SALAMANDRA 53(3) | 405–412 | 15 August 2017 | ISSN 0036–3375

Habitat use by peripheral populations of a lizard with a highly restricted distribution range, the Spanish algyroides, *Algyroides marchi*

José Luis Rubio & Víctor Martín

Departamento de Ecología, Universidad Autónoma de Madrid, Cantoblanco, 29049 Madrid, Spain

Corresponding author: José Luis Rubio, e-mail: joseluis.rubio@uam.es

Manuscript received: 15 August 2016
Accepted: 27 December 2016 by Stefan Lötters

Abstract. Peripheral populations are considered vulnerable but important for conservation. The Spanish algyroides is a small and endangered lacertid lizard, endemic to a small area in the southeastern mountains of the Iberian Peninsula. It is a stenotopic species that will typically inhabit shaded and humid microhabitats in enclosed rocky situations. These habitat preferences relate to a very low thermal inertia and high evaporative water loss consistent with its small body size. Its patchy distribution is delimited by dryer and warmer lowlands. Newly detected localities seemed to expand its known distribution range, providing a contact zone with core populations. We studied the habitat selection and conservation status of populations living in the border zone, produced a species distribution model of the new area, and compared border versus core structural and environmental variables. The results confirmed the predicted occurrence, showing no differences in border vs. core selected habitat characteristics. From the perspective of habitat selection alone, edge effects and local adaptation seem insignificant. This could be related to the 'hard-type edge' and 'two-patch system' of the small distribution of this species. Detected alterations of the habitat in this border area were mainly road and forest track construction, urbanisation, and livestock grazing. In the longer term, aridification of the area due to the global climate change could potentially gain importance, considering the dependency of the species on humid habitats, and the proximity of the edge of its distribution to the uninhabitable lowlands that determine its range limits. It is of great importance to identify the shape of the whole edge of this species' range, effect in-depth evaluations, and monitor its conservation status.

Key words. Edge populations, habitat selection, reptile conservation, species distribution model, Spain.

Introduction

Peripheral populations are considered of great importance for species conservation (e.g., Channel 2004) since they would be more vulnerable to environmental fluctuations compared with those in the core areas. Populations at the border of their species' distribution would be typically smaller, more isolated, less genetically diverse, and more susceptible to inbreeding and genetic drift. Thus, they would be less resilient in the face of environmental changes (e.g., Lesica & Allendorf 1995, Böhme et al. 2006, Sexton et al. 2009, Bill & Gómez 2011, Cuervo & Moller 2013, Antunes et al. 2006, Volis et al. 2016, but see Gonzalez-Guzman 2001, Channel 2004 for a discussion). On the other hand, populations adapted to peripheral environmental conditions have been regarded as potential reservoirs of adaptive genetic variation (e.g., Blows & Hoffman 1993, Lessica & Allendorf 1995, Eckstein et al. 2006, Willi et al. 2007, Ledoux et al. 2014), and local adaptation to conditions at the distribution limits has been reported and discussed in detail (e.g., Kawecki 2008, Bell & Gómez 2011).

The Spanish algyroides, *Algyroides marchi* Valverde, 1958, a small lacertid lizard, is an Iberian endemic with a very restricted distribution. It is restricted to the southeastern mountains of the Iberian Peninsula, the Prebetic System (sensu Sánchez 1982; in general terms: Alcaráz, Cazorla and Segura ranges; Sánchez-Videgaín & Rubio 1996, Rubio 2002, Carretero et al. 2010). These occurrences amount to one of the smallest distribution ranges among continental European lacertid lizards (< 5,000 km²). Within this area, suitable habitat seems to be patchy, and some declines in both the quality of habitat and number of populations have been reported (Rubio 2002, Rubio et al. 2006). All this makes the species very vulnerable; it is ranked as 'Endangered' by the IUCN (IUCN, Pérez-Mellado et al. 2008).

Algyroides marchi is a remarkably stenotopic species. It typically occupies (geomorphologically) enclosed, rocky, shaded and humid localities (Rubio & Carrascal 1994). These characteristics would reflect a high sensitivity of the species to high humidity and low temperature (Rubio & Carrascal 1994, García-Muñoz & Carretero 2013,

J. L. Rubio unpubl. data). This habitat preference has been related to the small size of the lizard (snout–vent length ≤ 50 mm) with its inherent high surface/volume ratio, high heating/cooling rate, and high evaporative rate (Rubio & Carrascal 1994). The mountain massif occupied by the species would constitute a form of continental island, surrounded by lower warmer and drier territories that limit the species distribution (Rubio 2002).

Recent surveys (Brakels et al. 2010, Carretero et al. 2010) revealed new localities of occurrence of the species (Moratalla Range, Murcia Region, and Taibilla and Zumeta Ranges, Albacete Province) at the previously known southeastern limits. This new area is a generally arid region where the populations appear to be rather isolated. The new data interestingly suggested some expansion of the previously known general distribution area, and could help to identify the shape of the peripheral limits in that sector. They also opened the possibility that an important contact zone may exist between the core and the southeastern peripheral populations. The vulnerability of *A. marchi* due to its stenoicity and its reduced area of distribution would be greater in these border populations as they might be more exposed to external stress factors. The study of mitochondrial markers (Carretero et al. 2010) revealed differences in these *A. marchi* edge populations, suggesting the existence of old (Pleistocene) fragmentation/retraction processes in this area, although nuclear markers indicated a genetic flow between core and edge populations. Very preliminary estimates of abundance within border populations of *A. marchi* suggest that they could be less abundant compared to their core counterparts (Carretero et al. 2010).

In this paper, (1) we studied the distribution of marginal populations of *A. marchi* at its southeastern limits (Taibilla and Zumeta headwaters, Albacete province), (2) we carried out a habitat selection research within the peripheral area and tested possible differences in habitat selection patterns at a regional scale between core and peripheral populations, (3) we then produced a distribution model to predict the localities that were most favourable for its presence in the study area, (4) we took into account only habitat preferences and preliminarily discuss our results for the species in the context of edge effects, and finally (5), we consider the main threats for the species in this area.

Materials and methods

Study area

The study of peripheral populations of *Algyroides marchi* was conducted in July and September of 2012 for ten days each in the southeastern periphery of its distribution, i.e., at the headwaters of the rivers Taibilla and Zumeta (Albacete Province, Spain; 38°07' N, 2°20' W; extension about 700 km²). This region is characterized by strong climatic contrasts (Sánchez 1982, Artiago 1984), with high daily and annual variation of temperatures (annual range: 10–16°C), with dry and hot summers and rainy and freezing winters (mean annual precipitation: 350–650 mm).

The general configuration of the mountains, mainly SW-NE, and the general altitude (700–2,100 m a.s.l.) hamper the crossing of precipitation-bearing clouds from the west, producing a strong gradient of aridity eastwards (towards the Murcia Region; Vidal-Abarca et al. 1987). The study area contains a variety of lithological materials such as limestone, dolomite and siliceous sands. The resultant carbonaceous character has produced a rugged landscape with narrow valleys with a high degree of enclosure that provide shaded and humid microhabitats, often within a more arid landscape matrix. The vegetation is mainly composed of open forest formations of pines (*Pinus nigra*), juniper trees (*Juniperus thurifera*), oaks (*Quercus ilex, Q. pyrenaica, Q. coccifera*), and Mediterranean shrubs and pasturelands with poplar and walnut trees (*Juglans regia*) on the riverbanks (Alcaráz & Sanchez-Gómez 1988, Gómez et al. 1992).

Study design

We surveyed the study area during the activity period of the lizards for a total of 20 days, and registered with GPS the exact UTM coordinates of the localities occupied by the species. We generated a distribution map based on 18 occurrence localities over a 30-m resolution Digital Elevation Model (ASTER GDEM; NASA government; asterweb.jpl.nasa.gov). For the study of habitat selection, we established sample plots of 25 × 25 m in 13 localities; one plot per locality. We located the centre of our sample plots at those sites with the highest observed abundance of *Algyroides marchi* individuals. Thirteen variables were measured in each sample plot: altitude, cardinal aspect, geomorphological enclosure, availability of water, percentage of area occupied by cliffs, rocks (diameter > 70 cm) and stones (diameter < 70 cm), as well as percentage cover of trees, bushes, forbs, grams, litter and bare ground. We measured the altitude and the cardinal aspects by GPS-altimeter and compass respectively. The degree of enclosure was scored as (1) flat terrain, (2) moderately sloped, (3) open gully and (4) closed gully. We calculated an index of water volume by multiplying length, average width and average depth of any water body within the plot. We estimated covers visually as percentages (after previous training). Additionally, we evaluated the degree of anthropogenic alteration in every location, ranking it by consensus among the authors in four categories: (1) high, (2) medium, (3) low and (4) very low to nil. We systematically assessed the physical structure of the landscape at 22 sites located at the intersections of the UTM coordinates of 5 × 5 km. We measured the same variables using the same methods described above. By means of a Mann-Whitney U test ($\alpha \leq 0.05$), we compared the variables of the occurrence localities versus the systematically selected localities in the study area (headwaters of rivers Taibilla and Zumeta). We also compared the peripheral occurrence localities, as well as the systematically selected localities, with those in the core area (Alcaraz Range, Albacete Province; data available from a previous study; Rubio & Carrascal 1994). Data analyses were performed with IBM SPSS Statistics 21.

To predict the most favourable localities of presence of the species at a regional scale, we generated a Species Distribution Model (SDM) (Elith & Leathwick 2009). The model was produced from occurrence records of *A. marchi* available from previous studies (Sanchez-Videgaín & Rubio 1996, Carretero et al. 2010), and a set of environmental variables. These variables were obtained from the Worldclim dataset at a spatial resolution of 1 km², andcomprised annual precipitation, maximum temperature of the warmest month, and altitude, and another four topographic variables derived from the Digital Elevation Model (DEM, 1 km² resolution; WorldClim dataset, http://www.wordlclim.org): slope (%), curvature, aspect and insolation received in 2012. All transformations of variables were computed with ArcMap 9.3.

Species distribution was modelled using the maximum-entropy machine learning SDM (Species Distribution Model) algorithm MAXENT v. 3.3.3k (Phillips et al. 2006), which is applicable to presence-only data and considered one of the most accurate SDM algorithms (Elith et al. 2011). We used the default settings of MAXENT with logistic output that would provide an estimated suitability between 0 and 1 (interpreted as the probability of presence). In order to evaluate the predictive ability of the model, the Area Under the receiver-operating characteristic Curve (AUC) was computed using MAXENT's internal validation procedure (Phillips & Dudík 2008). Jackknife test and response curves were selected in a way to measure the importance and contribution of the variables to the models. After running MAXENT and obtaining probability distributions (from 0 to 1), the output distributions were reclassified in categories according to their degrees of habitat suitability: low values (< 0.33), medium values (0.34–0.66), and high values (< 0.66).

Results

Distribution, evaluation and habitat selection

Our survey in the border area produced 18 new localities of occurrence of *Algyroides marchi* (Fig. 1). These data allowed us to draw a map of available potentially suitable habitat in a potential contact zone. In general, the localities were found mainly in relatively enclosed and humid gullies. The evaluation of anthropogenic alteration of the occurrence localities showed that 33% were exposed to very low or no impact, whereas the remaining localities showed signs of greater impact, mainly due to the construction of roads and tracks (60%), followed by urban constructions (22%) and livestock grazing (16%).

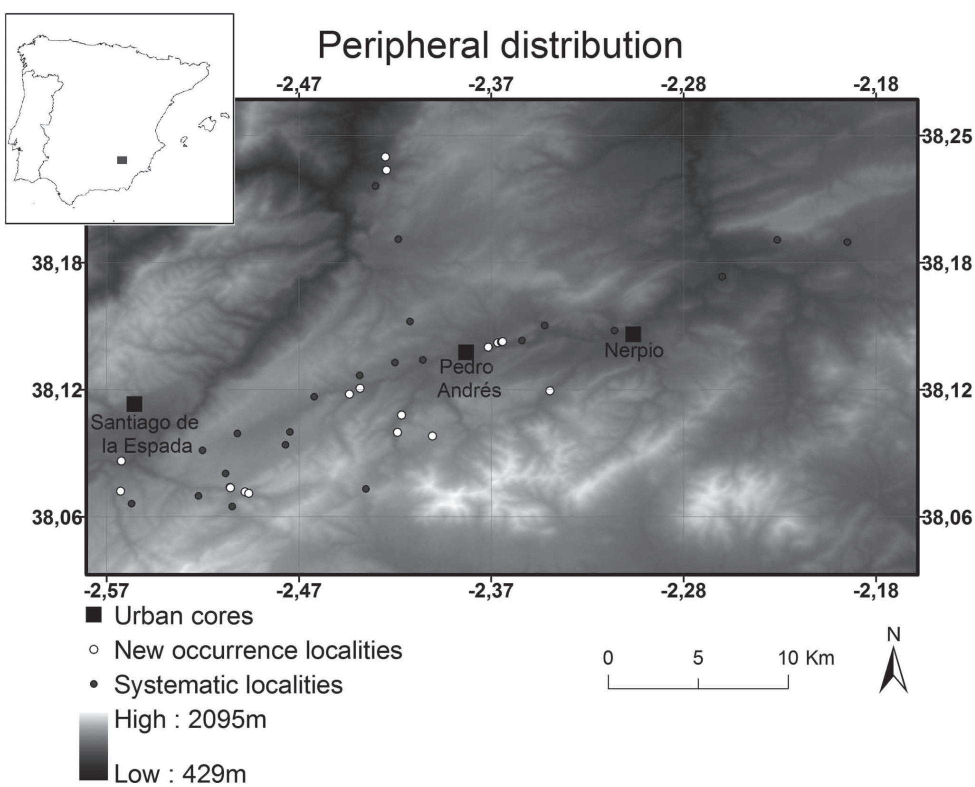

Figure 1. New occurrences of *Algyroides marchi* (white dots) and systematically selected localities (dark grey dots) at the southeastern border of the distribution (headwaters of the rivers Taibilla and Zumeta, Albacete, Spain). Urban cores in black squares. Insert in the top left corner: the study area on the Iberian Peninsula. Map based on 30-m resolution; ASTER Global Digital Elevation ranging from 429 to 2,095 m a.s.l.

Table 1. Comparison of the structural characteristics (mean and standard deviation, abbreviated SD) of systematically selected localities with those of occurrence of *Algyroides marchi* in the border populations at the headwaters of the rivers Taibilla and Zumeta (Abacete, Spain).

	Localities with *A. marchi*		Localities systematically selected		Mann-Whitney U test
	mean	SD	mean	SD	p
Altitude (m)	1282.73	212.48	1366	193.25	0.191
Cliff cover (%)	29.91	21.10	0.00	0.00	0.000
Rocks cover (%)					
Rocks, diameter > 70 cm	29.73	23.64	10.46	25.64	0.002
Stones, diameter < 70 cm	9.00	10.11	7.77	14.96	0.257
Canopy cover (%)	17.91	14.44	23.47	22.00	0.601
Bush cover (%)	20.36	9.97	28.73	24.70	0.578
Forbs cover (%)	5.73	7.63	7.18	7.18	0.801
Grams cover (%)	7.90	14.56	20.73	26.09	0.087
Trash cover (%)	2.45	5.91	3.41	7.08	0.631
Bare ground (%)	0.34	0.65	6.27	8.08	0.001
Water volume index (%)	1.41	3.37	0.31	1.44	0.049
Degree of enclosure	3.45	0.52	1.82	0.85	0.000
Sample size	13		22		

Table 1 presents the values of the variables in the localities of occurrence of the species, and those in the localities selected systematically at a regional scale in the new border area (Taibilla and Zumeta headwaters). The Mann-Whitney U test results show that degree of enclosure, water volume index, and percentage of surface occupied by rocks and cliffs were all significantly elevated in the occurrence localities of *A. marchi*. Bare ground was less common in the occurrence localities than in those systematically selected. The cardinal aspects of the occurrence localities tended towards the northern aspects (NW-N-NE, 62%). The remaining variables showed not significant differences.

Comparison of the structural variables of the occurrence localities in the core area with those in the border area showed a significantly higher degree of enclosure in the occurrence localities in the border zone (mean = 3.54 vs. 2.16; U = 206.5; P = 0.001). Grass and bare ground were less common in the occurrence localities in the border area (U = 61.5, P = 0.032 and U = 18.0, P < 0.001, respectively). The remaining studied variables did not show any significant differences. On the other hand, our comparison of the variables that describe habitat availability (systematically selected localities) in the core area vs. the border area, show a lower coverage of rocks in the border zone (U = 63, P < 0.001). The available altitudes are higher in the border area (U = 295, P = < 0.001), and cliffs were absent in our sample of systematically selected localities (mean surface in core area = 10%).

Species Distribution Model

The SDM, obtained from occurrence data in the general distribution area with a resolution of 1 km^2 (see Study design above), showed the main areas of habitat suitable for *Algyroides marchi* in the new border zone (Fig. 2A). The prediction for the border study area (Fig. 2B) shows consistency of the species' occurrence zones with the scores predicted by the model as suitable. Sixteen localities match with the suitable habitats predicted for the species. Only two localities offered habitats that were less adequate than predicted by the model in that they had lower suitability scores. Additionally, our model predicts other zones (Fig. 2) that could also be conducive to the presence of the species (e.g., gullies in the south of the Taibilla Range and zones to the north of the Taibilla and Zumeta headwaters).

The applicability of our model was evaluated through the AUC score (Area Under the Curve). We obtained an AUC of 0.991, indicating a very precise prediction (Swets 1998). The most influential variables in the model were altitude (39.4%) and the maximum temperature in the month of July (34.3%). The remaining variables contributed to a lesser extent to the model (slope = 10.4; curvature = 8.1; annual precipitation = 6.6), with insolation and cardinal aspect contributing the least (0.8 and 0.4, respectively). In fact, altitude and maximum temperature are also the variables that better explain the model when they are used alone, but it is the maximum temperature in July that will most affect the model when it is removed from it (Fig. 3).

Discussion

Considering the small expanse of the species' distribution, the new 18 occurrence localities of *Algyroides marchi* found in the study area constitute a noteworthy expansion of its known southeastern peripheral distribution. These data increase our knowledge of the potential connectivity be-

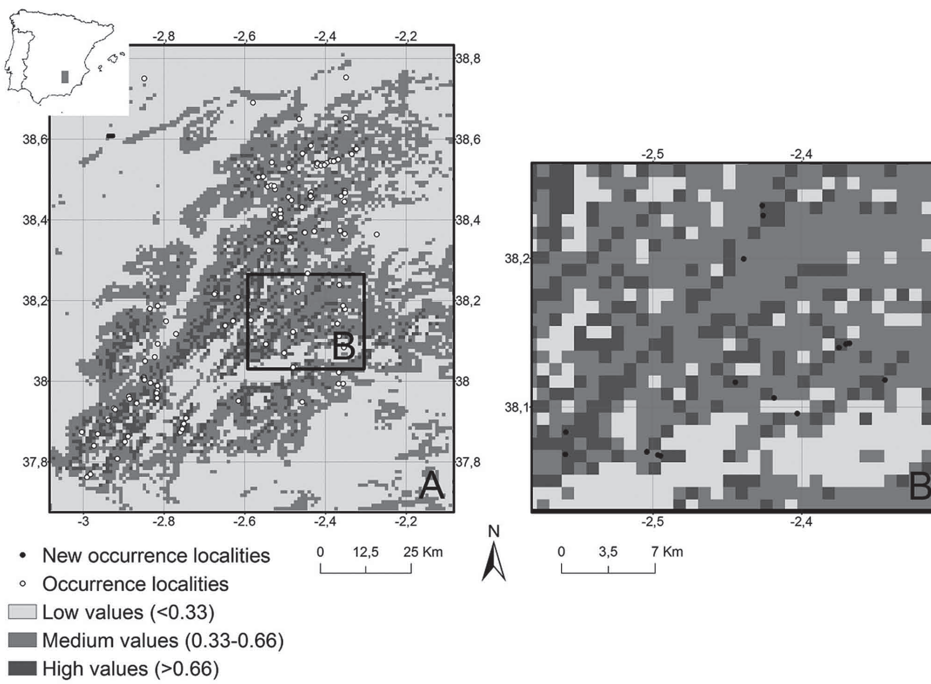

Figure 2. Species Distribution Model (SDM) of *Algyroides marchi* with a resolution of 1 km². Dark grey areas represent suitability values > 0.66, medium grey areas suitability values 0.33–0.66, and light grey areas suitability values < 0.33. (A) Representation of the total distribution range as predicted by the model. The occurrences used to develop the model are presented in black. (B) Extension of the model for the study area. White dots represent main villages, and black dots locations where the species was found.

tween populations, help to identify the shape of the species' distribution limits, and are important for future conservation plans (e.g., Burkey & Reed 2006).

The results of this study confirm the predictions for the habitat selection patterns at a regional scale from previous studies (Rubio & Carrascal 1994, Carretero et al. 2010). In the study area, *A. marchi* appears mainly in localities with rocky limestone gullies that provide water and a high degree of enclosure, and, hence, low exposure to solar radiation. Such characteristics are frequently associated in the area with rocky riverbeds. The limestone materials that characterize the area facilitate a way of landscape modulation that will create numerous small caves, holes and crevices usable to the lizards; rocky screes with associated humidity and ambient moisture underneath are also found.

Our comparison of localities of *A. marchi* occurrence in the border study area with the localities occupied by the species in the core area shows no variation in habitat use, indicating that habitat conditions in the localities occupied by *A. marchi* do not vary significantly throughout its distribution. Only the degree of enclosure was significantly higher in the peripheral study area than in the core area. The relatively arid and flattened matrix between suitable localities that characterize the landscape in the border range at the Taibilla and Zumeta headwaters could explain the high degree of enclosure found in the localities of occurrence of *A. marchi* in this peripheral zone. The Foehn effect generated by the Prebetic Mountains blocking the westerly winds (see area of study) create arid environmental conditions towards the southeastern distribution border (Vidal-Abarca et al. 1987). The localities with very high degrees of enclosure would provide enough humidity and suitable temperatures to allow the species to persist in this zone. Localities with the structural characteristics preferred by the species are scarcer in the border zone than in the more core-orientated range, where *A. marchi* furthermore appears to use a wider range of habitats that provide the shaded and humid conditions preferred by the species (crags, dolines, lapiés [lapiaz], large screes etc.; Sanchez-Videgaín & Rubio 1996).

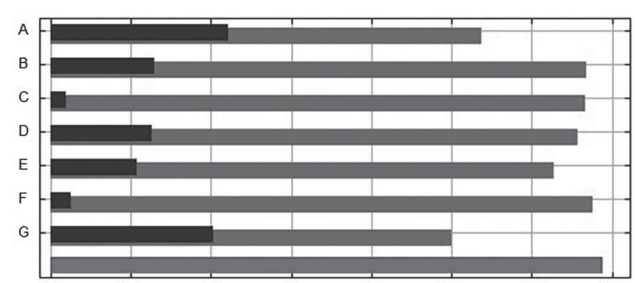

Figure 3. Contribution of every variable when used alone to calculate the model (dark grey), and when removed from it and keeping the remaining variables to calculate the model with a resolution of 1 km² (light grey). The last bar represents the full model. Key to variables: (A) altitude in m above sea level; (B) curvature index of the surface; (C) cardinal direction; (D) slope; (E) mean annual precipitation; (F) insolation; (G) maximum temperature in July.

The species' preference for a habitat with such characteristics confirms in this area the importance of temperature and humidity in its distribution proposed in previous studies (Rubio & Carrascal 1994, Carretero et al. 2010, García-Muñoz et al. 2010). Small lizards like *A. marchi* have a fast rate of heat exchange with the environment (e.g., Stevenson 1985, Carrascal et al. 1992, Garrick 2008) and a high relative evaporative water loss (Mautz 1982) due to their high surface-to-volume ratio. The short time available for diel and annual activity, derived from the environmental conditions in enclosed localities, may be of great importance in relation to the small size of the species, as well as for its reproductive strategy: typically a small cultch size in a single oviposition period (Rubio & Palacios 1986). Its selection of large rocks provides opportunities for thermo- and water regulation (e.g., Huey et al. 1989, Shah et al. 2004). The cool, humid and moist conditions under these rocks furthermore provide a good source of arthropod prey (mainly small spiders and flies; J. L. Rubio unpubl. data). Although a forest-dwelling character has been attributed to the species (Arnold 2002, Carretero et al. 2010), the results of our habitat selection studies portray *A. marchi* more as a species of shaded rocky sites where water will be available, not necessarily one of forest situation. High tree cover, and the associated humid and moist microclimate might help in the dispersal of this species, however.

The model prediction for the study area sees occurrence localities and the highest values of suitability coincide, and thus provides a map relevant to conservation planning. The model provides an image concordant with the habitat selection study, and is coherent with the SDM in the general distribution (Carretero et al. 2010). It signalled the importance, at various geographical scales, of a tall and rough relief in the maintenance of high humidity, through attracting precipitation, and reduced temperatures that would minimize the summer thermal stress.

Algyroides marchi exhibits little capacity to colonize suboptimal sites (although juveniles might use them for dispersal; see below). The results of the SDM obtained from the data of the general distribution together with the results of the study of habitat selection indicate that *A. marchi* will select the same habitats, at a regional scale, throughout its entire distribution range, including the periphery. Edge effects and local adaptations are thus unapparent in these populations, unlike in other reported instances (e.g., Díaz et al. 2006, Vergeer & Kunin 2013, but see, e.g., Bjorndal & Balten 2010, Peñalver et al. 2010). We hypothesize that this might be linked to the reduced and sharply edged expanse of the distribution range of *A. marchi*, which is restricted to the Prebetic Mountains. In this regard, Holt et al. (2005), following Carter & Prince (1981), indicated the possibility that individuals would experience the same environmental conditions in core and suitable patches in edge habitats. Larger distribution ranges may present greater spatial variation and environmental gradients that thus can promote local adaptation (sensu Fortin et al. 2005; Kawecki 2008, but see Ledoux et al. 2014). Diaz et al. (2006), for example, reported stable differences in life history traits in *Psammodromus algirus*, a large lacertid lizard with a wide distribution in the Iberian Peninsula (e.g., two vs. single clutches) between edge and core populations (see also Sinervo 1990). Although further study is needed on the *A. marchi* periphery, our data show a 'hard-type edge' sensu Stamps et al. (1987) or, as classified by Kawecki (2008), a 'two-patch system' (a little-studied model). The aridity of the surrounding land would limit this species' distribution, and has been related to extinction-recolonisation processes in the past, as apparently is reflected in the genetic differences reported for the extant border populations (Carretero et al. 2010). This last work also demonstrated, from nuclear markers, the existence of gene flow between edge and core populations, a factor able to counteract local selection (Barton & Partridge 2000, Lenormand 2002, Kawecki 2008). More specific studies about peripheral versus core populations are needed to investigate edge effects in *A. marchi*: on demography, life history, body condition, and biometry (including morphology and asymmetry), as are accurate studies of populations genetics.

In the light of our habitat selection study and species distribution model, the high predictability of occurrences of *A. marchi* facilitates the development of management plans for the conservation of this species. The immediate risk factors for *A. marchi* populations in the study area are related to direct alterations of their habitats: mainly the construction of roads and forest tracks, urban development, and livestock grazing. The alteration of the vegetation could also affect suitably shaded microclimates. The effect of livestock grazing, poorly known in lizards (Blevins & With 2011, but see Behroo et al. 2015 for vipers), may have some impact on this species, considering its potential sensitivity to environmental changes. However, many occurrence localities are relatively inaccessible to livestock. In addition, recent observations of individuals, mainly juveniles, in pastures (Carretero et al. 2010, J.L. Rubio unpubl. data) suggest that this vegetation might play a role in their dispersal, and grazing will not be a major problem as long as overexploitation would not lead to bare ground; however, further research on this issue is needed. Although *A. marchi* has sometimes been observed on the walls of old isolated houses (Carretero et al. 2010, J.L. Rubio unpubl. data), the process of construction itself would obviously drastically alter occurrence localities, and synanthropic species, such as domestic cats and rodents, are surely threats. The risk of forest fire is always present in this area. Other threats reported from other areas in the distribution range of *A. marchi* have not been found here, but should nevertheless be considered for future management measures in this border zone. The list includes stream canalising and/or silting by erosion after logging, replacement of traditional stone ponds (usable by the lizards) with metal or plastic tanks, small dams, and tourism facilities (Rubio & Carrascal 1994, Sánchez-Videgaín & Rubio 1996, Carretero et al. 2010). The study area is partly located within protected natural spaces (SPA of Alcaráz, Mundo and Segura Ranges), but, considering the afore-mentioned local impact factors, any management plan should focus on not altering humidity, moisture and temperature of the shaded rocky sites characteristic of the species' occurrence.

In a longer term, a potential aridification of the area due to global climate change (Summer et al. 2003) could gain importance considering the dependency of the species on humid habitats, and the proximity of the edge of its distribution to unsuitable lower, more flattened, and more arid areas that determine its range limit. Studies with climatic change sceneries will allow evaluating local perturbations of the habitat. Although SDMs have limitations (possible unaccounted biological factors, change of climatic variables with time, or other methodological factors; Thuiller et al. 2004, Sinclair et al. 2010, Sanchez-Fernandez et al. 2011), this tool surely will speed up finding new *A. marchi* localities in the future (cf. Guisan & Zimmermann 2000). As far as border populations are concerned, it will be of great interest to identify the shape of the whole distribution edge of this species, evaluate it in depth, and monitor its conservation status; this will enable us to detect and anticipate anthropogenically caused fluctuations so that preventive measures can be taken.

Acknowledgements

We thank M. Luzón and C. Díez for their help with fieldwork, and C. Mata and J. Traba for their comments on the SDM.

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