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History and new developments in the mapping and modelling of the distribution of the golden-striped salamander, *Chioglossa lusitanica*

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Geschichte und neue Entwicklungen der Kartierung und Modellierung der Verbreitung des Goldenstreifensalamanders

Die Entwicklung des Wissens um die Verbreitung von *Chioglossa lusitanica* auf der Iberischen Halbinsel wird dokumentiert und der Einfluss der Zunahme der Daten auf die Zuverlässigkeit und den Nutzen der ökographischen Modelle, im Besonderen in ihrer Bedeutung für den Naturschutz, analysiert. Nach der Erstbeschreibung der Art 1864 nahm die Zahl der Fundorte in Portugal allmählich zu: 1957 waren 13, 1995 54, 1999 202 und heute sind 278 Funde bekannt. In Spanien stieg die Zahl im gleichen Zeitraum auf 168 Funde. Die 10 x 10 km-UTM-Rasterfeld-Kartierung zeigt eine gleichmäßige Verbreitung in Portugal, in Spanien dagegen eine diskontinuierliche. Beschreibende Verbreitungsmodelle erbrachten AUC-Werte (Area Under the Curve statistics) von 0,89–0,99 in Portugal und 0,97–0,98 in Spanien. Von einem Land zum anderen extrapolierte Modelle hatten AUC-Werte von 0,83–0,93 (Spanien nach Portugal) und 0,94–0,97 (Portugal nach Spanien). Wir schließen daraus, dass bereits kleine Datenmengen gute Verbreitungsmodelle erbringen und mehr Wissen nicht unbedingt zu verbesserten Modellen führt. Die wahrscheinlichste Erklärung für die einheitlich hohe Eignung der beschreibenden und extrapolierten Modelle ist die enge ökologische Nische von *Chioglossa lusitanica*. Sie lässt sich gut durch eine kleine Zahl von Umweltparametern beschreiben, unter denen die Menge jährlicher Niederschläge der wichtigste Faktor ist.

Schlüsselbegriffe: Kartierung, Verbreitung, Modellierung, Umweltparameter, Portugal, Spanien, Goldstreifensalamander, *Chioglossa lusitanica*.

Summary

We document the development of knowledge regarding the distribution of *Chioglossa lusitanica* on the Iberian Peninsula and we analyse how the data increase affects the reliability and usefulness of ecographical models, e.g. as guidance for conservation measures. In Portugal the number of records increased from just the type locality in 1864, to 13 in 1957, to 54 in 1995, to 202 in 1999 and to 278 at the present day. In Spain the number increased over the same period from zero to 168. At the UTM10 grid cell scale the recorded distribution is continuous in Portugal and patchy in Spain. Descriptive distributions models yielded AUC scores of 0.89–0.99 in Portugal and 0.97–0.98 in Spain. Models extrapolated from one country to the other had AUC scores of

0.83–0.93 (Spain to Portugal) and 0.94–0.97 (Portugal to Spain). We conclude that small data sets produced good distribution models and more knowledge did not translate into markedly improved models. The most likely explanation for the consistent high fit of the descriptive as well as extrapolated models is the narrow ecological niche of *Chioglossa lusitanica*, which seems to be well described by a small set of environmental parameters, among which a high level of annual precipitation is the most important one.

Key words: Mapping, distribution, ecographical model, environmental parameters, Portugal, Spain, golden-striped salamander, *Chioglossa lusitanica*.

Introduction

The golden-striped salamander *Chioglossa lusitanica* Bocage, 1864 is a species endemic to the northwest of the Iberian Peninsula. It inhabits streamside habitats, mostly in humid mountain areas. It is the only living representative of its genus and possesses some unusual morpho-physiological traits, including a thin body and a long tail (of about 2/3 of the total length), potential autotomy of the tail and the absence of functional lungs. These peculiar characters are shared with its sister-species, the Caucasian salamander *Mertensiella caucasica* (family Salamandridae) and with several Nearctic plethodontid salamanders (family Plethodontidae), revealing a remarkable convergent adaptation to streamside habitats.

Following its discovery and formal description in 1864, knowledge on the life history of *Chioglossa lusitanica* has progressed slowly through the accumulation of mostly incidental observations. The first dedicated attempt to elucidate the species' ecological requirements, life history parameters and distribution was that of GOUX (1957). Comprehensive autecological studies were carried out in the late 1970's and the '80's by ARNTZEN (1981, 1984, 1994 a, b, 1995) and VENCES (1990). For an overview of the currently available knowledge on the natural history of the species see ARNTZEN (1999); on conservation status see TEIXEIRA et al. (1999). More recently, the emphasis in research has shifted from the gathering of ecological and natural history data towards the study of populations genetic structure and diversity (ALEXANDRINO et al. 1997, 2000, 2002, SEQUEIRA et al. 2005a, b) and the extensive surveying and rigorous spatial modelling of distribution data, starting with TEIXEIRA et al. (2001). Essentially the same distribution data set is further explored for modelling the potential effects of climate change on the species distribution (TEIXEIRA & ARNTZEN 2002) and the modelling of an internal subspecies border (ARNTZEN & ALEXANDRINO 2004). The distribution data set also contributed to the comparative analyses of ecographical methods (TEIXEIRA & FERRAND 2001, SEGURADO & ARAÚJO 2004) and, in combination with genetic data, to phylogeographic and hybrid zone research (ALEXANDRINO et al. in press, SEQUEIRA et al. 2005a). Aims of the present paper are to document the development of knowledge on the distribution of *Chioglossa lusitanica* and to analyse how data increase affected the reliability and usefulness of the resulting distribution models. The data will be re-evaluated with the help of a Geographical Information System (GIS) under the criterion of model predictive performance, meaning that models constructed for Portugal will be evaluated in Spain and vice versa. Whereas *Chioglossa* *lusitanica* in Portugal is well surveyed, records for Spain are less dense and unevenly distributed. We therefore investigated the effect of a weighting variable designed to counter the effect of search effort varying per grid cell.

Material and methods

Distributional data

Distributional data that we analyse are as published in AELLEN (1965), ARNTZEN (1981), MALKMUS (1995), TEIXEIRA et al. (2001) and PLEGUEZUELOS et al. (2002) at the UTM10 grid cell system and MALKMUS (2004) at the UTM5 grid cell system. The more or less exact localities from dot maps were fitted to the UTM10 grid cell system prior to analysis. Most efforts were restricted to either Portugal or Spain whereas other studies dealt with both countries. Doubtful records and potential introductions were deleted from the analysis. The data at the UTM20 scale in PLEGUEZUELOS (1997) that appear to be shifted out of the correct latitudinal position were adjusted on the basis of the UTM100 grid.

Environmental data

Twenty-three ecologically meaningful environmental parameters were pre-selected for analysis. For 18 variables information was available in digital format for Portugal (DGA 1995). A vegetation map (normalised difference vegetation index or NDVI) was obtained courtesy of the Royal Dutch Meteorological Institute (KNMI). An altitude map was taken from the internet[1] and used to produce a relief map by a set of filter operations (ILWIS 3.0 2001). Maps on the mean January and July temperature were digitised from the Portuguese climate atlas (SCN 1974). Variables were (de)selected using criteria of i) redundancy at $r_s > 0.8$, ii) availability for both Portugal and Spain and iii) promise in terms of the species' life history. The following 13 variables were retained: acidity of surface water (ACID, pH in 14 classes), altitude (ALTI, in m asl), frost days (FROD, in days), frost months (FROM, in months), hardness of the water (HARD, $CaCO_3$ mg/l in 17 classes), humidity of the air (HUMI, in %), insolation (INSO, in hours), lithology (LITH, in the classes, sedimentary, sedimentary and metamorphic and igneous), vegetation index (NDVI), annual precipitation (PRET, in mm), relief (RELI, in arbitrary scale), average temperature over the year (TEMP, in °C) and for July (TJUL, in °C). Data for Spain were digitised from the Atlas Nacional de España (IGN 1992). All variables (except LITH) were standardized to an average of zero and standard deviation of unity, to increase the comparability of their effects. The variables were introduced into ILWIS (ILWIS 3.0 2001) GIS analytical software as raster layers with 1 km spatial resolution. Mean values for UTM10 and UTM5 grid cells were obtained by averaging the data (modal values for the categorical variable LITH).

[1] http://edcwww.cr.usgs.gov/

Analysis and modelling

Logistic regression analyses were performed with SPSS 12 (SPSS 2003) with a forward stepwise addition of independent variables, with Bonferroni correction to the initial $\alpha = 0.05$ (HOLM 1979). The impact of presences and absences was equilibrated through a weighting variable. Each of the thirty-four records at the UTM10 scale in MALKMUS (2004) were dealt with as four records at the UTM5 grid and in the statistical analyses downweighted by a factor 4 each. Extrapolation of the models for Spain was performed on the basis of nine environmental variables for which data were available (all but ACID, FROM, HARD and LITH). The strength of agreement among distribution data and distribution models was summarized with the 'Area Under the Curve' statistics (AUC, determined from so-called Receiver Operated Character plots; FIELDINGS & BELL 1997, PEARCE & FERRIER 2000) in SPSS.

Search effort is defined as $E = (N_{obs}/N_{max})^2$, with N_{obs} = the number of amphibian and reptile species actually observed and N_{max} = the maximum number of species that could be observed in a grid cell, according to grid cell data and range maps from national surveys (GODINHO et al. 1999, PLEGUEZUELOS et al. 2002), respectively. E_{Cl} equals E with data for *Chioglossa lusitanica* taken out of consideration. These functions incorporate the notion that cells with greater surveying effort will have more species reported, but that, once the effort becomes substantial, new species will be added only slowly.

Results

Mapping history

Eighteen studies dealing with the distribution of *Chioglossa lusitanica* are listed in Table 1. The number of records in Portugal increased from just the type locality 'Buçaco' 'near Coimbra' in Portugal in 1864, to n = 13 in 1957, to n = 54 in 1995 and to n > 200 in 1999 (Fig. 1). Inspection of the map reveals that the data currently available for Portugal form a continuous or near-continuous recording at the UTM10 grid cell spatial scale. The further increase to n = 278 by 2004 (MALKMUS 2004) does not represent an extension of the range, but a four times more detailed representation at the UTM5 scale. The number of records in Spain increased over the last half century from n = 7 to n = 168 and appears as yet patchy. Some observations were reported out of the known range of the species: BOSCÁ (1880, 1881) cites the species for Elvas in the Alentejo, PÉREZ ARCAS (1874) and BOSCÁ (1877) cite the species for the mountains of La Serrota near Avila, Spain and VIEIRA (1886) cites the species in the Serra de Sintra near Lisbon whereas SEABRA (1943) mentions the introduction of some individuals from Buçaco in this area half-century later.

Descriptive and predictive distribution models

The one and only parameter consistently selected in all models is PRET, in which the presence of *Chioglossa lusitanica* is associated with high levels of precipitation (Table 2).

Tab. 1: Publications concerned with mapping the distribution of *Chioglossa lusitanica* in Portugal and Spain. UTM10 is the Universal Transverse Mercator grid with 10 x 10 km sized grid cells. n. a. = not applicable.
Veröffentlichungen zur Verbreitung von *Chioglossa lusitanica* in Portugal und Spanien. UTM10 ist das Universal Transverse Mercator-Gitternetz mit 10 x 10-km Rasterfeldern. n.a. = nicht anwendbar.

	number of data points		representation	distribution model (DM) and remarks
	Portugal	Spain		
BOCAGE 1864	1	0	descriptive	type locality
GOUX 1957	13	7	descriptive	
AELLEN 1965	15	9	dot map	
CRESPO 1971	23	n.a.	dot map	
ARNTZEN 1981	34	21	dot map	DM by overlap analysis, entire species range
MALKMUS 1982	33	n.a.	quarter military maps	
SALVADOR 1985	33	36	dot map	
CRESPO & OLIVEIRA 1989	44	n.a.	UTM10	
MALKMUS 1995	54	n.a.	UTM10	
PLEGUEZUELOS 1997	21	52	UTM20	
GODINHO et al. 1999	206	n.a.	UTM10	
SALVADOR & GARCIA-PARIS 2001	70	51	UTM20	
TEIXEIRA et al. 2001	202	none	UTM10	DM by logistic regression, entire species range
PLEGUEZUELOS et al. 2002	n.a.	168	UTM10	
TEIXEIRA & ARNTZEN 2002	202	n.a.	UTM10	DM by logistic regression and discriminant analysis, potential distributions under climate change
ARNTZEN & ALEXANDRINO 2004	202	n.a.	UTM10	DM by logistic regression, contact zone of potential subspecies in Portugal
MALKMUS 2004	278	n.a.	UTM5	
SEGURADO & ARAUJO 2004	207	n.a.	UTM10	comparison of analytical methods

Low altitude (ALTI), low insolation (INSO), low summer temperatures (TJUL) and high humidity (HUMI) figure in most but not all of the models. The parameter relief (RELI) is frequently selected, but, depending the model, with a positive or a negative sign. The parameter annual number of frost days (FROD) is selected in the three Spanish models and in none of the Portuguese models.

Distribution models for Portugal derived with data from Portugal – that is, descriptive models – yielded AUC scores ranging from 0.89–0.99. Descriptive models for Spain had AUC ranging from 0.97–0.98 (Table 3). When applying the predictive models to the neighbouring country, i.e. in predictive mode, AUC-values ranged from 0.94–0.97 for Portuguese models that where extrapolated over Spain and from 0.83–0.93 for Spanish models that were extrapolated over Portugal. All models suggest the presence of *Chioglossa lusitanica* in the eastern Cantabrian mountains and the western part of the Pyrenees, that is far outside the known range of the species (Fig. 2). Conversely, not all models suggest the presence of the species in the mountains of central Portugal (e.g., Serra de Estrela, Serra de Lousã) even though this area is known to be inhabited by *Chioglossa lusitanica*. Application of a weighting factor reflecting search affort (E_{CI}) did not markedly improve either the descriptive modelling results for Spain or the predictive modelling results for Portugal.

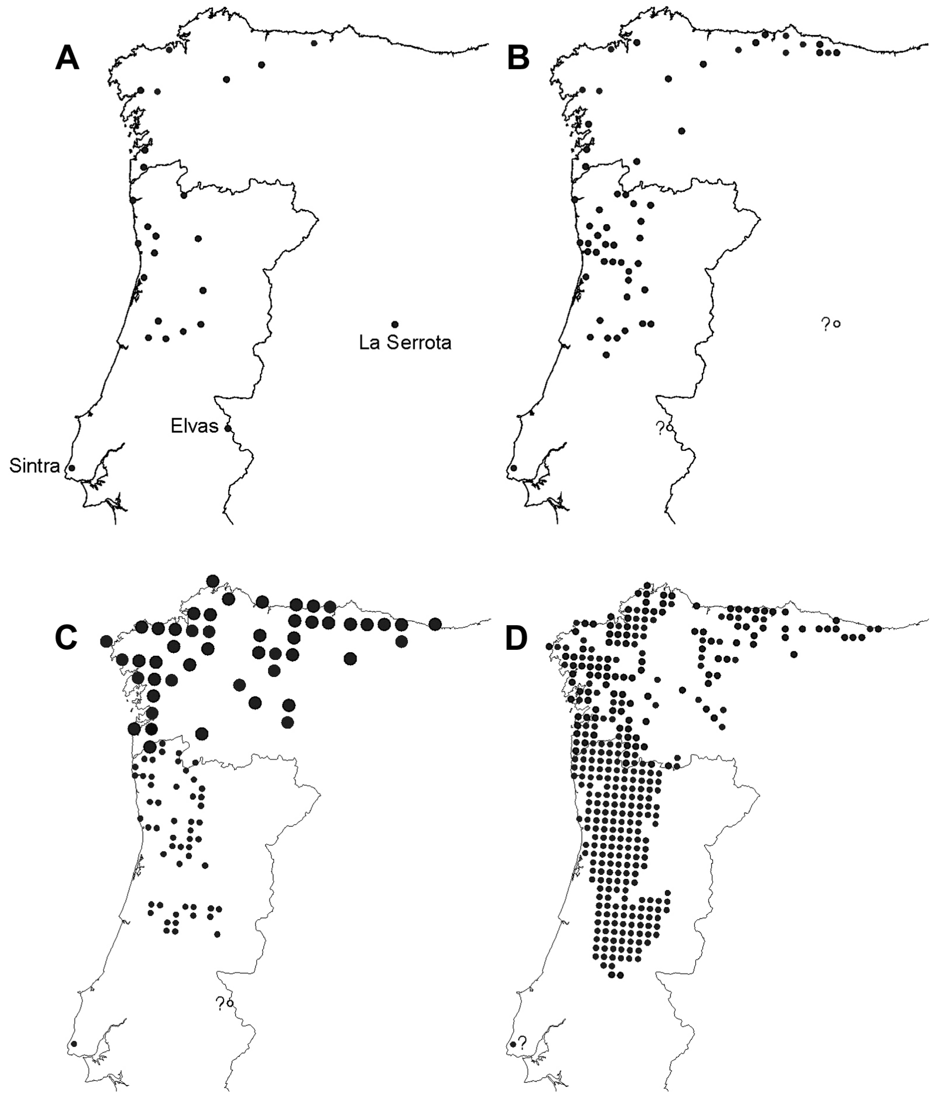

Fig. 1: Development of knowledge on the distribution of *Chioglossa lusitanica* presented at the UTM 10 x 10 km scale, adapted from: A – AELLEN (1965), B – ARNTZEN (1981), C – MALKMUS (1995) and PLEGUEZUELOS (at UTM 20 x 20 km, 1997) and D – TEIXEIRA et al. (2001) and PLEGUEZUELOS et al. (2002).
Fortschritte der Kenntnis der Verbreitung von *Chioglossa lusitanica* auf der Basis des UTM 10 x 10 km-Gitternetzes, nach A – AELLEN (1965), B – ARNTZEN (1981), C – MALKMUS (1995) und PLEGUEZUELOS (UTM 20 x 20 km, 1997) und D – TEIXEIRA et al. (2001) und PLEGUEZUELOS et al. (2002).

Discussion

The knowledge on the distribution of *C. lusitanica* has dramatically increased over the last half-century, starting with Goux' seminal publication (GOUX 1957). Most of the gain can be attributed to the surveying programme carried out in the framework of

Tab. 2: Distribution models for *Chioglossa lusitanica* made with logistic regression and increasing numbers of observations (see Table 1). Models for Portugal are made with 13 or 9 environmental variables available for selection (see text). Environmental data are standardized, except for LITH. Parameters with large effect (values >1) are shown in boldface type.
ACID = acidity of surface water (pH in 14 classes), ALTI = altitude (in m asl), FROD = frost days, FROM = frost months, HARD = hardness of the water ($CaCO_3$ mg/l in 17 classes), HUMI = humidity of the air (in %), INSO = insolation (in hours), LITH = lithology (in the classes, sedimentary, sedimentary and metamorphic and igneous), NDVI = vegetation index, PRET = annual precipitation (in mm), RELI = relief (in arbitrary scale), TEMP = average temperature over the year (in °C) and TJUL = temperature for July (in °C)

Modelle der Verbreitung von *Chioglossa lusitanica* mit logistischer Regression und größer werdender Zahl von Beobachtungen (vgl. Tab. 1). Die Modelle für Portugal wurden mit 13 und 9 Umweltvariablen (siehe Text) gerechnet. Die Umweltdaten wurden standardisiert, außer LITH. Parameter mit großer Wirkung (Werte >1) sind fett hervogehoben.
Abkürzungen: ACID = Säuregehalt des Oberflächenwassers (pH in 14 Stufen), ALTI = Höhe (in m NN), FROD = Frosttage, FROM = Frostmonate, HARD = Härte des Wassers ($CaCO_3$ mg/l in 17 Klassen), HUMI = Luftfeuchtigkeit (in %), INSO = Einstrahlung (in Stunden), LITH = Gesteine (in den Klassen sedimentär, sedimentär und metamorph und eruptiv), NDVI = Vegetationsindex, PRET = jährliche Niederschläge (in mm), RELI = Relief (in beliebiger Skalierung), TEMP = Jahresdurchschnittstemperatur (in °C) und TJUL = Temperatur im Juli (in °C).

	Available for	Model equation*														Con-
Data source	selection***	ACID	ALTI	FROD	FROM	HARD	HUMI	INSO	LITH**		NDVI	PRET	RELI	TEMP	TJUL	stant
Portugal																
AELLEN 1965	13 variables						0,891	**-1.243**	-0,623	1,450	-0.796	**1.277**	**-1,543**			-2,240
	9 variables	…			…	…	0.676	-0.880	…		-0.800	**1.505**	**-1,179**			-1,586
ARNTZEN 1981	13 variables	**-1.734**	-0.640					-0.935			-0.564	0.821				-2.309
	9 variables	…			…	…	0.595	**-1.031**	…		-0.813	**1.355**	-0.496			-1.677
MALKMUS 1995	13 variables				-0.445			-0.858				**1.413**				-1.624
	9 variables	…	**-1.123**		…	…	0.386	-0.656	…			**1.050**	0.644	-0.826		-1.847
TEIXEIRA et al. 2001	13 variables				**-1.112**	**-3.613**						**3.215**	**1.051**		**-1.186**	-4.422
	9 variables	…	-0.859		…	…			…			**3.424**	**1.556**		**-1.006**	-2.237
MALKMUS 2004	13 variables					**-2.297**		0.383				**1.207**	0.609		-0.886	-2.434
	9 variables	…			…	…			…			**1.505**	0.669		-0.582	-1.300
Spain																
AELLEN 1965	9 variables	…		**-1.430**	…	…		**-4.974**	…			**3.686**	**-2.654**			-15.634
ARNTZEN 1981	9 variables	…	**-1.091**	-0.382	…	…	0.439	-0.687	…		0.449	0.665		0.761	**-1.744**	-4.593
PLEGUEZUELOS et al. 2002	9 variables	…	-0.983	-0.473	…	…		-0.360	…			**1.775**	-0.498		**-1.653**	-4.363
	idem#	…	**-1.595**		…	…			…			**1.900**	-0.480		**-2.140**	-4.838

* Model equation for e.g. AELLEN (1965) with nine variables available for selection is:
probability of occurrence = (1/(1+exp(-0.676*HUMI+0.88*INSO+0.8*NDVI-1.505*PRET+1.179*RELI+1.586))).
** The categorical variable 'LITH' Is represented by two binary variables.
*** Remember that 13 and nine environmental variables are documented for Portugal and Spain, respectively.
… Variable not available for selection.
With search-effort weighting applied.

the EC-Life Programme on five Iberian amphibians and reptiles (see TEIXEIRA et al. 1999 for *C. lusitanica*, and furthermore ARAÚJO et al. 1997, BRITO et al. 1998, MOREIRA et al. 1999 for data on *Emys orbicularis*, *Mauremys leprosa*, *Lacerta schreiberi* and *Archeolacerta monticola*). The documented range of *C. lusitanica* in Portugal is nearly continuous at the UTM10-scale. Moreover, a string of UTM-grid cells bordering the perceived range of *Chioglossa lusitanica* was documented in which the species was not found, despite surveying efforts no less intense then where its presence was documented. The current status in Portugal is that of few perceived 'false absences' (grid cells for which the species was not recorded despite its actual presence). The distribution data for Spain in contrast appear uneven as observations are more or less clumped along the western and northern Atlantic coastline, with few records in between and no records east of the Picos the Europa.

Tab. 3: Fit of various distribution models to the presence/absence data of *Chioglossa lusitanica*, expressed by the AUC-statistic and asymptotic standard error (SE). Descriptive distribution models are derived with data from the very country whereas predictive models are derived with data from the neighbouring country. N. a. = not applicable.
Eignung verschiedener Verbreitungsmodelle zur Erklärung der An- und Abwesenheit von *Chioglossa lusitanica*, ausgedrückt mit der AUC-Statistik und dem asymptotischem standardmäßigen Fehler (SE). Beschreibende Verbreitungsmodelle leiten sich aus Daten des von der Art besiedelten Landes, während sich vohersagende Modelle aus Daten benachbarter Gebiete ableiten. N. a. = nicht anwendbar.

Data source	Variables available	AUC-values ± SE in models	
	for selection	Descriptive	Predictive
Portugal			
AELLEN 1965	13	0.908 ± 0.024	N. a.
	9	0.886 ± 0.024	0.968 ± 0.003
ARNTZEN 1981	13	0.888 ± 0.017	N. a.
	9	0.886 ± 0.015	0.963 ± 0.003
MALKMUS 1995	13	0.921 ± 0.011	N. a.
	9	0.927 ± 0.011	0.959 ± 0.004
TEIXEIRA et al. 2001	13	0.991 ± 0.002	N. a.
	9	0.986 ± 0.003	0.958 ± 0.005
MALKMUS 2004	13	0.908 ± 0.006	N. a.
	9	0.904 ± 0.006	0.944 ± 0.005
Spain			
AELLEN 1965	9	0.979 ± 0.004	0.911 ± 0.010
ARNTZEN 1981	9	0.966 ± 0.005	0.833 ± 0.015
PLEGUEZUELOS et al. 2002	9	0.978 ± 0.002	0.932 ± 0.009
	9*	0.977 ± 0.002	0.923 ± 0.010

* With search-effort weighting applied.

The presence of *C. lusitanica* at two localities deep inland is contradicted by the modelled distribution data (Elvas, Portugal; BOSCÁ 1880), or weakly supported at best (La Serrota, Spain; PEREZ ARCAS 1874). With no confirmation for well over a century we consider the records erroneous. Its presence in Serra de Sintra, only confirmed once in 1993 by G.-D. GUEX (in ARNTZEN 1999), poses the questions if there is still a viable population and whether the surviving population is autochtonous as cited by VIEIRA (1886) and suggested by some of the distribution models, or the descendant of a c. 60-year old introduction with animals stemming from Buçaco as mentioned by SEABRA (1943). The area has been intensively searched prior to as well as after 1993 (ALMAÇA 1959, TEIXEIRA et al. 2001) with no sightings of the species. Once relocated, this population should be investigated with the help of molecular genetic markers. The null hypothesis of an autochtonous presence of *C. lusitanica* in the Serra de Sintra is that the mitochondrial DNA composition is compatible with the phylogeographic pattern across the range (ALEXANDRINO et al. 2000, 2002, SEQUEIRA et al. 2005a). Spatial variation at highly polymorphic nuclear loci (SEQUEIRA et al. 2005b) should behave similarly. Tests based on population demographic parameters (e.g., genetic bottleneck) are less promising, considering the long period of population isolation and marginal existence under both – autochtonous and allochtonous – scenarios.

We consider the range of *Chioglossa lusitanica* in Portugal well-documented. The near-complete surveying at the UTM10 scale did not, however, affect much the fit of the

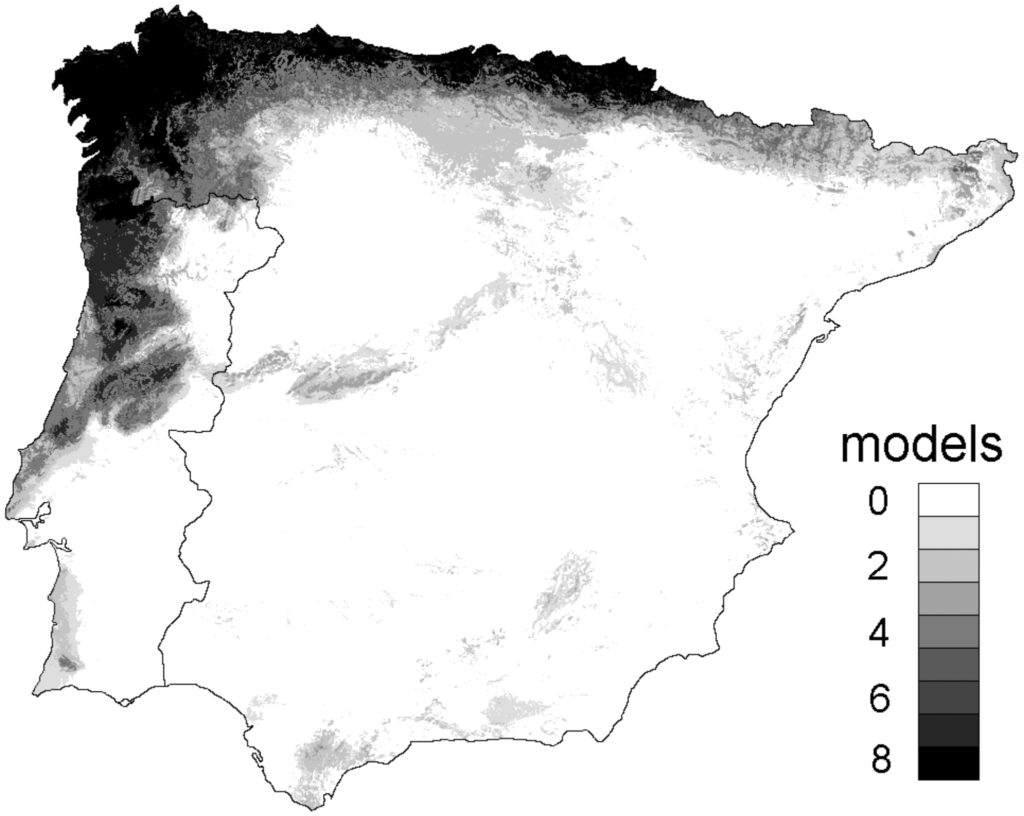

Fig. 2: Cumulative representation of the eight distribution models of *Chioglossa lusitanica* described in Table 2. Shading represents the number of models supporting the presence the species.
Je dunkler die Fläche desto mehr der acht Verbreitungsmodelle von *Chioglossa lusitanica*, beschrieben in Tabelle 2, erklären kumulativ die Anwesenheit der Art.

descriptive distribution models that was high across all analyses (0.89 < AUC < 0.99). The model on the basis of 15 Portuguese data points documented by AELLEN (1965) yielded an AUC-value at 92% of the highest value obtained with the modelling of 202 data points (Tables 1 and 3). In other words, in this species sets with few observations gave rise to good predictive models, as did small, moderate and large data sets. A similar result was obtained when testing the effect of sample size on the accuracy of distribution models in Mexican birds, with 90% of maximum accuracy obtained with ten data points and near-maximum accuracy obtained with 50 data points (STOCKWELL & PETERSON 2002). Interestingly, the distinctly incomplete surveying of *Chioglossa lusitanica* at the UTM5 scale (in MALKMUS 2004) reintroduces false absences and causes a concomitant drop in AUC-values to 0.91. Comparison of the available models indicates that those derived with logistic regression of a large number of observations yield more spatial resolution than does e.g. overlap analysis with few data. Nevertheless, all models are fairly similar and it appears that the progress made by simply adding more and more distribution records was not substantial.

The most likely explanation for the consistent high fit of the distribution models is the narrow ecological niche of *Chioglossa lusitanica*. Intuition and field observations would point to annual precipitation as a prime parameter positively associated with the species' presence, as did the first formal but fairly unsophisticated model produced by Overlap Analysis (ARNTZEN 1981) and indeed all models ever since (Table 2). The single parameter annual precipitation encompasses most local environmental factors that are considered important for the species' presence, namely a high humidity of soil and air, rich riparian vegetation and a strong and well-oxygenated water current. The other variables frequently selected in the models, namely altitude (low), insolation (low), summer temperature (low) and humidity (high) describe an environmental envelope characteristic of humid hilly and low mountainous regions with mild summers. In a laboratory study *C. lusitanica* demonstrated a clear preference for high humidity substrata (GOUX 1957) and in a local field study the parameters affecting activity and abundance were precipitation, humidity and the availability of shelter (SEQUEIRA et al. 2001). Considering the entire range, *C. lusitanica* is rarely found at altitudes of over 1000 m (ARNTZEN 1981, MALKMUS 1995, TEIXEIRA et al. 1999). The negative effect of high altitude on the presence of *C. lusitanica* may reflect low temperature and physiological drought and the thinning out of shade and shelter, provided by riparian and streamside vegetation. High summer temperatures and high levels of insolation describe dry regions that are clearly unsuitable for the species. Moreover, high summer temperature affects the availability of water (through evaporation) and reduces the potential amount of dissolved oxygen in the brooks with a negative effect on the survival of the larvae.

The inclusion of the variables lithology, pH and hardness of the water in some of the models point to characters of the substratum directly or indirectly affecting species occurrence. In those models *C. lusitanica* appears more often absent on sedimentary soils, including limestone with typically mineral-rich and slightly alkaline surface water. VENCES (1990) mentions that *C. lusitanica* is normally associated to brooks of high acidity (pH 4.5–6.5), even though low pH is among the parameters affecting larval growth negatively (HARTE & HOFFMAN 1989, JUTERBOCK 1990, LIMA et al. 2000). Interestingly, the absence of the species in eastern Asturias has been attributed to calcareous soils that would act as a barrier to range expansion (VENCES 1997), probably because the limestone does not keep the water and moisture. Another example is provided by JAEGER (1971) who studied the tolerance limits of two American salamanders and suggested that soil humidity is a key factor to explain their ranges.

Hilliness of the terrain is widely seen as a typical characteristic of the *C. lusitanica* habitat (e.g. TEIXEIRA et al. 2001) and the inclusion of this parameter with a negative sign in some models is puzzling (Table 2). Our tentative explanations are as follows. (i) It is a chance effect due to few data. This explanation applies to four models out of five. (ii) Low relief compensates for low altitude. This explanation also applies to four models out of five. (iii) Low relief and/or low altitude are selected in models for Spain, to capture the absence of *C. lusitanica* in the Cantabrian mountains, from the Picos de Europa to the Pyrenees. This applies to three models out of three. (iv) Relief compensates for a parameter for which we have no data, such as for example LITH in Spain. The absence of *C. lusitanica* east of the Picos de Europa seems real, but is not captured by any of the distribution models. It is conceivable that *C. lusitanica* is still in the process of expanding its range over this area (ALEXANDRINO et al. 2000, 2002) and obviously, non-equilibrium situations are difficult to model accurately. Alternatively, the discrepancy between the observed and predicted distributions could be due to the unavailability of prime environmental variables in the analysis (e.g., LITH for Spain; TEIXEIRA et al. 2001). As a way forward, the two alternatives to proceed are: i) Working with abundance data, that is, the density of *Chioglossa lusitanica* instead of its presence/absence. This is a demanding task because with the currently available techniques for capture-mark-recapture even a single population size estimate involves extensive field work. ii) Working with the exact localities of presence and absence within the species range, coupled with accurate and precise environmental data. This appears a promising approach that could be targeted to test a priori formulated hypotheses generated by documented knowledge on the environment, such as, for example, calcareous vs. non-calcareous mountains, the presence of a competitor species, etc. In addition to the present study on a habitat specialist, it would be interesting to analyse the effect of an increase in distribution data on ecographical models for habitat generalist species.

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