Potential distribution of the endangered spider *Macrothele calpeiana*（Araneae，Hexathelidae）and the impact of climate warming *

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Abstract　The aims of this contribution are i）to identify major climate correlates of the distribution of *Macrothele calpeiana*（Walckenaer，1805）in the Iberian Peninsula in order to predict its potential distribution；ii）to elaborate a hypothesis for the distribution of the spider in the Iberian Peninsula；iii）to identify suitable places for the species in both North Africa and the entire Mediterranean region through extrapolation of model predictions；and iv）to predict the impact of climate warming on the potential spider distribution．Generalized Linear Models were used to develop a potential distribution predictive model．Potential Iberian Peninsula distribution extends through a large part of Portugal where the spider has not been found．Historical factors are proposed as contributors to the absence of *M．calpeiana* from suitable areas．Existence of suitable conditions for the species in North Africa，and the absence of the genus there，favours the oriental origin of a *Macrothele* ancestor．Extrapolation to the Mediterranean region highlighted suitable territory in the Aegean area，where *M．cretica* Kulczynski，1903，the other European *Macrothele* species，is found．Climate warming will negatively affect the existing Iberian *M．calpeiana* populations because it will reduce and fragment potential North African habitat．Confirmation of species presence，or absence，in much of Portugal and North Africa is a priority，as well as the development of phylogenetic studies of the genus to establish a solid hypothesis of *Macrothele* origin and dispersion history［*Acta Zoologica Sinica* 53（5）：865 – 876，2007］.

Key words　Climate warming，Iberian Peninsula，*Macrothele calpeiana*，Mediterranean region，North Africa，Potential distribution model

一种濒危大疣蛛的潜在分布区域以及气候变暖的影响 *

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摘　要　本研究的目的是 i）确定伊比利亚半岛一种大疣蛛（*Macrothele calpeiana*）分布的气候相关性以预测其潜在分布，ii）详细阐述该物种在伊比利亚半岛的分布假说，iii）通过推断模型预测确认该物种在北非和整个地中海地区的适合区域，iv）预测气候变暖对蜘蛛潜在分布区的影响。基于物种的存在、远离目前环境条件下的可能缺失以及其它的气候参数，使用广义线性模型发展了潜在分布的可预测模型。蜘蛛在伊比利亚半岛上的潜在分布远大于目前已知的分布区，延伸到尚未发现蜘蛛分布的葡萄牙广大地区。本文提出了该种大疣蛛在适合分布区域内没有分布的历史因素。北非具有适合该物种的条件但却没有该属物种的分布支持了大疣蛛（*Macrothele*）祖先的东方起源假说。对地中海地区蜘蛛分布的推断突出显示了阿根廷地区有合适的分布区，该地区也发现有另一种欧洲大疣蛛。气候变暖将对现存于伊比利亚的 *M．calpeiana* 种群产生负面影响，因为气候变暖将减少并破碎化蜘蛛在北非的潜在栖地。目前，急需确认在葡萄牙广大地区是否存在蜘蛛物种，发展对该属的系统发育研究以确定大疣蛛属起源和扩散史的理论［动物学报 53（5）：865 – 876，2006］。

关键词　气候变暖　伊比利亚半岛　大疣蛛　地中海地区　北非　潜在分布模型

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The genus *Macrothele* Ausserer, 1871, is composed of 26 species distributed from Western Europe to Japan, and belongs to the family Hexathelidae, a spider family with a supposedly Gondwanic origin (Raven, 1980). The family is composed of 11 genera, the majority occurring in the Australian region (Platnick, 2006) and only two (*Mediothele* Raven and Platnick, 1978 and *Scotinoecus* Simon, 1892) endemic to South America (Platnick, 2006). As with some Asian species, the taxonomic status of four central African *Macrothele* species (Platnick, 2006) is uncertain due to lack of proper descriptions and unknown males (Snazell and Allison, 1989). One of these African *Macrothele* species was described in 1903, while the other three where described in 1965, with no new data since. Descriptions of the two European species, *M. cretica* Kulcyznski, 1903, endemic to the island of Crete, and *M. calpeiana* (Walckenaer, 1805) from the Iberian Peninsula, have recently been revised (see Blasco and Ferrández, 1986; Snazell and Allison, 1989).

M. calpeiana is included in the Bern and Habitat directives. The purpose of the Bern directive, signed in 1981, is to protect the wildlife and habitats in Europe by the creation of national policies and the cooperation of member states. The Habitat directive was signed in 1992 in Rio de Janeiro, with the aim of protecting characteristic and rare habitats as well as endangered and endemic species in the European Union. Since the work of Blasco and Ferrández (1986), new *M. calpeiana* locations in the Iberian Peninsula have slowly been elucidating its distribution. Currently, *M. calpeiana* is known from six apparently isolated core Iberian areas (Fig. 1). In the Iberian Peninsula the distribution of this species seems to be mainly determined by climate variables. Its occurrence is favoured by high annual precipitation, high precipitation seasonality, warm winters and cooler summer temperatures (Jiménez-Valverde and Lobo, 2006a). Of the two North African records, the first, published in 1849 in El Arrouch, Algeria, is doubtful due to the deterioration of the specimen (Lucas, 1849); the second, from the city of Ceuta, has recently been confirmed (Ferrández and Fernández de Céspedes, 1996). These African records have led some authors to hypothesize the possible existence of this species in North Africa (Helsdingen and Decae, 1992), and to suggest that *M. calpeiana* could have colonized the Iberian Peninsula from there in recent times. However, Ferrández et al. (1998) proposed that the species colonized the Iberian Peninsula during the early Tertiary, and Ferrández and Fernández de Céspedes (1996) suggested that given the anthropogenic habitat of the record from Ceuta, this particular population may be a recent introduction. A recent phylogenetic analysis proposes an African colonization during the Messinian crisis (Arnedo and Ferrández, 2007), but the population from Ceuta was not included in the study so its origin remains unknown. Arnedo and Ferrández (2007) also suggested that reduction of wider *M. calpeiana* Iberian distribution in the past could have produced the present-day apparent isolation of populations.

Recent developments in acquisition of GIS data and techniques, as well as statistical analyses, enable quantification of species-environment relationships and prediction of geographic distribution from confirmed occurrences (Guisan and Zimmermann, 2000; Scott et al., 2002). Existing distribution maps are improved by such prediction modelling (Bustamante and Seoane, 2004), while their automatic fitting procedures have even outperformed models based on expert opinion (Seoane et al., 2005). Distribution modelling has been widely employed to design field surveys and focus sampling efforts aimed at locating new species or populations (e. g. Raxworthy et al., 2003; Guisan et al., 2006) as well as to explore biogeographic questions (Gallego et al., 2004; Anderson et al., 2002; Lobo et al., 2006; Jiménez-Valverde et al., 2007), among many other uses (see Guisan and Thuiller, 2005 for an overview).

In recent times, model predictions have also been used to simulate the effects of climate warming on species distribution (Peterson et al., 2002; Peterson, 2003; Thuiller et al., 2005a). There is broad agreement among researchers of a direct climate-warming link with greenhouse gas emissions (Oreskes, 2004; King, 2005). Climate change will modify many environmental factors that determine species distribution and abundance (Hulme, 2005; Lovejoy and Hannah, 2005) and there is now undeniable evidence of the impact of climate warming on species range shifts (Parmesan and Yohe, 2003; Root et al., 2003; Hickling et al., 2006). Estimates of potential extinction risks (Thomas et al., 2004; Malcom et al., 2006), most likely from habitat loss and especially pronounced in species with narrow geographic ranges (Thuiller et al., 2005b), point to the seriousness of climate warming.

In this paper we use a modelling technique: i) to identify major climate correlates of *M. calpeiana*, ii) to estimate its potential distribution in the Iberian Peninsula, iii) to extrapolate this distribution to the whole Euro-Mediterranean region, and iv) to simulate changes in extent and location of probable suitable areas under a climate warming scenario. The possible existence of climatically favourable places in North Africa can help us to elaborate a more reliable hypothesis about the presence of this spider in the Iberian Peninsula. We also hope that the improvement of knowledge on the determinants of distribution and the delimitation of potential ranges under climatic warming will facilitate conservation planning for this endangered species.

1　Material and methods

1.1　Biological data

　　M. calpeiana presences（total number of presences: 92）in the Iberian Peninsula were extracted from the literature（Blasco and Ferrández, 1986; Snazell and Allison, 1989; Helsdinge and Decae, 1992; Santos

Lobatón, 1996; Rodríguez and García-Villanueva, 2000; Calvo-Hernández and Santos-Lobatón, 2001; Luque, 2001; Calzada, 2002; Ferrández, 2004）and located in 100 km² UTM squares（Fig.1）. As the appearance of the species is quite distinctive, all presence data were considered reliable.

Fig.1　Distribution of *Macrothele calpeiana*（Walckenaer, 1805）in the Iberian Peninsula

Six core areas are identified. Dots represent known 100 km² UTM squares. Names of rivers mentioned in the text are given. The circle marks the two presence points wrongly predicted by the model as absences. The small map shows a digital elevation model.

1.2　Environmental data

　　Seven potential explanatory environment variables, selected to reflect climate variation in each 100 km² Iberian Peninsula UTM square and based on previous knowledge of the ecology of the spider（Jiménez-Valverde and Lobo, 2006a）are: mean annual temperature（temp）; mean annual maximum temperature（tmax）; mean annual minimum temperature（tmin）; mean annual precipitation（precp）; seasonal precipitation variation（coefficient of variation, precpsea）; precipitation in the wettest month（precpw）; and precipitation in the driest month（precpd）. All variables were obtained from WORLDCLIM interpolated map database, version 1.3（http://biogeo. berkeley. edu/worldclim/worldclim. htm; see Hijmans et al., 2005）.

1.3　Creating probable absences

　　As only *M. calpeiana* presence data is reliable, probable absences were created for modelling the potential distribution. Although there are methods for modelling potential species distribution from presence-only data, these methods tend to overestimate distributions, because of the lack of true absences that would constrain

predictions（Ferrier and Watson, 1997; Zaniewski et al., 2002; Engler et al., 2004）. To reduce such overestimation, use of probable absences has been encouraged（Engler et al., 2004; Lobo et al., 2006; Jiménez-Valverde et al., 2007）.

　　Eight hundred and twenty-eight probable absences（giving a prevalence = 0.1）were selected at random from the area falling outside the envelope defined by the seven environment variable maximums and minimums within the observed presence localities. This so-called niche-based envelope model（see Busby, 1991 and Beaumont et al., 2005）is made up of those environmental conditions, at presence points, suitable for the species. The number of probable absences was selected in order to get a sample size as large as possible while not decreasing prevalence below 0.1, which could otherwise compromise model performance（A. Jiménez-Valverde, J. M Lobo and J. Hortal, unpublished data）.

　　The application of a modelling technique to obtain probable absences distant from the environmental conditions of the presences, and the posterior use of a regressive method, may be considered a circular

procedure. The inevitable consequence is that the final model will show high predictive accuracy. This is inevitable when modelling the potential distribution with climate variables. Potential distributions can be considered as the probable whole distribution ranges in which the species have favourable conditions according to the environmental variables used in the simulations, i. e., geographical simulations in which we try to eliminate the role of restrictive distribution forces such as biotic interactions, historical factors or dispersal limitations (Ricklefs and Schluter, 1993; Hanski, 1998; Pulliam, 1998, 2000). Potential distributions are never known because they do not exist unless the species is in equilibrium with the environmental conditions (it occupies all the *a priori* favourable environmental sites). Thus, strictly speaking, the only validation objective of potential models is not to have a high omission error rate (presences predicted as absences). Obviously, the geographical projections of these models are quite similar to those performed with presence-only methods. The two main reasons for using discrimination methods and probable absences are: 1) regression techniques are well-known by the vast majority of researchers and they are old procedures with a huge literature and a well-established methodology; 2) these methods avoid the use of cells without information, which are indirectly used by presence-only methods, and thus are presumably less affected by false absences, environmental biases and aggregation of occurrence data.

1.4　Modelling process

Among existing modelling methods (see, for example, Guisan and Zimmermann, 2000), regression methods are probably the most popular, due to ease of implementation and interpretation of their results (Lehmann et al., 2002a). Correctly applied, they perform relatively well with a training data set free of major errors (Manel et al., 1999a, b; Moisen and Frescino, 2002; Elith et al., 2006). This study used two regression methods, Generalized Additive Models (GAMs) and Generalized Linear Models (GLMs), the former to explore and the latter to predict.

We applied GAMs (Hastie and Tibshirani, 1990) with a logit link function to explore the relationship between *M. calpeiana* presence/probable absence data and the seven selected environment variables. GAMs are semi-parametric extensions of GLMs, dealing with non-linear and non-monotonic relationships by applying smoothing functions to each predictor (Guisan et al., 2002; Lehmann et al., 2002b). In other words, GAMs can be applied to more complex response shapes than GLMs and fit data more closely for a given number of degrees of freedom (Wintle et al., 2005). This makes GAMs ideal for exploring the shape of the response of spider data to each explanatory variable, in order to subsequently define variable relationship for GLMs model

parametrization (see, for example, Olivier and Wotherspoon, 2005). GAMs with penalized regression splines were used, where the smoothing parameter is estimated by using the Un-Biased Risk Estimator criterion (UBRE), an approximation of the Akaike Information Criterion (AIC; Wood, 2000; Wood and Augustin, 2002). Smoothed terms with four initial degrees of freedom were regressed against the response variable. GAMs were fitted in R (R Development Core Team, 2004) using the mgcv package (Wood, 2004).

Multi-colinearity of independent variables negatively affects automated stepwise variable selection in regression analysis (Feinstein, 1996). To reduce the number of possible correlated factors, Pearson's correlation coefficient (r) was calculated for variables, and groups of correlated factors were defined using an r value $\geqslant 0.8$ (Silva and Barroso, 2004). Variables were replaced by just one factor per group. Factors explaining the smallest deviance in GAMs, or relating in a complex or unrealistic way with presence-absence data, were dropped.

GLMs (McCullagh and Nelder, 1997) were then used to fit the environmental model to the factors selected. GLMs are extensions of linear regressions, able to deal with non-Gaussian probability distributions. Logistic regressions (GLMs with binomial distributions and logit link functions) were selected for the prediction step, as they are less prone to overfitting than GAMs, and so are more likely to produce more reliable generalizations and extrapolations (Reineking and Schröder, 2003; see Olivier and Wotherspoon, 2005 for a case example). Variables selected in the previous step were introduced in the model and further selected by a backward-stepwise procedure (Harrell, 2001). Nested models were tested using AIC criterion (Buckland et al., 1997), a method that penalized the log-likelihood of the model as a function of the number of degrees of freedom. GLMs were fitted in R (R Development Core Team, 2004).

Autocorrelation of residuals was examined to detect possible spatial patterns in the residuals of the prediction function, indicative of any major unaccounted-for variable. Residuals were calculated after correcting for the prevalence bias in logistic probabilities (see below). Moran's I coefficient, which describes the degree of spatial autocorrelation for distinct distance classes, was employed with a lag distance of 30 kilometers. Moran's *I* test was checked for significance with the Bonferroni-corrected significance level (Sawada, 1999).

1.5　Evaluation

Accuracy in model predictions was assessed using a jackknife procedure, a technique which yields relatively unbiased estimates of model performance (see Olden et al., 2002). This procedure excludes one observation, and then the model is parametrized again with the remaining n_1 observations to obtain a predicted probability for the excluded observation. This procedure is repeated n times

（one per observation）, and the receiver operating characteristics（ROC）technique is applied, using the area under the curve（AUC）as a measure of overall accuracy （Fielding and Bell, 1997; Pearce and Ferrier, 2000）. In addition, sensitivity and specificity（presences correctly predicted as presences, and absences correctly predicted as absences, respectively）were also calculated from these new jackknife probabilities. As these two accuracy measures depend on a threshold value, above which probabilities are considered as presences, we applied the threshold which minimizes the difference between sensitivity and specificity（MDT threshold; Jiménez-Valverde and Lobo, 2007）. All validation computations were run in R（R Development Core Team, 2004）.

1.6　Extrapolation of models

The predictive model was projected on North Africa and the entire Mediterranean region. As extrapolation of model predictions beyond the range of values of the variables used in parametrization is quite unreliable, areas within the ranges were first defined and extrapolation was limited to them. To assess the impact of climate warming, models were projected onto a future Iberian Peninsula and North African climate dataset（CCM3 climate model for 2100）, predicting a doubling of CO_2 concentration（see Govindasamy et al., 2003 for details）. Variables for these extrapolation scenarios were obtained from WORLDCLIM（http: //biog eo. berkeley. edu/worldclim/worldclim. htm）.

1.7　Map representations

Probabilities derived from logistic regressions are inevitably affected by prevalence; mean probabilities are biased towards the most common outcome（Cramer, 1999）. Thus, these probabilities cannot be considered indicative of habitat suitability, and they must be rescaled （Jiménez-Valverde and Lobo, 2006b）. For this purpose, we used the favourability function developed by Real et al.（2006）to eliminate the random element from the logistic equation:

$$F = 1 - \frac{1}{1 + e^{\left(\ln\frac{P}{1-P} - \ln\frac{n_1}{n_0} \right)}}$$

where F is the favourability value, P is the logistic probability, n_1 is the number of presences and n_0 is the number of absences.

2　Results

Relationships of the seven variables with *M. calpeiana* presence/probable absence data were statistically significant（χ^2 test, all P values < 0.001, Fig.2）. Precipitation-related variables explained the greatest amount of deviance. Seasonal precipitation variation was the most important variable（66.2% of explained deviance）, with a positive linear relationship. Precipitation in the driest month was the second variable in relevance, explaining a bit less than the former （52.8%）, and with a negative, linear relationship with

spider presence-absence. Mean annual precipitation and precipitation in the wettest month explained 37.7% and 26.4% of deviance, respectively; relations of both with spider presence（maximum probability of presence at ~ 800 mm and ~ 125 mm, respectively）were bell-shaped. Mean annual temperature and mean annual minimum temperature relations with *M. calpeiana* presence-absence were positive, quasi-linear, explaining 26.8% and 24.9% of deviance, respectively. Mean annual maximum temperature was the variable that explains the least deviance（14.6%）. Probability of presence is positively, linearly related with this variable below ~ 25°C, above which the probability reaches an asymptote.

Correlation analysis identified three pairs of highly-correlated variables（$r \geqslant 0.8$）: average monthly precipitation and precipitation in the wettest month; precipitation in the driest month and average monthly maximum temperature; and average monthly mean temperature and average monthly minimum temperature. From the first pair, wettest-month precipitation was discarded as it explained less deviance than its partner. From the second pair, even though it explained less variation than its partner, maximum temperature was selected, since its non-linear relation with *M. calpeiana* suggests better characterization of spider environmental requirements. Additionally, driest-month precipitation was highly correlated with seasonal variation in precipitation（$r = -0.77$）. From the third pair, minimum temperature was selected, as its relation with probability of presence was simpler than that of mean annual temperature, while deviance explained was similar.

As a result of the above-mentioned analysis, the following variables were introduced in the GLM: seasonal variation in precipitation（linearly related with dependent variable）, average monthly precipitation（a second-term polynomial）, average monthly maximum temperature （second-term polynomial）and average monthly minimum temperature（linear）. The final GLM environmental model retained all variables（Table 1）, accounting for

Table 1　Summary of results of the GLM model

Terms	estimate	Std. Error	z value
Intercept	− 38.32	8.23	− 4.65[***]
Tmax	810.69	209.45	3.87[***]
tmax²	− 605.21	141.78	− 4.27[***]
Tmin	− 0.97	0.46	− 2.10[*]
Precp	− 337.91	155.77	− 2.17[*]
precp²	− 632.58	162.50	− 3.89[***]
Precpsea	0.50	0.14	3.50[***]
Measures of fit and predictive accuracy			
$D = 89.98$	AUC = 0.99	Sens = 0.97	Spec = 0.97

D, explained deviance（［null deviance-residual deviance］/null deviance * 100）; AUC, area under the ROC curve; Sens, sensitivity（proportion of presences predicted as presences）; Spec, specificity（proportion of absences predicted as absences）（ [*] < 0.05, [***] < 0.001）.
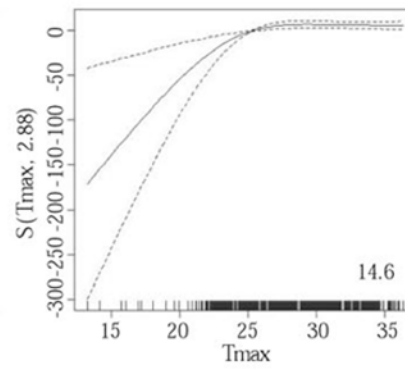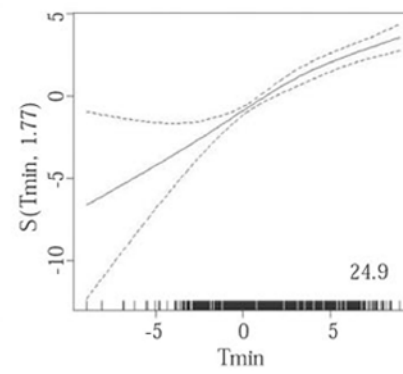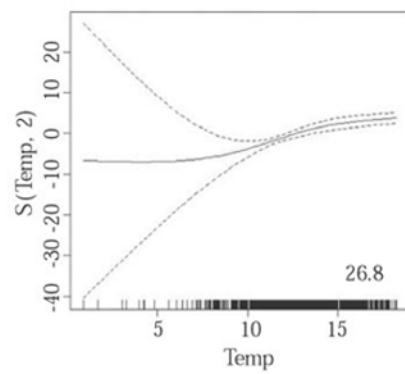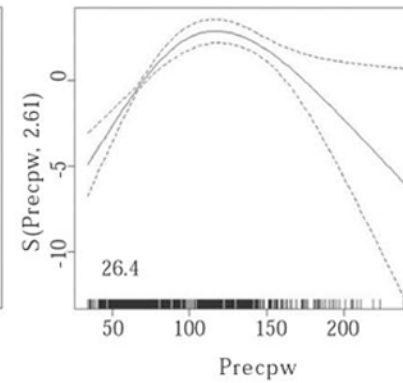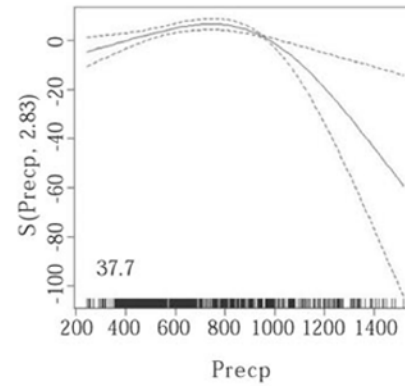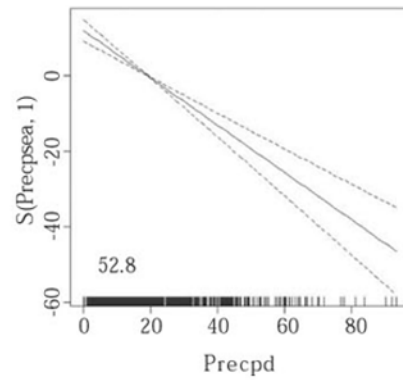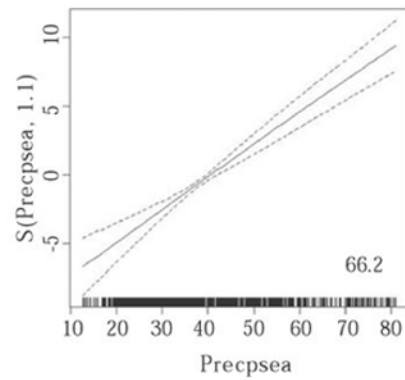
89.98% of deviance, and yielded accuracy measures greater than 0.96. Positive and significant autocorrelation scores, present in the two first distance lags, persisted even though such spatial terms as the third degree polynomial term of latitude and longitude are added (Legendre and Legendre, 1998); addition of these spatial variables after climatic ones did not increase the explained deviance.

Fig.3 illustrates the importance of accounting for prevalence in the mapping of probabilities as an index of habitat suitability, and in the selection of a cut-off to convert probabilities into presence-absence maps. Fig.3A shows the logistic probabilities predicted for the entire Iberian territory. The MDT cut-off yielded the presence-absence map of Fig.3B. The classic 0.5 threshold would yield the map of Fig.3C, which clearly differs from the previous one. Application of the favourability function produced the map of Fig.3D, which can be considered a habitat suitability map due to the elimination of the random element of logistic regression. As expected, application of the 0.5 cut-off to these favourability values produces a presence-absence map virtually identical to the one produced using the MDT criterion. In all the following representations, favourability scores will be used.
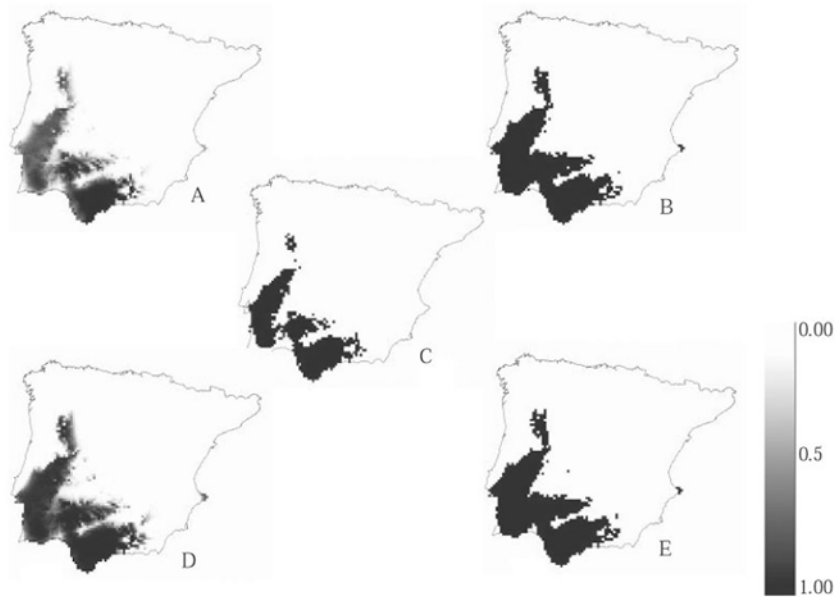

Fig.3   A. Logistic probabilities estimated for the Iberian Peninsula; B. Presence-absence map after applying the cut-off that minimized the difference between sensitivity and specificity to logistic probabilities; C. Presence-absence map after applying the 0.5 cut-off to the logistic probabilities; D. Favourability values estimated after deleting the random element of the logistic equation (Real et al., 2006); E. Presence-absence map after applying the 0.5 cut-off to the favourability values. Note that E is nearly the same as A.

In the Iberian Peninsula, the model predicted broader potential *M. calpeiana* distribution than that presently known (Fig.3); apparently isolated core areas are joined and predicted distribution extends halfway up the Iberian Peninsula and through southern and mid-Portugal, touching the Sierras of Nogueira and Mogadouro in the north. Potential climate distribution does not include the Guadalquivir Valley, except around the river mouth.

Extrapolation to North Africa (Fig.4) identified environmentally suitable areas in: Morocco, through the Tangier Peninsula, the Rif and most of the Atlas Mountain Range; north of Algeria and Tunisia; and two small areas in the north of Libya. Extrapolation to the Mediterranean region (Fig.5), within model parameter

environmental limits, identified potential distribution area in: Sardinia and Sicily; some southern areas of Italy and Greece; Crete, most of the Aegean islands and Cyprus; and a large part of Turkey, Syria, the Lebanon, Israel and Jordan.

Climate warming simulation (Fig.6) led to a general reduction in potential Iberian Peninsula distribution area, from 11 740 km^2 to 9 600 km^2, affecting an area mainly in the north of the Guadalquivir Valley, while potential distribution through the north of Portugal remained unaffected. There was also a slight reduction of potential North African area, from 15 520 km^2 to 14 920 km^2, in spite of the potential Moroccan area increase (though fragmented in three sections) from 9 040 km^2 to 9 260 km^2.
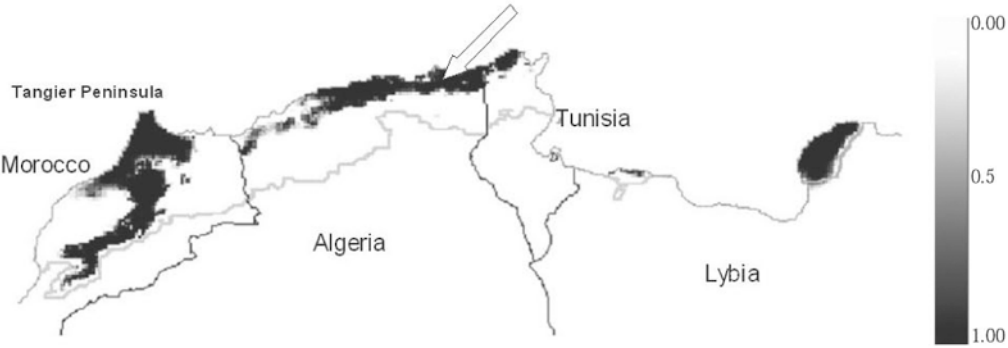
Fig.4　Extrapolation of the climatic model of *Macrothele calpeiana*（Walckenaer，1805）to North Africa
Values are favourability scores. Grey line delimits the area outside of which environmental variables are beyond the values used to parameterize the GLM model. The arrow points to El Arrouch，locality of Algeria from where Lucas（1849）cited *M. calpeiana*.
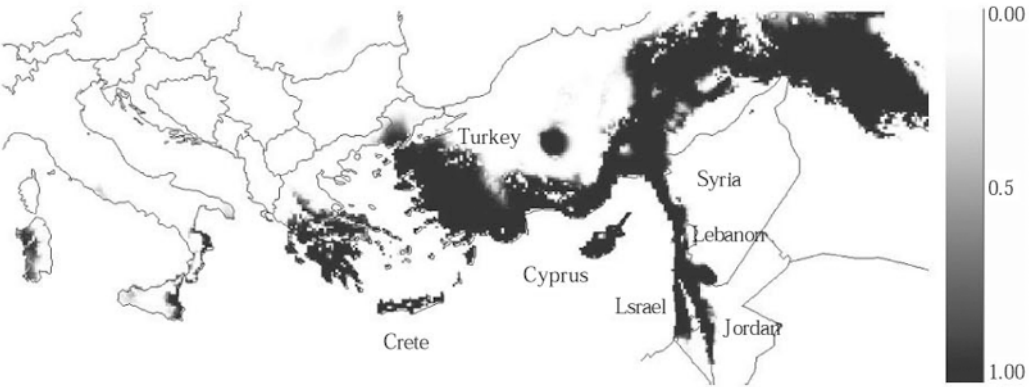

Fig.5　Extrapolation of the climatic model of *Macrothele calpeiana*（Walckenaer，1805）to the Western Palaeartic
Values are favourability scores. The picture window delimits the area out of which environmental variables are beyond the values used to parametrize the GLM model.
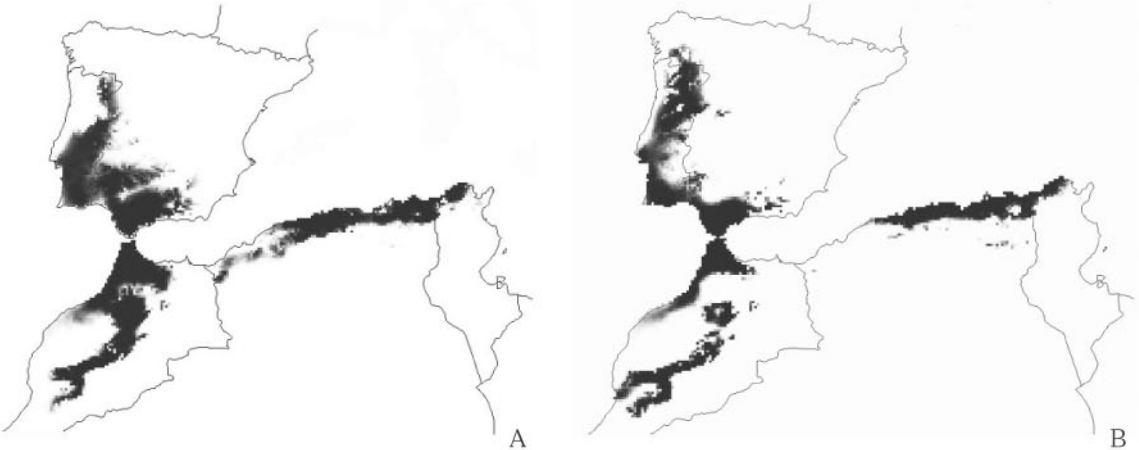
Fig.6　Potential distribution（A）and predicted changes in the potential distribution of *Macrothele calpeiana*
（Walckenaer，1805）in the Iberian Peninsula and North Africa after climate change（B）
Values are favourability scores.

3　Discussion

Given that species show climate optima，the climate envelope of a species can be considered the first constraint on its geographic distribution，at the top of scale-dependent，determinant factors（Mackey and Linden-

mayer，2001）. Elucidation of that envelope is an essential first step in the understanding of any species distribution. For the moment，in the absence of detailed physiological and ecological information， correlation methods such as the one used in the present study provide the best estimations of potential distributions. In the case of *M. calpeiana*， precipitation seems to play a primary role in determining its potential geographic range across the Euro-Mediterranean region. In particular， high seasonal precipitation variation seems to be the most relevant constraint；the greater the seasonal variation，the more favourable the habitat for the spider. These results agree with those of Jiménez-Valverde and Lobo（2006a） who， using variation partitioning techniques， identified precipitation-related variables as the main environmental determinants at a smaller resolution and extent. Nevertheless，the potential distribution shown in Jiménez-Valverde and Lobo（2006a）for Spain is slightly narrower than the one depicted in the present study，probably due to the differences in resolution and the inclusion in the cited work of land use factors which restrict the climate potential distribution.

The two main core areas of *M. calpeiana*（1 and 5，see Fig.1）coincide with the southern Atlantic Spanish distribution of the cork oak（*Quercus suber*；see Costa Tenoio et al.， 1998 ）. In Portugal， potential *M. calpeiana* distribution matches core areas of the cork oak，mainly in Alentejo and Algarve provinces（see Costa Tenorio et al.，1998）. The match of the distributions of other taxa with potential *M. calpeiana* distribution in the Iberian Peninsula suggests an environmental constraint common to all their distributions. This is also the case，for example， of the leaf-beetle *Orestia punctipennis*（Lucas，1849）（see Gruev and Döberl，1997；Baselga and Novoa， 2003 ）， and the dung-beetle *Scarabaeus cicatricosus*（Lucas，1846）（see Martín-Piera and López Colón，2000；J. M. Lobo，unpublished data），among others. These distribution areas correspond with some of the Iberian regions which acted as a refuge for many species（Carrión et al.，2000）.

During the editing process of this manuscript，the first author found *Macrothele calpeiana* in the Algarve province（southern Portugal），thus supporting the results presented in this study and showing the practical application of distribution predictive models for discovering new populations of poorly-known species（details of the first records for Portugal will be published elsewhere）. Absence of records of the spider in the rest of Portugal is curious in light of a possible ancient origin and wider distribution of the spider in the past. However，if its absence from central and northern areas in Portugal is genuine， *M. calpeiana* is not in equilibrium with the environment within the Iberian Peninsula， and its geographic range would be constrained by climate as well as by unique geographical and/or historical factors.

Mygalomorph spiders show low dispersal capabilities（Reichling， 2000；Hendrixson and Bond，2005 ）and juveniles of *M. calpeiana* in particular are believed not to leave their nest far behind（Santos Lobatón， 1996 ）. Thus， under the assumption that *M. calpeiana* could have occupied these areas in the past，their recolonization may have been impossible for the spider after going locally extinct due to palaeoclimate changes. This factor is also suggested by Arnedo and Ferrández（2006）to explain the apparent isolation of known populations. Nonetheless， in addition to historical factors， other agents such as biotic interactions（competition，predation）may be causing the absence of the species from suitable areas.

With regard to the absence of the spider in the Guadalquivir valley， Helsdingen and Decae （ 1992 ） suggested that open，unshaded areas may act as a barrier to *M. calpeiana* . We agree that this barrier could exist but that this absence is also due to large-scale climate factors，as shown by our model，which could interact with the lack of suitable habitat. In this case， other factors apart from macroclimate， could also have been influential. For example， the southern part of the valley was under water during all of the Tertiary and most of the Pleistocene （ López-Martínez， 1989； Hevia， 2004 ）， clearly a barrier to *M. calpeiana* colonization.

Two records from core area 4， wrongly predicted by the model（see circle in Fig.1），could indicate that these localities are at the species range limit. Alternatively， an important predictor variable could be lacking in our model， as autocorrelation in the residuals in the first lag distances seems to suggest. Failure by trend surface analysis to increase deviance explained by the environmental model could indicate that unaccounted-for variables may be acting on local scale（Diniz-Filho et al.，2003）.

Although extrapolation of models from the area of their training data may be of interest，this can produce unreliable results. Models extrapolated from ostensibly direct variables，such as climate variables，can be more reliable than those from indirect ones （ *sensu* Austin，1980）such as altitude，which is usually a surrogate for other related factors whose relationships may vary according to region（Austin，2002）. Extrapolation from our model， based entirely on climate variables， which presumably have a direct influence on species physiology，should be more robust than extrapolation from others based on indirect variables. Nevertheless，truncated responses to some variables indicate incomplete characterization of those spider environmental requirements， so reliable extrapolation is limited to areas within training-area environmental ranges. As already pointed out， an important consideration is that historical and biotic factors may cause the absence of the species from suitable areas. Extrapolations outside the area where the model has been trained should be considered distributional simulations

hypothesis in which these restrictive distribution forces do not act.

Extrapolation to North Africa identified environmentally suitable areas for *M. calpeiana* in that region, matching cork oak distribution there quite well (see Costa Tenorio et al., 1998), although forests of *Cedrus atlantica*, *Quercus pyrenaica* and *Pinus pinaster* are also common. Interestingly, this potential suitable region comprises northern Algeria and Tunisia, in which the dubious Lucas (1849) record is located (see arrow in Fig.4). At present, *M. calpeiana* is supposed to be of African origin and to have colonized Spain from there. After going extinct with the palaeoclimate change in many areas of Africa, it should still occur where climate remains suitable. These places still exist in North Africa, and they harbour well-preserved habitats (which make improbable a recent extinction event). If we accept the anthropogenic origin of the population from Ceuta, given that the presence of *M. calpeiana* in North Africa remains possible but uncertain, and considering the doubtful taxonomy of central African *Macrothele* species, we propose a new hypothesis for the colonization of the Iberian Peninsula by the species. The Mediterranean would have been colonized by *Macrothele* from south Asia maybe during the late Oligocene-early Miocene (Oosterbroek and Arntzen, 1992; Rölg, 1999). In this case, the Iberian colonization process could have happened during the Messinian salinity crisis (as proposed by Arnedo and Ferrández, 2007) through a Mediterranean dispersal route (Sanmartín, 2003), instead of an old African colonization event as proposed by Ferrández et al (1998).

This new hypothesis is supported by the presence of the other Mediterranean species *M. cretica* of the same genus within the potential suitable Mediterranean area. *M. cretica* could be a leftover stepping-stone vestige of the ancestral *Macrothele* species that colonized the Euro-Mediterranean region. In the Late Miocene, Crete belonged to a large land mass that the Tethys Sea later flooded, except for the highest altitudes (Welter-Schultes, 2000). Afterwards, in the Pliocene, uplifting of what had been many small islands gave Crete its present coastline. Given the favourability of the area, survival of *M. cretica* or other *Macrothele* species on other Aegean Islands, or in the Greek and Anatolian Peninsulas, would not be surprising because many suitable areas occur in this region (see Fig.5).

Despite their limitations, model predictions are still the most reliable forecaster of climate change effects on species distributions (Pearson and Dawson, 2003; Martínez-Meyer, 2005). Our climate model should be considered the null hypothesis in the absence of other interactive factors such as biotic interactions, land use effects or dispersal limitations (Peterson et al., 2002; Brooker et al., 2007). Potential habitat area for Iberian

populations north of the Guadalquivir valley (core area 5; see Fig.1) will be reduced, and that of core areas 2 and 3 will probably disappear under the climate change scenario considered. Although isolated populations could possibly persist in refuges undetected by our broad-resolution climate model (see Pearson, 2006), climate warming will not benefit such populations. Main core area 1 environment will remain highly favourable. In Portugal, potential habitat will be reduced in the south, while it will increase in the north. Given the known distribution of *M. calpeiana*, and its probably poor ability to disperse, it is not expected to undertake distribution shifts (along the Atlantic coast) to track optimal climatic conditions. Its distribution area is predicted to be reduced, although the main core area will remain habitable. In North Africa, potential distribution will be reduced and fragmented, reducing potential habitat, especially in Morocco.

The model predicts suitable habitat over a great part of the Iberian territory, connecting the apparently isolated known populations of *M. calpeiana*. These suitable areas should be a priority for future field surveys aimed at discovering new populations. New records of the spider in these suitable areas could change our present knowledge of the spider. Statistics can be used to support one biogeographic hypothesis or another, but models will never replace natural history data. Thus, research priorities are to: i) confirm the presence or absence of the spider in central and northern Portugal as well as in North Africa; ii) clarify the taxonomic status of central African *Macrothele* species; iii) estimate separation time among presently-known core Iberian populations, and between these Iberian populations and the population of Ceuta, via molecular data, and; iv) generate a reliable phylogenetic hypothesis for the genus.

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