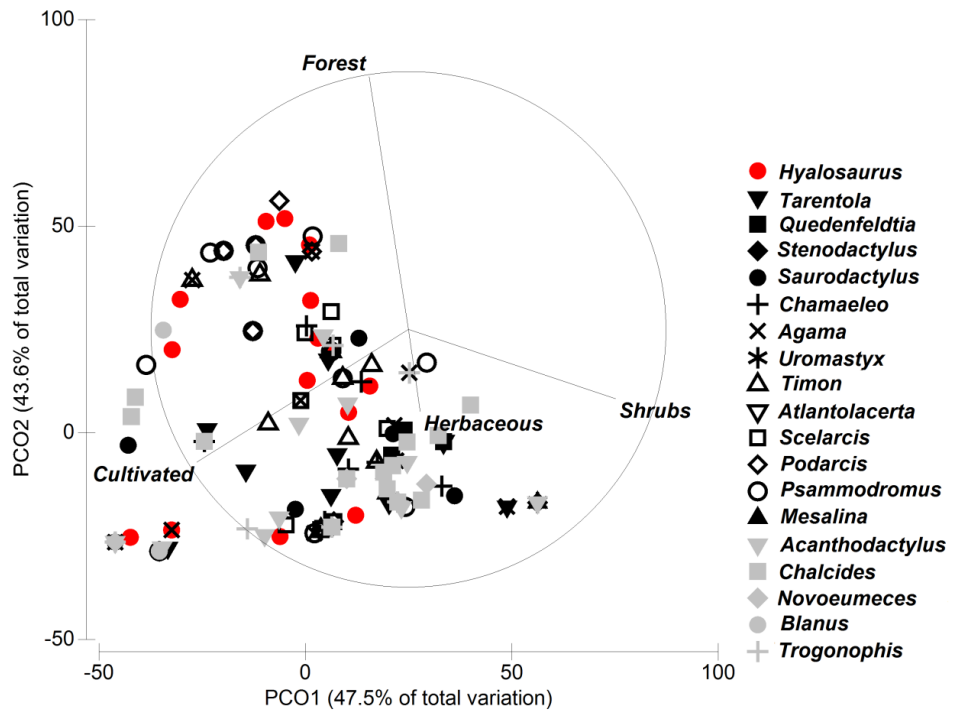
**APPENDIX 2**. Principal coordinates ordination plot, showing the association between vegetation cover and occurrence of several lizard genera in the region.